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Cognitive movement ecology

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Cognitive movement ecology

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Table of contents

Concepts and Reviews

Theoretical Studies

Heuristic Innovations

Empirical studies

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Editorial: Cognitive movement ecology

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Editorial on the Research Topic
Cognitive movement ecology

1 Introduction

Papers, dissertations and books devoted to the analysis of animal movement often invite interest in the subject with the incontrovertible claim that *all animals move*. It is no less true and no less obvious that *all animals perceive, remember, and think* (though cognitive scientists seem less obligated to remind everyone of the fact). Perception, memory, orientation, and navigation are all cognitive components that have been identified, in a zeitgeisty collection of simultaneous independent studies, as central to animal movement (Mueller and Fagan, 2008; Nathan et al., 2008; Schick et al., 2008). And yet, the cognitive causes and consequences of animal movement remain nearly as understudied now (Joo et al., 2022) as then (Holyoak et al., 2008).

There are several reasons behind the apparent chasm dividing these fields. Advances in movement ecology often “chase” both the data and the telemetry technology, the rapid development of which is often driven in support of concrete needs to monitor animal populations for management or conservation. Although biologists are generally aware, and often in awe, of the cognitive ability of their study species, the very thought of trying to measure or quantify something as unobservable as cognition is daunting and of limited apparent practical utility.

In contrast, the history and pedigree of ethological studies on animals is much longer. One might argue that, as an applied exercise, it includes all human groups that have ever engaged in the domestication of wild animals. In the Western scientific tradition, notably contributors include Darwin, Pavlov, and Lorenz. However, as a scientific endeavor, ethology has focused on animals that are easy to observe and therefore amenable to controlled experimentation, in almost all cases captive or domesticated (Wynne and Udell, 2020). Much as the wildlife manager may wonder what practical information can be obtained from considering cognition in a wild deer, an ethologist may wonder what can possibly be inferred about the cognition of an animal that can only be indirectly observed through blips of satellite locations and upon whom experimental manipulation is impractical. With the exception of a handful of neurological phenomena, cognitive processes are latent, and there are good reasons to shy away from studying what we cannot observe.

And yet, in the past decade there has been growing theoretical and empirical evidence that perception (Fagan et al., 2017), spatial memory (Fagan et al., 2013; Merkle et al., 2014; Avgar et al., 2015; Schlagel et al., 2017), and social and experiential learning (Mueller et al., 2013; Berdahl et al., 2018; Jesmer et al., 2018; Abrahms et al., 2021) are all fundamental to the way that free-ranging animals use space. It therefore felt timely and important to collect original research under the novel rubric of "*Cognitive Movement Ecology*" into a single Research Topic. We invited a wide array of conceptual, theoretical, and empirical papers, reflecting a wide range of approaches to this relatively new field of study. In so doing, we hoped to identify common themes, standardize some jargon, and generally facilitate dialog among cognitive movement ecologists.

The resulting Research Topics includes 15 contributions which strike an admirable balance between concepts, theory, methods and applications. Specifically, our Research Topic is comprised of: 2 high-level reviews, 4 explicitly theoretical contributions leaning on numerical analysis and simulation, 2 articles that propose novel heuristic approaches to inferring cognition from movement data, and, finally, 7 articles that bravely seek to make direct inference and even predictions about cognitive processes of free ranging animals based primarily on movement data. We provided no explicit guidelines outside the general rubric and were struck by the ways in which important themes emerged and similar goals were set in papers with markedly different approaches. In this editorial, we summarize the four sections of this Research Topic, making an effort to link the common themes across sections, and conclude with our view of the future of this young, but important, branch of ecology.

2 Reviews and concepts

The Research Topic opens with a comprehensive review of the cognitive ecology of animal movement (Kashetsky et al.), setting the stage with a clear definition: that cognition is one of several *processes* that deal with the *acquisition*, *retention*, and *use* of information. The authors further explore several critical mechanisms by which such acquisition occurs, with an emphasis on the important role of *social learning*. The authors consider several observable spatial phenomena – all direct consequences of movement – that are exhibited by animals, in particular *migration*, *homing*, *home ranging*, *trail following*, and *spatial learning*. There is emphasis on the *perceptual mechanisms* and *ranges* (e.g. *viewsheds*, *soundscapes*, and *smellscapes*), including a consideration of the complexity and "*cognitive costs*" of different kinds of learning. These themes are laid out with several compelling published examples, and are all returned to explicitly and specifically (though largely independently) in almost every subsequent paper in the Research Topic. It bears noting, however, that the examples and synthesis provided are based primarily on experimental studies such as pigeon (*Colomba livia domestica*) releases and manipulated spatial feeding configurations for domestic sheep (*Ovis aries*).

The second major conceptual contribution (Lewis et al.) narrows the focus on *learning* (i.e. the *acquisition* and *use* of information), while broadening the disciplinary scope by pulling in vernacular, metaphors, and approaches from such fields as machine learning and robotics, as well as in psychology and behavior (their Box 1 provides a comprehensive glossary). Again, a clear definition rooted in the psychology literature is provided: that learning is a process of *information acquisition* that occurs via experience and leads to consistent and predictable *neurophysiological* or *behavioral* change. In the context of this Research Topic, the relevant observable behavioral change is specifically movement data. Much effort goes into covering the various mechanisms of learning (individual, social, positively reinforced, negatively reinforced, etc.). A set of rigorous criteria are proposed to identify whether actual learning is observed in a given study. Important distinctions are made between the kind of *"fundamental learning"* that occurs in a novel, or significantly perturbed, environment, compared to the kind of "*maintenance learning*" that is continuously ongoing in a dynamic but stochastically stationary environment. The former is more dramatic and categorical and can occasionally be inferred from "uncontrolled experiments" like translocations, introductions, or major environmental perturbations like habitat fragmentation or destruction. The second kind of learning is more subtle and reflects the ability of animals to continuously update information and make decisions. These two papers provide crucial conceptual context for later contributions in the Research Topic, all of which slot neatly into themes anticipated by these two overviews.

3 Theoretical contributions

Theoretical studies lean on numerical studies and simulations and have the freedom to essentially create universes from scratch. In so doing, researchers can explore processes that are impossible to observe over a range of conditions that stretch the credible, potentially leading to profound insights into fundamental principles that produce patterns that are, in fact, widely observed in the wild.

Swain et al.– focusing on the *evolution of perception* – used millions of agent-based models to incorporate the relatively unexplored *costs* of perception to constrain the simulated emergence of optimal evolutionary scales of perception ranges. In identifying the conditions under which non-local perception is selected for, the authors found unintuitive interactions between, among others, resource density and energetic costs. Notably, low-resource environments led to the evolution of either *zero* perceptual range, or *large* perceptual ranges – pointing towards two divergent and apparently contradictory strategies in low-resource environments, consistent with observations (e.g., deep-water crustaceans either are entirely blind, or have exceptionally large eyes). The dramatic evolutionary trade-offs inherent in the evolution of perception (steep costs, high returns), leading to the wide range of evolutionary outcomes, is likely mirrored in the emergence of cognitive properties, like spatial memory and social learning, and the dizzying range of those adaptations. Indeed, it can be argued that memory itself is a kind of "temporal perceptual range", that uses information from the past to "perceive" the future.

Gurarie et al., ask a complementary question: what possible *non-genetic* mechanisms can lead to the emergence, maintenance, and resilience of seasonal migrations, a very widespread and successful strategy that involves considerably uncertainty, risk, and energetic cost. Using a different computational approach from the other three theoretical studies (partial differential equations rather than agent-based simulations), the authors explore how *collective memory*, *sociality*, *exploration*, *resource following*, and *learning* all interact to exploit a highly seasonal and disconnected resource environment; i.e. one where the "patchiness" is extreme, but the predictability is high. For migration to emerge, all these ingredients are required, but mixed in just the right proportions: social cohesion to share information must be balanced against exploratory behavior to acquire new information, and a deep well of reference memory to lean on must be balanced against the ability to modify that reference in response to new information. Even in the highly synthetic conditions of the model, striking optimal balance is not easy; but, much as in the evolutionary model of Swain et al., the rewards can be considerable. Furthermore, though there is no selection in the model *per se*, it is clear that social learning as a mechanism can operate at time scales that are much more rapid than genetic selection.

Cognition is, however, not only about what the animals know (perception and memory), it is also about what they do not know, and how they might learn and make movement decision in the face of uncertainty. In the absence of perfect information, animals must rely on approximations to update their knowledge of their environment, as well as the expected outcomes of their decisions. Using individual-based simulations in a dynamic depleting and regenerating resource landscape, Avgar and Berger-Tal examine the role of two types of *optimism* as adaptive strategy for partially informed optimal foragers. Using a simple agent-based model, they show that moderate discounting of information from undesirable outcomes ('positivity biased learning' or 'valence-dependent optimism') results in improved fitness in environments characterized by high resource variability.

As if expressly to punish any irrationally optimistic foragers, Bracis and Wirsing introduce predators into a similar simulated dynamic resource environment to study the widely reported phenomenon of the "Landscape of Fear". The authors build on a versatile continuous-time, continuous-space framework developed for the exploration of the role of spatial memory in guiding mobile foragers navigating dynamic landscapes (Bracis et al., 2015; Bracis et al., 2018). Within this habituated prey/resource system, the authors then release predators in high resource areas. The prey are left to learn from near escapes, and eventually to associate high quality habitat with increased risk. Somewhat analogous to Gurarie et al. This method of learning relies on two memory streams – a long-term "*reference memory*" (e.g. of fundamentally suitable habitat) and a short-term "*working memory*" which pushes the forager from recently depleted patches. Interestingly, these apparently simplistic two streams of memory are capable of both *fundamentally learning* about the new predator element, and of continuous *maintenance learning* (*sensu* Lewis et al.). The authors find that landscape of fear effects, in particular more time spent searching and less net consumption, do emerge with the presence of predators. However, the factors that lead to the most dramatic effects are primarily *intrinsic*, i.e. related to memory and personality, rather than *external*, i.e. related to the configuration of the environment. Specifically, the effects are greatest when animals are initially naïve to their environment and when they are highly conservative (akin to Avgar and Berger-Tal's *pessimists*). This result is important as a reminder that in real systems intrinsic states can easily be as important as the kinds of external, environmental factors that are most commonly used to model animal movements.

While very different in purpose and technique, a clear theme emerges from this suite of theoretical explorations: that the value of perception, memory, and learning for fitness is a direct consequence of the spatial structure and temporal dynamics of the environment the animal moves through. Thus, a somewhat unexpected corollary emerges: cognitive abilities serve above all else to compensate for *constraints* and *limitations* in the ability to move across the landscape itself.

4 Heuristic innovations

While all the empirical studies rely to varying extents on methodological innovations, two contributions to this Research Topic stand out for proposing purely trajectory-based approaches to analyzing movement data, pointing towards widely observed spatial patterns that – the authors claim – can only emerge from memory-driven movement process.

Gautestad explores the topological properties of movement tracks that emerge from a model of self-reinforcing (i.e. memory-driven) returns to previously visited locations. This ultimately very simple model leads to patterns of space use that can be represented as a "scale-free network". In other words, it has rare "dominant nodes" and very many "rarely visited" nodes, distributed in such a way that the frequency of degree centrality scores has a predictable log-log relationship. Gautestad shows that – when decomposed to a node-to-node type – empirical data on black bear movements (*Ursus americanus*) consistently show precisely the scale-free properties expected by this memory-driven random walk. A fascinating analogy is made with the global internet network, which is also scale-free and therefore susceptible to targeted attacks on dominant nodes. In similar ways, Gautestad makes an unexpectedly applied conclusion: that the movements and habitat-use of a free-ranging animal is structurally sensitive to disruptions to dominant nodes of patch use. There is an implicit corollary to this conclusion: if a movement track lacks these scale-free properties, this may indicate a perturbation in "normal" memory-inflected movement patterns.

Alavi et al. have a similar goal: to study the impact that simple cognitive processes have on the spatial, topological, and statistical properties of emergent movement tracks. Rather than focus, as Gautestad, on *patches* (network nodes) Alavi et al. focus on *routes* (network edges). They propose a set of metrics that can be computed directly from data that capture those properties related to linearity, absolute directionality, and recursion rates. Using a set of memory-driven simulations, the authors show the conditions under which these patterns emerge, and finally apply the methods to a set of four medium-sized tropical mammals moving in a forest in Panama. The differences in the movement patterns of these animals are striking, and well-captured by the metrics the authors proposed. Those differences are then compellingly related to very specific hypotheses about the kinds of learning and perceptual capacities (another recurring theme) that the animals likely rely on.

Notably, both of these highly original analyses depend entirely on the spatial properties of a movement track, without any environmental covariates, or even particular regard to displacement durations. Both lean on the fundamental fact that movement tracks never actually really resemble the kinds of naïve random movements that form the basis of most empirical movement modeling. In an echo of Bracis and Wirsing, they underscore the fact that a good amount of the structure of the observed animal movements can, in fact, emerge from purely intrinsic properties. Furthermore, they point to ways in which the generally unobservable process of cognition can nevertheless be inferred from movement data.

5 Empirical studies

Inferring cognitive process based on observational data of free-ranging animals is a tremendous challenge (Lewis et al.). Nevertheless, seven contributions to our Research Topic attempt to do just that for a diverse set of taxa: three ungulate species (elk *Cervus elaphus*, mule deer *Odocoileus hemionus*, and bighorn sheep *Ovis canadensis*; Falcón-Cortés et al., Rheault et al., and Berger et al.), 2 terrestrial carnivores (fisher *Pekania pennanti* and wolves *Canis lupus*; Facka and Powell and Gurarie et al.), 1 flying mammal (Egyptian fruit bat *Rousettus aegyptiacus*; Lourie at al.), and 1 swimming fish (salmon *Oncorhynchus* spp.; Goodwin et al.). Rather than provide summaries of their findings (the authors do that in their abstracts much better than we could here), we focus on areas of notable overlap and divergence (Figure 1).

The processes analyzed in these studies span a range of taxa and of spatio-temporal scales. But the fundamental question – at the level of the individual – always boils down to: *where to move*? At the extremes, Berger et al. predict seasonal migrations of sheep, while Goodwin et al focuses on extremely fine-scaled (3 minute) decisions made by fish in a highly dynamic environment. Rheault et al. and Falcón-Cortés et al. deal with space use and selection within a seasonal range – i.e. selection on a temporal scale of hours, while Gurarie et al. and Lourie at al. examine selection of foraging sites on the scale of diel departures from a den or roosting site. Lastly, Facka and Powell were interested less in details of movement than in large-scale interactions among conspecifics.

Six of the seven empirical contributions consider memory as a potentially important driver of animal space-use patterns or movement decisions and directly or indirectly provide a data-informed estimate of a “memory coefficient”. The most straightforward form of memory is captured as a tendency to return to previously visited locations, with or without temporal decay (Rheault et al., Falcón-Cortés et al., Lourie at al.). In all these

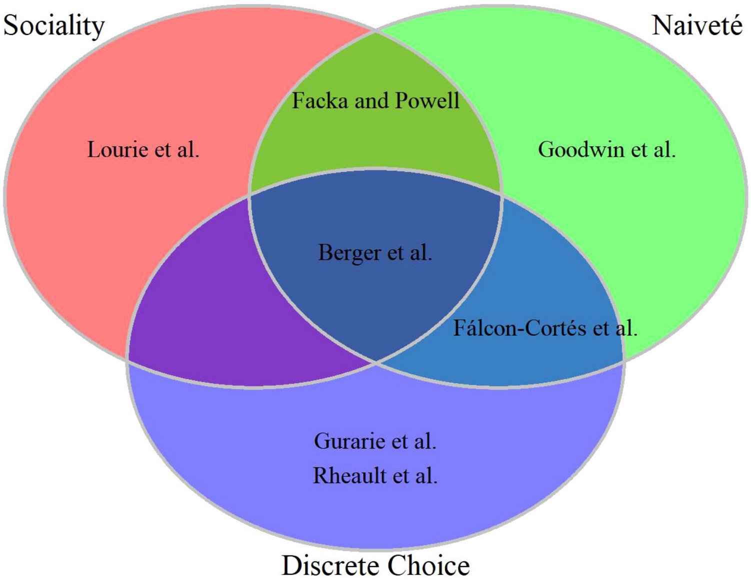

FIGURE 1
Venn diagram of seven empirical studies in the collection across three sets of commonalities. Three papers studied social interactions, four leveraged inference from “naive” animals (translocated ungulates, reintroduced predators, juvenile fish migrating downstream); four used some form of discrete choice modeling, whether choosing where to hunt, whether to migrate, where to move out of a discrete set of options.

cases, accounting for that tendency improved the ability of respective models to explain the data, or – equivalently – to match some of its emergent properties. Others add additional cognitive elements to simple attraction to previously visited locations; thus Berger et al. explicitly account for and estimate relevant perception ranges for decision-making, Gurarie et al. model multiple conflicting streams of memory that positively or negatively reinforce revisits, and Goodwin et al. incorporate a complex hierarchy of immediate behavioral responses to sensory input.

Three contributions are focused primarily on *social drivers* of space use (Figure 1, red set); Lourie at al. evaluate alternative hypotheses for foraging domain partitioning among neighboring bat colonies, Facka and Powell examine how established home ranges affected the formation of a newcomer's home range, and Berger et al. compare the relative importance of the effect of a social group's migratory culture to the effects of individual memory and sensory information. Inference on social factors requires simultaneous information on many individuals, an aspect that most observational studies lack. Each of these studies were able to examine these questions by using some innovation in their study design. Lourie at al. applied high-resolution tracking technology; they used a reverse-GPS system to track ~100 bats for an average of 24 days and at a resolution of 0.125 Hz (8 obs. x sec^{-1}). Berger et al. and Facka and Powell had the advantage of studying reintroduced species (incidentally, both in the Sierra Nevada mountains) where many (Berger et al.) or all (Facka and Powell) individuals were tracked.

To varying degrees, four of the studies took advantage of naiveté in the animals (Figure 1, green set). Facka and Powell, Berger et al., and Falcón-Cortés et al. leveraged the "uncontrolled experiment" of releasing animals in novel environments (fisher reintroductions, and sheep and elk translocations, respectively). Facka and Powell had the further advantage of having tracked every reintroduced individual, while Berger et al. augmented their observations with the intensive monitoring associated with a high-profile recovery program. Finally, the juvenile fish in Goodwin et al were migrating downstream and entering environments and conditions, like dams, that were completely novel to them. Reintroductions and translocations – common means of ecological restoration or rewilding, augmenting struggling populations, or resolving human-wildlife conflicts – are of incredible value for studying learning in particular (Lewis et al.). Since relocated animals are naïve to the landscape they find themselves in, no behaviors can be ascribed to specific prior experience, only a moving set of expectations. The same is true of dispersal events (which also describes the juvenile salmon outmigration), which have the advantage of not requiring any handling of animals. Dispersal events, however, are generally much harder to detect in wild populations, mainly because they are relatively rare and tend to occur among subadult males, an age-sex class that is generally understudied by wildlife biologists and managers whose focus is often on adult females. Nonetheless, as tracking and monitoring efforts increase, dispersal events will be ever more available for analysis of learning in movement (Barry et al., 2020).

Two empirical contributions join the theoretical paper of Gurarie et al. to focus on seasonal migration. Berger et al. investigated why only some sheep migrate to lower elevation ranges in the fall while others remain in high-elevation ranges. Rheault et al. examined the effect of memory gained in the previous year on the space use of deer returning to their seasonal ranges. While not as tidy as translocations or dispersal events, seasonal migration also has particular benefits with respect to cognition. Beginning and end points of migrations are often well-known, or at least identifiable from movement data, and questions can focus on the repeatability of their selection. Furthermore, in some systems, proximate drivers of migration are more or less known, e.g. niche tracking or "green-wave surfing" (Merkle et al., 2016; Aikens et al., 2017), providing a well-understood null model against which the influence of perception or memory-driven choices can be compared. Finally, given long-enough tracking durations, we may have reasonable information on the animal's prior knowledge and experience, provides researchers a null expectation about what the animal may or may not know. Studies where migratory animals are translocated and tracked as they do (or do not) adopt the migratory behavior, as was the case for several of the sheep in Berger et al., are of particular value (see also Mueller et al., 2013; Jesmer et al., 2018).

With respect to methodology, four of the contributions conducted some form of discrete choice analysis (Figure 1, blue set), where observed movement 'decisions' are contrasted against one or more alternative decisions that could have been made; e.g. to migrate or not to migrate (Berger et al.), which foraging area to move to (Gurarie et al., Falcón-Cortés et al.), or which "step" to take (Rheault et al.). These discrete-choice models were applied directly to observed data, and memory effects were assessed by including prior experience as a predictive covariate of the choice made. Discrete choice modeling is not often applied to wildlife studies, but echoes a long history of experimental approaches for studying memory and learning in animals (Tolman and Honzik, 1930; Wilkie and Willson, 1992; Thorpe et al., 2004). In contrast, two contributions constructed individual-based simulation models where some of the parameters are informed by observed data, but the simulation as a whole is tuned via likelihood-free (pattern-oriented) alignment with observed emerging patterns (Lourie at al.; Goodwin et al). Notably, Lourie at al. used the simulation-based approach to draw inferences about the relative contributions of individual memory vs. conformity, whereas Goodwin et al used it as a predictive tool. Lastly, Facka and Powell leverage the incredible strength of an experimental design: by simply comparing deliberate introductions of fishers into areas with and without the presence of conspecifics, a very strong signal of avoidance was detected without the need for overly complex analytical machinery.

Gurarie et al. conclude their analysis with a proposed five point checklist for the inference of memory driven processes from data on movements of free-ranging animals: (A) an observable behavior that might be driven by prior experiences; (B) identification of experienced cues that might influence that behavior; (C) a cognitive model; i.e. a plausible functional relationship between movement response A to experience B; (D) a statistical method (or pattern-matching heuristic) to estimate the model C; and (E) a metric for comparing the cognitive model against a non-cognitive model. It is instructive to apply this checklist to other studies. For example: in Berger et al. a sheep's choice to migrate (A) is a consequence of perception viewsheds (B) which predict the probability of migration via a linear mixed model (C,D) which takes into account other potential covariates, and can be compared against a suite of non-cognitive models using maximum likelihood (E). Or, in Lourie at al., the observed property of spatially non-overlapping neighboring bat colonies (A) is hypothesized to be a consequence of prior visitations (B), a suite of agent-based models is developed to account for that behavior (C) and emergent properties of those simulations are compared to the observations (D) for agent-based simulations with and without the memory component (E). The empirical studies in this Research Topic checked off most, if not all, of these requirements, indicating that the framework may be useful for further empirical investigation into cognitive roots of movement.

6 Concluding remarks

Editing this Research Topic has reinforced our conviction that the cognitive processes of perception, memory and learning are fundamental to understanding any animal movements. But it may still not be clear why wildlife practitioners should care. Here, it bears noting that in two of the empirical studies (Rheault et al., Falcón-Cortés et al.) where time-scales of memory were estimated, memory was essentially infinite, consistent with prior findings (e.g., Avgar et al., 2015). Similarly, in both of the heuristic contributions (Alavi et al., Gautestad), the essential argument was that fundamental patterns of movements can be explained almost entirely by memory. These results suggest that, at least in some cases, the most effective way to predict where an animal might show up (an important goal for monitoring, conservation, and management) is not to model movement against some complex set of habitat covariates, but to simply study where the individual has been before. With that in mind, the global reality is that environmental conditions for many populations are changing extremely rapidly, whether through disturbance, habitat fragmentation, or climate change. These rapid changes put major pressures on the adaptability and behavioral plasticity of organisms. Or, to apply the jargon (and some of the paradigms) of animal cognition, the question of a population's persistence can be summarized as its ability to modify a *reference memory* with updated *working memories*, such that the resulting *behavioral innovations* are adaptive with respect to fitness.

The two foundational models that underlie much of theoretical animal movement ecology are almost diametrically opposed. On the one extreme, the *random walk* (Berg, 1993; Turchin, 1998; Codling et al., 2008) assumes that animals move blindly and completely randomly in a restricted, slow to "diffuse" manner. On the other extreme, the *ideal-free distribution* (Fretwell and Lucas 1969; Křivan et al., 2008; Avgar et al., 2020) assumes that completely omniscient and optimal animals can appear anywhere and anytime, distributing themselves in proportion to resource availability. The reality is, of course, somewhere between the two: real animals in real-life scenarios are capable of moving in directed and informed ways, but not at infinite speed, and only with partial information about the environment. Cognitive movement ecology can be viewed as an essential bridge between these theoretical constructs. What does it mean to be partially informed? How does an organism act on that partial information? And how does it distribute itself through space, given its goals and given its constraints? How, in the end, do organisms manage to navigate, survive, even thrive in environments that are complex, heterogeneous, and dynamic? These questions, which are very much the realm of cognitive movement analysis, are also at the very foundation of animal ecology.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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REVIEW
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The Cognitive Ecology of Animal Movement: Evidence From Birds and Mammals

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Cognition, defined as the processes concerned with the acquisition, retention and use of information, underlies animals' abilities to navigate their local surroundings, embark on long-distance seasonal migrations, and socially learn information relevant to movement. Hence, in order to fully understand and predict animal movement, researchers must know the cognitive mechanisms that generate such movement. Work on a few model systems indicates that most animals possess excellent spatial learning and memory abilities, meaning that they can acquire and later recall information about distances and directions among relevant objects. Similarly, field work on several species has revealed some of the mechanisms that enable them to navigate over distances of up to several thousand kilometers. Key behaviors related to movement such as the choice of nest location, home range location and migration route are often affected by parents and other conspecifics. In some species, such social influence leads to the formation of aggregations, which in turn may lead to further social learning about food locations or other resources. Throughout the review, we note a variety of topics at the interface of cognition and movement that invite further investigation. These include the use of social information embedded in trails, the likely important roles of soundscapes and smellscapes, the mechanisms that large mammals rely on for long-distance migration, and the effects of expertise acquired over extended periods.

Keywords: cognition, expertise, philopatry, spatial learning, social learning, navigation

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INTRODUCTION

The factors necessary for maximizing growth, survival and reproduction vary in time and space. To accommodate this temporal and spatial variation, most animals possess the physical means for moving toward beneficial resources and away from harm. In addition to the ability to move, however, animals must frequently decide about the timing, direction and duration of movement as well as its final destination. To make such decisions, animals rely on their cognitive system, which consists of the structures and processes concerned with the acquisition, retention and use of information (Dukas, 2004, 2017). Research in the past few decades has integrated mechanistic information on animal cognition with functional knowledge on animal ecology and evolution (Dukas, 1998; Dukas and Ratcliffe, 2009; Morand-Ferron et al., 2016; Ratcliffe and Phelps, 2019). Our contemporary understanding of animal cognitive ecology, however, is still not well incorporated within the field of movement ecology.

Scientists across a wide range of disciplines have engaged in insightful research on organismal movement for a long time. Examples range from laboratory analyses of movement in bacteria at the micrometer scale (Adler, 1976; Koshland, 1980; Eisenbach and Lengeler, 2004) to field work on whale migration over thousands of kilometers (Pike, 1962; Rasmussen et al., 2007). The young field of movement ecology adds to this knowledge by relying both on new technologies for monitoring natural animal movement over vast areas, and on modern computational tools for analyzing the large data sets acquired through automated tracking (Nathan et al., 2008; Abrahms et al., 2021). Only recently, however, movement ecology has increased the consideration of animal cognition (Fagan et al., 2013, 2017; Avgar et al., 2015; Lewis et al., 2021), an approach that typically requires controlled experimental settings.

Animal cognition can be divided into a few interconnected categories. The first component is perception, which involves capturing information from the environment and converting it into internal representations retained by neuronal networks. Information acquisition is carried out by receptors specialized to capture cue attributes emitted by or associated with relevant objects including patterns of reflected light, sound, odors, flavors and texture. Newly acquired information may either fade away immediately, remain for brief periods, or consolidate into long lasting internal representations that can persist for many years. The process of adding new representations into neuronal networks is termed learning, and the information retained is referred to as memory. The only utility of information acquisition and retention is to determine and execute action. To this end, individuals have to continuously assess relevant environmental features and their experience to decide about their subsequent action (Rolls, 2014; Anderson, 2015; Dukas, 2017).

The framework of movement ecology laid out by Nathan et al. (2008) clearly recognized the crucial role of cognition in general and navigational abilities in particular for the obvious reason that cognition underlies all animal decisions regarding when and where to travel. Although one can study movement while ignoring its underlaying internal mechanisms, a thorough understanding of individuals' movement decisions requires us to quantify the cognitive processes that drive them. Chief among the cognitive abilities relevant to animal movement are the mechanisms that enable spatial orientation. Such mechanisms allow individuals to both navigate their local surrounding while engaging in their daily routines, and to undertake long-distance seasonal migrations.

To keep our review within the space constraints, we will focus here on experimental research in birds and mammals as these groups have been the subject of most studies in movement ecology. While we will aid our analyses with a few examples from insects, we cannot encompass here the rich body of research on insect navigation (Dyer, 1998; Collett and Collett, 2002; Wehner, 2020). Our review has five parts. In the first two sections, we focus on individual cognition and ignore social influences. First, we discuss the roles of learning and memory in movements within the local settings of one's home range. Second, we take the broader perspective of the innate mechanisms, learning and memory involved in long-distance movements typically associated with seasonal migration. Most birds and mammals have parental care, many species live in groups (Wilson, 1975; Clutton-Brock, 2016), and even the ones classified as solitary show rich social interactions (Caro, 1994; Elbroch et al., 2017). Hence, our third section assesses the multiple effects of the social environment on the cognitive features that guide movement. The fourth part briefly integrates the previous three sections to address the understudied topic of animal expertise, defined as the traits that enable individuals to show superior performance after a long period of individual and social learning (Dukas, 2019). Finally, our prospects section focusses on a few suggestions for promising research at the interface of cognition and movement.

INDIVIDUAL LEARNING AND MEMORY WITHIN THE HOME RANGE

Most animals can benefit from learning about the attributes of relevant environmental settings, resources and individuals. Examples include food sources, shelters, temperature, predators and other hazards, kin, social partners, competitors, and prospective mates. Key features associated with such variables include unique, identifying cues such as odor, color, sound, taste, size and shape, and their location in space and time. It is thus not surprising that all animals subjected to critical experimental tests show learning when tested under the controlled conditions designed to distinguish learning from relevant alternatives (Dukas, 2008a, 2017). Critical evidence for learning, however, requires strict experimental protocols because learning can only be inferred indirectly through a change in behavior. This means that one has to carefully rule out non-learning alternatives including changes in perception, satiation, physiology, and motivation. For example, while GPS movement data on a single mule deer (*Odocoileus hemionus*) suggested reliance on spatial memory (Jakopak et al., 2019), the study could not critically rule out alternatives including the use of trails or other cues, or following other individuals. Nevertheless, evidence such as the ability of an individual to return to its summer range after moving about 100 km away is instructive regardless of the mechanism employed. That is, we encourage researchers to modulate their vocabulary based on their evidence where the settings and priorities do not allow for critical tests of learning. Additionally, future research may continue to develop protocols that allow critical tests of cognitive abilities in the field (Morand-Ferron et al., 2016). We provide examples of such field tests throughout our review.

Most relevant for movement ecology is animals' abilities to learn and remember the spatial locations of resources and individuals. Spatial learning and memory merely means having the ability to acquire and later recall information about distances and directions among relevant objects. This allows individuals to navigate, i.e., find their way among these objects. Controlled laboratory studies indicate robust spatial learning and memory in key model systems including fruit flies (*Drosophila melanogaster*) (Ofstad et al., 2011) and rats (*Rattus norvegicus*) (O'Keefe and Dostrovsky, 1971; Moser et al., 2008). Many field studies over the past several decades, which included controlled experiments as well as observations using individually tagged individuals, have revealed exceptional navigational abilities in honey bees (*Apis mellifera*) (von Frisch, 1967; Seeley, 1996; Dyer, 1998; Menzel et al., 2005; Riley et al., 2005). In addition to routinely traveling to flower patches up to several km away from their nests, honey bees communicate to nestmates the direction and distance to both flower patches and prospective new nests (Dyer, 2002; Visscher, 2007). These skills allow honey bees to dynamically adjust to changes in the spatial and temporal distribution of floral rewards, and to locate the best locally available tree cavities for new nests (Visscher and Seeley, 1982; Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003; Seeley, 2010).

It is fair to assume that all birds and mammals possess spatial learning and memory as good as or better than that experimentally demonstrated for honey bees in the field. Controlled laboratory and enclosure studies typically confined to up to several meters indeed demonstrate excellent spatial learning and memory in a variety of birds and mammals (e.g., Morris, 1981; Sherry et al., 1981; Balda and Kamil, 1992). Much of the field work is either limited or suggestive owing to the lack of a large body of controlled experiments. A notable exception is the homing pigeon (*Columba livia domestica*) discussed in the section below (Wallraff, 2005; Wiltschko and Wiltschko, 2015).

Consider the following example for study design that has enabled strong inference on cognitive processes. A well controlled field study (Edwards et al., 1996) tested spatial memory in domestic sheep (*Ovis aries*) in a 30 by 45 m pasture. There was a grid of 4 by 8 plastic bowls with randomly chosen 4 bowls containing food pellets (**Figure 1A**). The food could not be seen until a sheep was within 0.5 m of the bowl. Each sheep was tested individually 11 times over about a week. In trials 1–6, the position of the bowls containing food remained constant, and sheep reduced the number of bowl visits required to locate the four bowls containing food (**Figure 1B**). In trial 7, half the sheep had no food in any bowl, and half the sheep had food in four new randomly chosen bowls. This probe trial tested whether sheep relied on spatial memory or on cues emanating from the food. The sheep in both groups mostly searched first in the four bowls that had previously contained food and then searched randomly among the other bowls. This resulted in no change in the number of visits needed to locate the previously food-containing bowls in the no-food group, and in a large increase in the number of visits needed to locate the four new food containing bowls in the location-switching group (**Figure 1B**). Trials 8–10 consisted of retraining, where the no-food group from trial 7 received food again in the same bowls as in trials 1–6, while the location-switching group received food at the same bowls as in trial 7. Sheep from the previously no-food group maintained their small number of visits required to locate the four food bowls, while sheep from the location-switching group reduced again the number of visits required to find the new locations of the four food bowls (**Figure 1B**). Trial 11 tested spatial memory after longer than the retention period of 12 h used previously. Here half the sheep were tested after 24 h while the other half were tested after 72 h. Both groups showed the same high performance as in the earlier trials (**Figure 1B**). The sheep study illustrates how one can critically assess spatial memory in the field. Similar work may be conducted at larger spatial scales with a variety of wild animal populations that are habituated to feeding near humans.

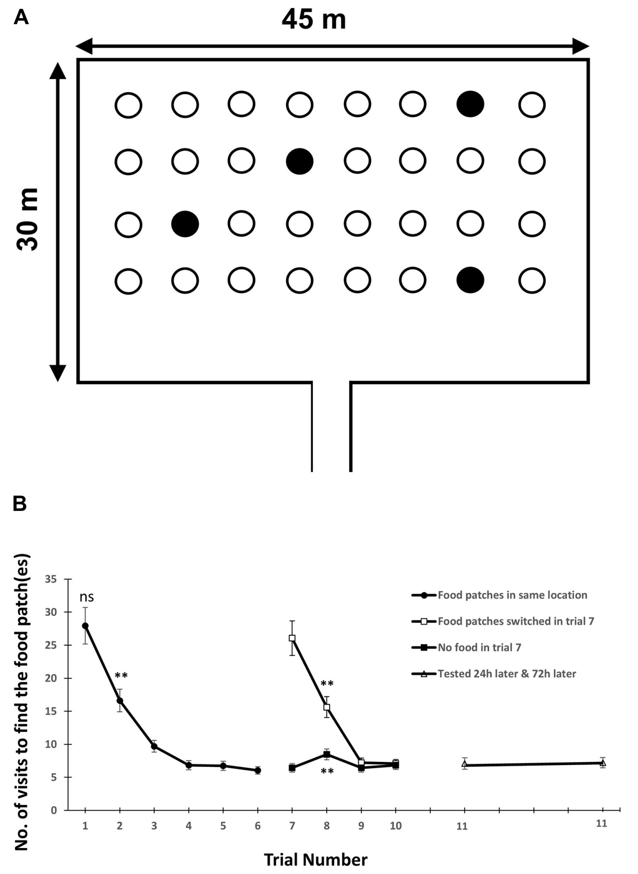

FIGURE 1 | (A) The layout of food bowls in the sheep spatial memory experiment. Open circles illustrate empty bowls while filled circles depict the four bowls containing food. **(B)** The mean ± SE number of visits required to locate all food bowls. In trials 1–6, the food was always in the same 4 bowls. In trial 7, half the sheep encountered food in 4 new bowls (□) and these bowls also contained food in trials 8–11. The other half of the sheep encountered no food in any bowl in trial 7 (■) and had food in the same bowls as in trials 1–6 in trials 8–11. In trial 11, half the sheep were tested 24 h after trial 10, and the other half were tested 72 h after trial 10. The asterisks indicate visit numbers statistically different from random search in tests conducted in trials 1, 2, and 8. Data from Edwards et al. (1996).

INNATE BEHAVIOR, INDIVIDUAL LEARNING AND MEMORY IN SEASONAL MIGRATION

Seasonal migration occurs in nearly all major animal groups. Traveling to exploit favorable conditions (e.g., food, warmth, or mates) and escaping adverse conditions (e.g., parasitism, predation, or competition) is a beneficial strategy that many animals adopt (Avgar et al., 2014; Somveille et al., 2015). To make navigational decisions during migration, animals use

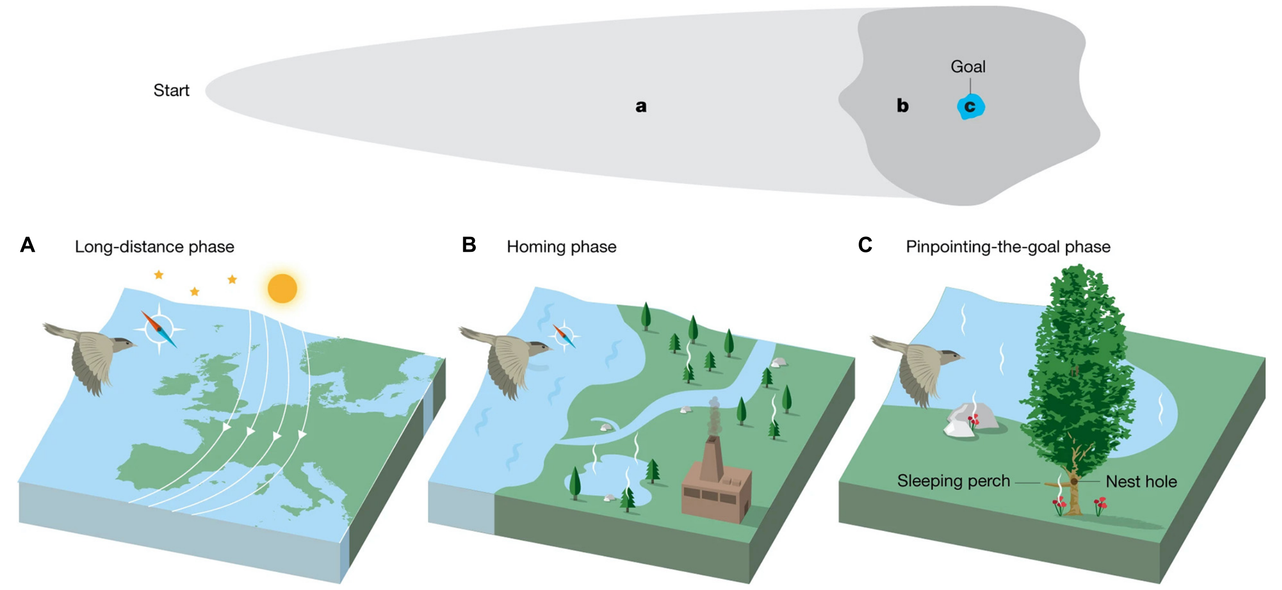

FIGURE 2 | Illustrated phases of long-distance navigation. **(A)** During the long-distance phase, individuals rely on celestial and magnetic cues as well as on large landmarks such as mountains, lakes, and coastlines. **(B)** During the homing phase, gradients, landmarks, and compasses are important. **(C)** During the pinpointing-the-goal phase, residential cues including beacons and the goal itself are valuable. Figure from Mouritsen (2018) with permission.

a combination of innate instructions, information they have previously learned either individually or gleaned from others, and cues they currently perceive (Spiegel and Crofoot, 2016). Seasonal migration consists of three phases in which animals use different cues to navigate (Mouritsen, 2018; **Figure 2**). During the long-distance phase, animals navigate using innate and learned information, and global/regional cues (Schmidt-Koenig, 1990; Gwinner, 1996). In the narrowing-in/homing phase, animals use compasses and landscape information (O'Keefe and Nadel, 1978; Toledo et al., 2020). For the pinpointing-the-goal phase, animals follow specific landmarks near the goal or the goal itself. We will focus on species that live long enough to partake in multiple migrations throughout their lives, providing good opportunity to discuss cognitive processes beyond innate instructions.

The vast literature on animal migration has revealed a multitude of innate mechanisms and learned features that guide individuals toward their long-distance goals. The number and complexity of processes involved as well as the variation among species precludes simple generalizations. We thus detail below several key elements. We will first assume no social interactions and focus on the combination of innate mechanisms and individual learning that guide navigation. Then we will discuss in the subsequent section social influences and social learning, which are prevalent in many species.

Compass Orientation

In many cases, orientation toward a long-distance goal can be aided by a compass mechanism. The three compasses—magnetic, sun, and stars—provide simple directional information regardless of the current location (Wiltschko and Wiltschko, 2015). Migratory birds, especially inexperienced individuals, rely on compasses during the long-distance and homing phases of long-distance movement (Mouritsen, 2018). The avian magnetic compass is primarily innate (Wiltschko and Gwinner, 1974), while celestial compasses are primarily learned (Wiltschko and Wiltschko, 1980; Michalik et al., 2014). Birds typically use one compass mechanism to calibrate another (Pakhomov and Chernetsov, 2020). For example, night-migratory songbirds update their star compass using their magnetic compass as a reference (Wiltschko and Wiltschko, 1975). Subsequently, the calibrated star compass can be used independently (Wiltschko and Wiltschko, 2015).

Information from multiple compasses is usually available concurrently, depending on the season, time of day, weather, and magnetic anomalies. Currently, there are various conflicting theories regarding the hierarchy of the compasses used for orientation (Johnsen et al., 2020; Pakhomov and Chernetsov, 2020). When multiple cue types are available, birds likely have preferences for which one to follow based on individual experience, current environment, and distance to their goal (Munro and Wiltschko, 1995; Wiltschko and Wiltschko, 2015; Chernetsov, 2017). If an in-use compass becomes unreliable, birds switch to cues with more accurate readings. For example, pigeons initially rely on magnetic cues, then attempt to compensate for disorientation during magnetic anomalies or experimental disturbance using celestial cues (Keeton, 1971; Ioalé, 1984; Wiltschko and Wiltschko, 2001; Schiffner et al., 2011).

Magnetic Compass

Geomagnetic fields stretching from poles to equator remain relatively consistent over animals' lifetime, making them informative for determining direction. Birds may rely on a few features of magnetic fields including intensity (strength of the magnetic field), inclination (the angle between the magnetic field and earth surface), direction (polarity), and declination (the difference between true north and magnetic north) (Wallraff, 2005; Wiltschko and Wiltschko, 2005, 2015; Mouritsen, 2018). While much of the research on magnetic compasses has been done in birds, there is growing evidence that mammals, specifically rodents and bats, also possess a magnetic compass (Holland et al., 2006, 2010; Oliveriusová et al., 2012, 2014; Finn, 2021). Some large terrestrial mammals can spontaneously align their bodies with magnetic fields (Begall et al., 2013; Obleser et al., 2016; Painter et al., 2016; Červený et al., 2017), but it is unclear if they use an established magnetic compass for navigation.

Birds inherit their ability to sense magnetic inclination (Wiltschko and Wiltschko, 1972, 2005; Wiltschko and Gwinner, 1974). In some cases, they must calibrate this compass using celestial cues (Able and Able, 1990; Cochran et al., 2004), or vice versa (Muheim et al., 2007, 2009). Magnetic compass orientation is dependent on the presence and wavelength of light (Wiltschko W. and Wiltschko R., 1981; Muheim et al., 2002), although night-migratory songbirds require less light than diurnal birds (Wiltschko and Wiltschko, 2015). The avian magnetic compass works in a functional magnetic intensity window; increasing or decreasing the magnetic strength by 25–30% is disorienting, until birds establish a separate functional window (Wiltschko, 1978; Wiltschko and Wiltschko, 2015). Because magnetic field intensity changes through space, an adjustable compass is advantageous for long-distance movements (Wiltschko and Wiltschko, 2015).

Solar Compass

The temporal cycles and perceived movement of the sun make it an excellent guide for orientation (Guilford and Taylor, 2014). Solar cues are valuable during the long-distance phase of movement (Wiltschko and Wiltschko, 2015; Mouritsen, 2018). Birds may use polarized light cues or the azimuth of the sun itself (Munro and Wiltschko, 1995; Wiltschko and Wiltschko, 2015; Muheim et al., 2016). The sun compass requires learning in juvenile birds. Pigeons establish their sun compass before they are 12 weeks old, while early experience flying can accelerate learning to 8–10 weeks (Wiltschko and Wiltschko, 1981).

Birds must integrate the sun's movements into their internal clock to orient themselves based on their perceived time-of-day (Wiltschko and Wiltschko, 1980, 1981; Schmidt-Koenig, 1990; Schmidt-Koenig et al., 1991; Åkesson et al., 2017). The integrated sun compass and internal clock must constantly be updated to account for daily and seasonal changes in the perceived location of the sun (Wiltschko and Wiltschko, 2015). Improper synchronization between the internal and sun compass is disorienting. For example, pigeons under experimental settings in which the light-dark cycles were shifted 6 h ahead flew 90 degrees counter-clockwise compared to control pigeons (Schmidt-Koenig, 1958). Once individuals recognize that their compass is shifted, they resynchronize their sun compass and internal clock. Such synchronization occurs naturally when birds travel to different locations (Schmidt-Koenig, 1958; Wiltschko et al., 1998). Yet in some cases, following the sun compass without updating it can be advantageous. Arctic shorebirds such as the American golden plover (*Pluvialis dominica*), semipalmated sandpiper (*Calidris pusilla*), pectoral sandpiper (*C. melanotos*), and the white-rumped sandpiper (*C. fuscicollis*) migrate without synchronizing their internal clock and sun compass. At high altitudes, non-stop flights attuned to the sun compass result in orthodomes, traveling the shortest distance between two points on a sphere (Alerstam et al., 2001).

Star Compass

The other celestial compass, which is based on stars, provides direction for nighttime navigation. Night-migratory songbirds learn to locate a north-south directional axis based on the fact that stars closer to the celestial axis move through smaller arcs (Emlen, 1970). In order for night-migratory songbirds to learn the compass, they require 2–3 weeks of exposure to a rotating star pattern (Able and Able, 1990; Michalik et al., 2014). Learning occurs during the pre-migratory period before autumn (Emlen, 1970, 1972), but can take place the following spring if needed (Zolotareva et al., 2021). Star patterns change seasonally because of the earth's rotation around the sun, so migrating birds must regularly update their celestial information (Wiltschko and Wiltschko, 2015). On the other hand, because birds learn the celestial axis rather than the time-dependent celestial location of stars, shifting birds' internal clock does not affect their star compass orientation (Emlen, 1970; Mouritsen and Larsen, 2001; Pakhomov et al., 2017). Once a star compass is established, it can be used independently of magnetic and solar cues.

Vector Navigation

Long-distance movement poses a considerable challenge for young, inexperienced individuals. First year avian migrants either follow experienced individuals (see Social Learning section below) or use vector navigation (Gwinner, 1996; Bingman and Cheng, 2005; Mouritsen, 2018). Vector navigation, also called the clock-and-compass strategy, uses at least one compass and a set of genetically encoded instructions for direction and distance rooted in their internal clock (Mouritsen et al., 2016). Garden warblers (*Sylvia borin*) deprived of any seasonal cues for a year displayed migratory restlessness only at the appropriate temporal windows for spring and fall migrations (Gwinner, 1996). The inherited migratory instructions are population specific. Crossbreeding individuals from separate populations with distinct migration routes results in hybrid offspring with intermediate migration patterns (Berthold and Querner, 1981; Helbig, 1991).

Circadian and circannual clocks are responsible for the onset, distance (duration), and direction of migration (Gwinner, 1996). Before learning alternative navigation strategies, naïve individuals rely on genetic instructions, effectively demonstrated by displacement experiments. Experienced birds can correct for displacement over extraordinary distances, while inexperienced juveniles typically fail to do this (Perdeck, 1958). For example, in an experiment involving the displacement of juvenile and adult white-crowned sparrows (*Zonotrichia leucophrys gambelii*), adults corrected for displacement by adjusting their route toward their usual wintering grounds. Juveniles neglected to reorient themselves, flying in the direction of the expected migration route (**Figure 3**; Thorup et al., 2007). Juveniles fail

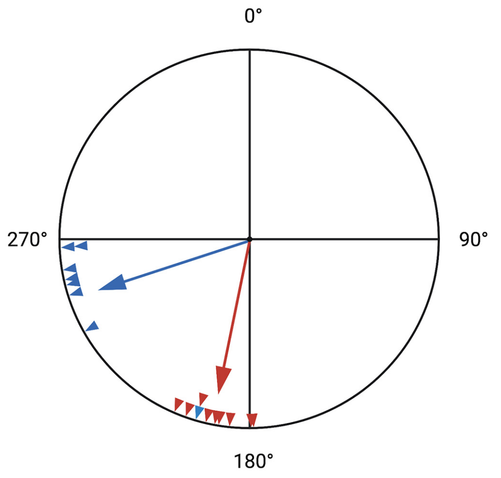

FIGURE 3 | Last observed direction of white-crowned sparrows after experimental displacement east of their location. Adults (blue, large arrow is the average) correctly reoriented southwest toward their original wintering grounds, exhibiting true navigation. Juveniles (red, large arrow is the average) failed to reorient, continuing southward using vector navigation. Based on Thorup et al. (2007).

to correct for displacement not because they lack that ability, but because they lack information required for compensation (Wiltschko and Wiltschko, 2015).

In some instances, juveniles can correct for displacement. Surprisingly, juvenile blackcaps (*Sylvia atricapilla*), willow warbles (*Phylloscopus trochilus*) and garden warblers could reorient themselves after experimental or natural displacement during their first migration to an unfamiliar goal (Thorup et al., 2011). Likewise, some juvenile common cuckoos (*Cuculus canorus*) corrected for experimental displacement at the same level as adults, traveling toward their expected wintering grounds (Thorup et al., 2020). These compensation mechanisms toward an unfamiliar goal remain unclear—juveniles may be following magnetic cues or using inherited signposts, which are discussed next (Thorup et al., 2011, 2020).

Signposts

Signposts are markers that trigger specific responses that aid in navigation (Wiltschko and Wiltschko, 2005; Freake et al., 2006). Behavioral responses to signposts can be genetically encoded or imprinted. Various species respond to signposts. These include birds (Beck and Wiltschko, 1988; Fransson et al., 2001), turtles (Lohmann et al., 2001), eels (Schabetsberger et al., 2016; Naisbett-Jones et al., 2017), salmon (Putman, 2015; Scanlan et al., 2018) and lobsters (Boles and Lohmann, 2003). Signature magnetic and physical properties act as signposts. Examples include region-specific magnetic intensity, temperature, odor, water salinity or currents (e.g., Fransson et al., 2001; Schabetsberger et al., 2016). For example, particular magnetic intensities can trigger animals to change directions during migration (Putman, 2015; Naisbett-Jones et al., 2017; Scanlan et al., 2018), reorient themselves to avoid ecological barriers and dangerous conditions (Beck and Wiltschko, 1988; Lohmann et al., 2001), or land at stopover sites for refueling (Fransson et al., 2001).

True Navigation

True navigators are individuals that can navigate to a goal after being displaced to an unknown location, at an unknown distance and direction (Griffin, 1952; Kramer, 1953; Keeton, 1974; Able, 2001; Thorup et al., 2007, 2020; Wikelski et al., 2015; Kishkinev et al., 2021). True navigation allows individuals to reach their goal when familiar landscape information is absent. Animals must determine their geographic location, then orient themselves toward the goal using a compass (Griffin, 1952). As mentioned in the vector navigation section above, displaced adult white-crowned sparrows flew toward their usual wintering grounds, exhibiting true navigation, while inexperienced juveniles relied on vector navigation, flying according to genetically encoded instructions (Thorup et al., 2007). Bi-coordinate position fixing, that is, navigation using at least two gradients, is a prerequisite for true navigation (Griffin, 1952; Freake et al., 2006). True navigation involves at least one compass and gradient-based or location-based navigation discussed in the section below.

Navigation Based on Learning and Memory

Animals may learn distinct information for guiding their navigation. Such learning may be egocentric, meaning that it is based on the animal's own movement, or exocentric, implying that it is based on features of the landscape (Klatzky, 1998). Based on the type of information learned, one can distinguish among four non-mutually exclusive navigation strategies (Fagan et al., 2013) detailed in the four sub-sections below (**Figure 4**).

Route-Based Navigation

During route-based navigation, also called path integration (**Figure 4A**), individuals record their movements relative to the starting point using a compass and return by reversing their net outward movements (Schmidt-Koenig, 1975; Wiltschko and Wiltschko, 2000, 2015; Wallraff, 2005; Fagan et al., 2013; Bidder et al., 2015). Learning is egocentric and structured around self-movement, thus the individual does not need to be familiar with the landscape because landmarks are not required (Wehner et al., 1996; Kimchi et al., 2004). Route-based navigation is a cognitively simple strategy that requires little memorization (Mittelstaedt and Mittelstaedt, 1982; Wehner and Wehner, 1986; Fagan et al., 2013). Additional distance and turns increase the cognitive demand of keeping track of the route, leaving more room for mistakes. Thus, we can expect route-based navigation to be used at smaller scales. During route-based navigation, individuals acquire information of the unfamiliar area *en route* to build their exocentric navigation strategies (Wiltschko and Wiltschko, 2015).

Location-Based Navigation

In location-based navigation (**Figure 4B**), one learns the spatial relationships between landmarks and goals (O'Keefe and Nadel, 1978; Bingman and Cheng, 2005; Wallraff,

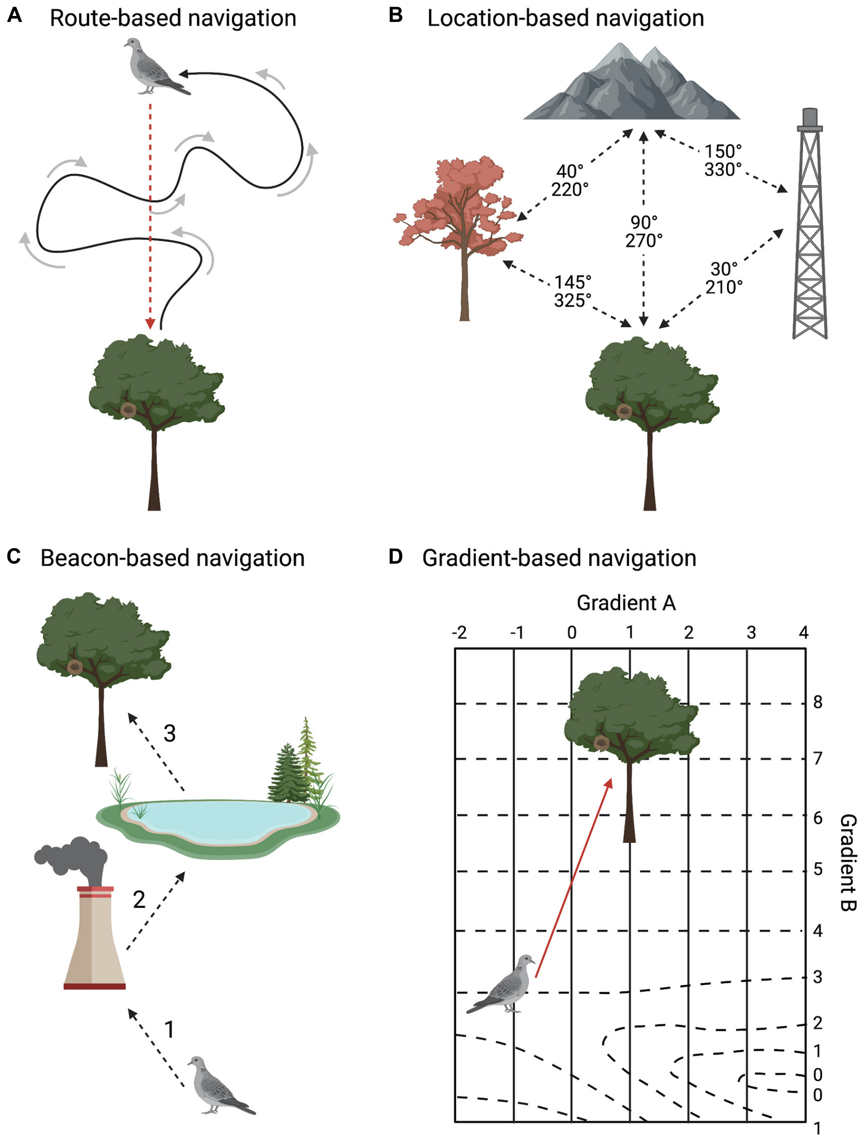

FIGURE 4 | Types of memory-based navigation. **(A)** In route-based navigation, the individual sums the distance and direction of its outward movements to estimate its current position and take a direct path to its starting point. **(B)** In location-based navigation, the individual memorizes spatial relationships between landmarks and goals. **(C)** In beacon-based navigation, specifically pilotage, the individual follows sequential landmarks leading to the goal. **(D)** In gradient-based navigation, the individual navigates with memorized gradients. In this illustration, both gradients are magnetic (solid and dash lines), with a magnetic anomaly in the southeast corner, which could initially disorient the individual. The scale of D is over 1000 km. Created with BioRender.com.

2005; Fagan et al., 2013; Wiltschko and Wiltschko, 2015; Toledo et al., 2020). This strategy may use simple memory snapshots (Cartwright and Collett, 1982; Alert et al., 2015) or complex cognitive representations of space (Bingman and Cheng, 2005). A compass is required for learning geographical directions in relation to landmarks (Wiltschko and Wiltschko, 1982, 2015). Although learning spatial relationships between landmarks and goals can produce a heavy memory load, repeated experience moving throughout the landscape should reinforce these memories, reducing cognitive load. Migratory animals probably learn spatial information at a larger scale but lower acuity compared to non-migratory navigators (Bingman and Cheng, 2005). This navigation technique is valuable during the homing phase of long-distance movement.

Beacon-Based Navigation

Individuals using the beacon-based strategy (**Figure 4C**) are guided to their goal by at least one familiar beacon, which is a landmark near the goal (Papi, 1992; Biro et al., 2004; Wallraff, 2005; Fagan et al., 2013; Wiltschko and Wiltschko, 2015). This includes traveling toward the goal itself or following a series of landmarks to reach the goal (Collett et al., 1986, 1992; Steck et al., 2009; Guilford and Biro, 2014; Yovel and Ulanovsky, 2017). While exploring unfamiliar areas, individuals use a compass to navigate until they learn which landmark(s) lead them to their goal. Once they have established a route, compasses become unnecessary as they can follow the landmark(s) directly (Papi, 1992; Biro et al., 2007; Guilford and Biro, 2014). Beacon-based navigation is most applicable during the homing and pinpointing phases of long-distance movement, as landmarks are typically too small to perceive at long distances, with the exception of massive geographical features such as coastlines or mountains.

Gradient-Based Navigation

Individuals that rely on gradient-based navigation (**Figure 4D**) have to learn perceptual signatures of at least one feature that changes gradually over space (e.g., magnetic or olfactory gradients) (Bingman and Cheng, 2005; Wallraff, 2005; Fagan et al., 2013; Wiltschko and Wiltschko, 2015). Navigating using gradients requires a compass (Wiltschko and Wiltschko, 2015). Magnetic cues provide both compass orientation and gradient-based navigational information through different perceptual mechanisms—interfering with magnetic cues for one does not impair the other (Munro et al., 1997; Deutschlander et al., 2012; Holland and Helm, 2013; Chernetsov et al., 2017). Gradients are functional during the homing phase and can be projected to longer distances beyond an individual's experience (Gagliardo et al., 2013; Wikelski et al., 2015). For example, birds learn the features of the magnetic field throughout their home or migratory range, then extrapolate that information to spatial scales beyond what they have experienced (**Figure 5**; Thorup et al., 2007; Kishkinev et al., 2021). Extrapolated gradients are not always accurate representations of nature (Wallraff, 2005). Individuals extrapolate to unknown locations based on memory of familiar gradients, leaving unfamiliar anomalies and gradient changes unaccounted for, which could result in navigation miscalculations. For instance, individuals displaced to the northwest corner of **Figure 5A** would move away from their true home because their extrapolated gradient is signaling them to fly in the opposite direction (Wallraff, 2005).

Selecting a Navigation Strategy

Strategies of navigation vary among species. In species that employ multiple strategies, their use depend on individual experience, preference, available information, distance from the goal, and energy expenditure (Filannino et al., 2014; Green et al., 2020). Furthermore, animals may use multiple navigation strategies simultaneously (Wiltschko and Wiltschko, 2015). Navigation strategies driven by landscape familiarity (location-, beacon-, or gradient-based, **Figure 4**) are generally preferred over route-based navigation (Wiltschko and Wiltschko, 2015), likely because these strategies are less prone to errors, and allow for short cuts and course corrections. Pigeons using gradient-based navigation modified their route depending on their current motivational state. Food deprived pigeons released at an unknown location flew to a known food source, while satiated pigeons released at the same location flew to their home loft (Blaser et al., 2013). Contrarily, route-based navigation does not allow individuals to revise their goal, and displacing individuals is disorienting, as their reversed net outward movements no longer lead to the return point (Müller and Wehner, 1988; Andel and Wehner, 2004). If information necessary for a preferred strategy is unavailable, animals revert to a simpler feasible navigation technique. For instance, rats revert to route-based navigation when beacons are unavailable (Shettleworth and Sutton, 2005).

Synthesis

Notwithstanding our precautionary note that both the multitudes of complex processes involved in navigation and the variation among species preclude simple generalizations, we wish to end this section with a synthesis. In many species, naïve individuals traveling alone can successfully execute long-distance migration based on innate instructions and one or more compasses. All three compasses typically include innate as well as learned information. Overall, navigation is greatly enhanced by learning, which may be solely based on an individuals' own movement, but typically also on a variety of environmental features including landmarks and gradients. Furthermore, individuals in many species acquire information related to navigation from others, a topic we discuss next.

SOCIAL INFLUENCES AND SOCIAL LEARNING

The traditional separation of animals into solitary and social species is rapidly fading as we learn to appreciate the sophisticated social skills of animals historically classified as non-social (Costa, 2006; Durisko and Dukas, 2013; Elbroch et al., 2017). It is fair to assume that individuals in most species can gain from information gleaned from conspecifics, and that such information may guide their movements. Social influence merely means that a focal's behavior is affected by the presence, activity, or cues left by other individuals. Social learning means that a focal acquires novel information based on the presence, activity, or cues left by other individuals. As we discuss below, a dominant source of information that young individuals should attend to is parents and other old individuals. While we focus here on species with parental care, direct or indirect cues left by parents are highly relevant in species in which young do not encounter their parents (Dukas, 2010). We begin by discussing philopatry and the importance of trails. We then review collective navigation, and the use of social learning for decisions regarding home range and migratory movement.

Philopatry

In birds and mammals, newborn rely on their parents for food and protection. When young are sufficiently mature, they typically travel farther from their nest or shelter and often follow their parents. The duration of parental feeding of fledgling varies widely among birds and is positively associated with the duration of practice required for reaching some threshold of foraging proficiency (Ashmole and Tovar, 1968; Heinsohn, 1991; Hunt et al., 2012). In mammals, post-weaning maternal care is brief in short-lived species but can last for years in long lived species (Clutton-Brock, 2016). At least in carnivores, the long duration of post-weaning maternal care is related to the low learning rate

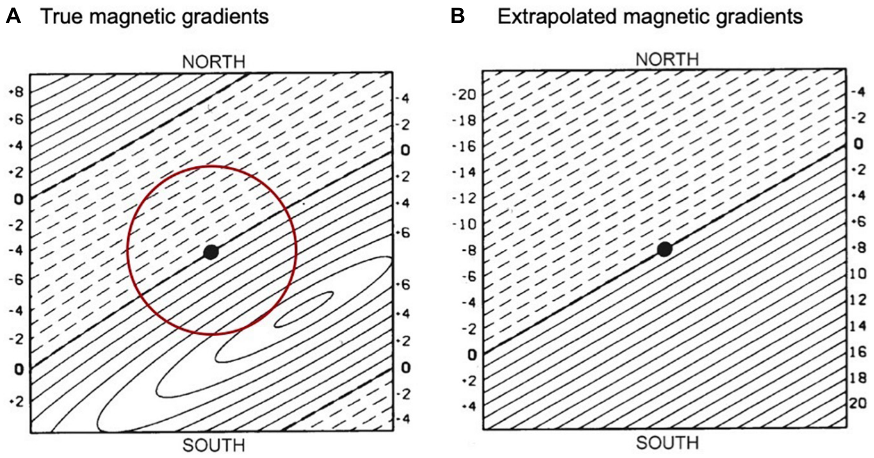

FIGURE 5 | An example of true and extrapolated magnetic gradients. A single gradient is showed for simplicity with positive (dashed line) and negative (solid line) values, on a scale over 1000 km. **(A)** True magnetic gradient values surrounding the individual's home (black dot) and its familiar range (red circle). **(B)** The individual extrapolates gradients based on experience, and incorrectly anticipates the gradient in the northwest and southeast corners. Based on Wallraff (1985).

associated with challenging hunting skills (Caro, 1994; Wachter et al., 2017). While there is wide variation among species, in the vast majority of birds and mammals, young have ample opportunities to learn many features of their natal environment including the food types preferred by their parents, foraging skills, and the spatial locations of food, shelters, and hazards (Slagsvold and Wiebe, 2007, 2011).

In most species, a large proportion of individuals do not reach reproductive maturity. Of those that reproduce, a large proportion of parents fail to lead their offspring to independence owing to either predation or starvation (Clutton-Brock, 1988). Hence the fact that young have reached independence is a solid evidence that their parents have chosen well their natal environment. Given their likely lack of knowledge about alternative sites and the costs of acquiring such information, the young should copy their parents' choice and show philopatry where possible (Stamps et al., 2009). Several other factors that promote philopatry include advantages of familiarity with biotic and abiotic features of the natal habitat, improvements to the environment by previous generations such as reusable burrow systems, tree cavities and trails, and the mortality risk associated with exploration of novel areas (Waser and Jones, 1983). Indeed, philopatry is prevalent in both birds and mammals (Greenwood, 1980; Waser and Jones, 1983).

A large cross fostering study tested the effects of early social experience on natal habitat preference in pied flycatchers (*Ficedula hypoleuca*) in Spain. Pied flycatchers are long-distance migrants who breed throughout Europe but spend the winter south of the Sahara. The experiment involved cross fostering nestlings between nests in a coniferous habitat and nests in a deciduous habitat one km away and, as a control, cross fostering nestling within each of the two distinct habitats. Most returning young birds came to the forest patch from which they had fledged, regardless of whether they had been cross-fostered within or between patches (**Figure 6A**). These results indicate a strong effect of early experience on habitat choice (Camacho et al., 2016), which is consistent with many other bird studies (Greenwood, 1980; Weatherhead and Forbes, 1994). The results also illustrate remarkable navigational and spatial memory abilities, which allowed 1 year old birds to relocate the small patch of their natal forest after a round trip migration of thousands of km. While the young birds receive no guidance from their parents (Mouritsen and Larsen, 1998), some reliance on social information cannot be ruled out.

Similar effects of early social influence were observed in a study involving 57 radio-collard moose (*Alces alces*) in Sweden, which revealed strong philopatry by calves. Ten of the 14 radio collard calves returned with their mothers to their summer range, and 9 out of the 10 subsequently separated from the mothers but remained within 2 km from them. The female offspring kept returning to that range in subsequent summers (Cederlund et al., 1987).

In both birds and mammals, site fidelity is even stronger in breeding adults than in young. The same reasons listed above can readily explain why adults remain in their current home range, or keep returning to it in species that show seasonal migration. Indeed, adult philopatry tends to increase with the temporal consistency in conditions, risks, and resources, and particularly their predictability from year to year (Riotte-Lambert and Matthiopoulos, 2020; Morrison et al., 2021). The factor of experience becomes stronger over time, because individuals can keep learning site-specific relevant information as discussed in the expertise section below (Dukas, 2019). Individuals, however, can rely on their experience to decide whether it pays to show site fidelity. Indeed in many bird species, individuals are more likely to show site fidelity if they succeed than fail in reproduction (Greenwood and Harvey, 1982). For example, an elegant experiment manipulated the nesting success of prothonotary warblers (*Protonotaria citrea*) that used nest boxes in southern Illinois (Hoover, 2003). Birds were randomly assigned into rearing zero, one or two successful broods within a season, with the failures manipulated via predation. Success

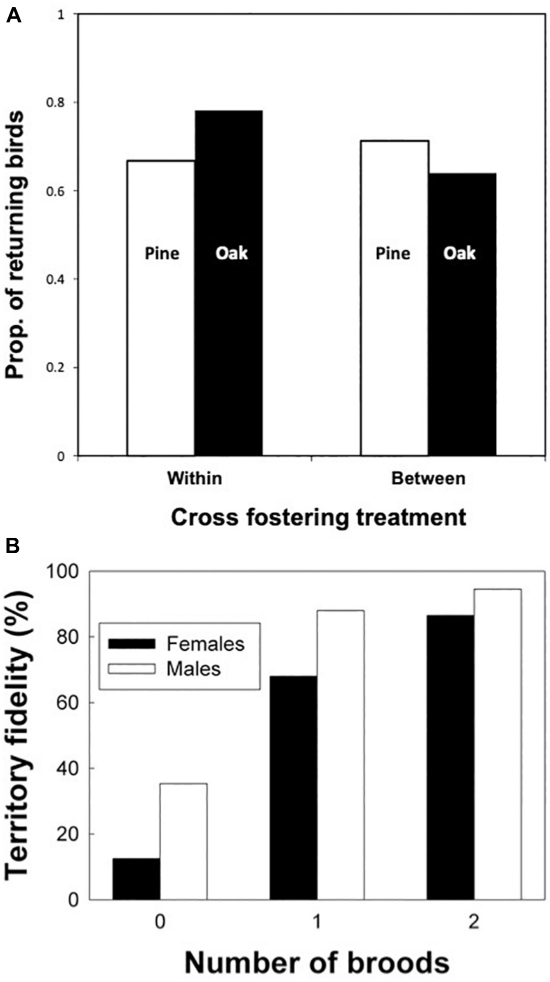

FIGURE 6 | (A) The proportions of pied flycatcher nestlings that returned to breed in the same patch where they had fledged after being cross-fostered within or between habitats containing either pines or oaks. Data from Camacho et al. (2016). **(B)** Territory fidelity of female and male prothonotary warblers that were experimentally manipulated to have 0, 1, or 2 successful broods in the previous year. Data from Hoover (2003).

rates strongly affected the return rates of birds in the following season, after their long-distance migration to Central or South America (**Figure 6B**). Intriguingly, males whose nesting attempts failed were three times more likely to show site fidelity if they had successful rather than unsuccessful neighbors. Because the males can monitor and even father offspring in neighboring territories through extrapair copulations, it is likely that neighbors' success affected their subsequent site fidelity (Hoover, 2003). In addition to their remarkable navigational and spatial memory abilities, the prothonotary warblers also showed sophisticated skills in optimizing decisions affecting future reproductive success based on both their own and their neighbors' experience.

To synthesize, while there are clear benefits to philopatry and obvious costs to dispersal, the social and genetic trade-offs vary among species, leading to a large within and between species variation in the overall and sex-specific patterns of philopatry (Greenwood, 1980; Waser and Jones, 1983; Smale et al., 1997; Clutton-Brock, 2016; Morrison et al., 2021). There are many unresolved issues ripe for investigation, which can take advantage of modern movement ecology tools. Specifically, the causes and consequences of within species variation in philopatry provide intriguing questions. On the cognitive ecology side, in species where one sex remains and the other sex disperses, are there between sex differences in cognitive traits such as spatial abilities, tendencies to explore, attachment to kin, and openness to new experiences? On the movement ecology side, current tracking techniques can help us quantify the sex-specific trade-offs that underlie philopatry versus dispersal.

Trails

Trails can be perceived as social information left from previous generations owing to their usefulness in connecting multiple sites containing resources such as food, water, minerals and shelters while minimizing effort and perhaps danger. Similarly, trails may be used for migratory movement. Trails are also a rich source of contemporary social information, as olfactory and visual cues left by previous trail users can provide information on their identity, number, reproductive state, condition, and the time and direction of travel (Mutinda et al., 2011). Finally, established and well maintained trails allow fast, efficient travel between feeding areas, and between feeding patches and shelters. Indeed, as noted above, an established trail system is one factor that can promote site fidelity in walking species. For example, elephant shrews (*Elephantulus rufescens*) restrict much of their travel to a network of trails from which they regularly remove plant material and other obstacles. It has been suggested that their rapid running along these trails is an effective anti-predatory strategy (Rankin, 1965; Rathbun, 1979). In larger animals, trails have been studied primarily in elephants (*Loxodonta africana*) (Vanleeuwe and Gautier-Hion, 1998; Mutinda et al., 2011) and mentioned in a few other studies (Di Fiore and Suarez, 2007; Noyce and Garshelis, 2014; Trapanese et al., 2019). Despite the prevalence and potential importance of animal trails in shaping animal movement, however, they remain understudied.

Aggregations, Information and Individual Movement

A fair number of animals live their whole or part of their lives in aggregations. Examples include bird and bat roosts, and nesting aggregations in solitary bees and birds (Allee, 1931; Michener et al., 1958; Rolland et al., 1998; Beauchamp, 1999; Fenton and Simmons, 2015). Philopatry, discussed above, can readily lead to aggregation. Additional factors include the rarity of appropriate sites, anti-predatory advantages and social information about food and predators (Galef and Giraldeau, 2001; Danchin et al., 2004; Evans et al., 2016). The most likely effect of social information on movement is via local enhancement, whereby individuals searching for food join others whom they observe feeding (Thorpe, 1963; Krebs et al., 1972; Thiebault et al., 2014). Another possibility is that individuals from the aggregation follow departing, apparently informed individuals to food patches. Some field observations agree with this possibility while others do not (Brown, 1986; Mock et al., 1988; Marzluff et al., 1996; Danchin and Richner, 2001; Sonerud et al., 2001; Harel et al., 2017; Urmy, 2021). It is fair to assume, however, that socially biased movement occurs in many species.

Both philopatry and the rarity of satisfactory aggregation sites should lead to large spatial variation in the distribution of aggregating species. Because members of the aggregation can save time and energy as well as incur lower mortality by foraging closer to the aggregation, one would expect lower individual densities farther from the aggregation (**Figure 4** in Dukas and Edelstein-Keshet, 1998). Bumblebees in the field indeed showed such pattern of spatial distribution (**Figures 3**, **4** in Osborne et al., 2008). Reliance on social information would further increase the spatial variation in individual densities. This can lead to cascading spatial effects on other trophic levels. For example, bumblebee wolves (*Philanthus bicinctus*), sphecid wasps that prey on bumblebees, nest in rare, large aggregations that persist over decades as indicated by the fact that an aggregation studied in the early 1960s (Armitage, 1965) still existed in 2004 (Dukas, 2005). Bumblebee densities at flowers were much lower within 4 km than farther than 5 km from the bumblebee wolf aggregation (**Figure 7A**). Consequently, fewer flowers of the bumblebee pollinated plant, western monkshood (*Aconitum columbianum*), set fruit within a few hundred m from the bumblebee wolf aggregation than 6 km away from the aggregation (**Figure 7B**; Dukas, 2005).

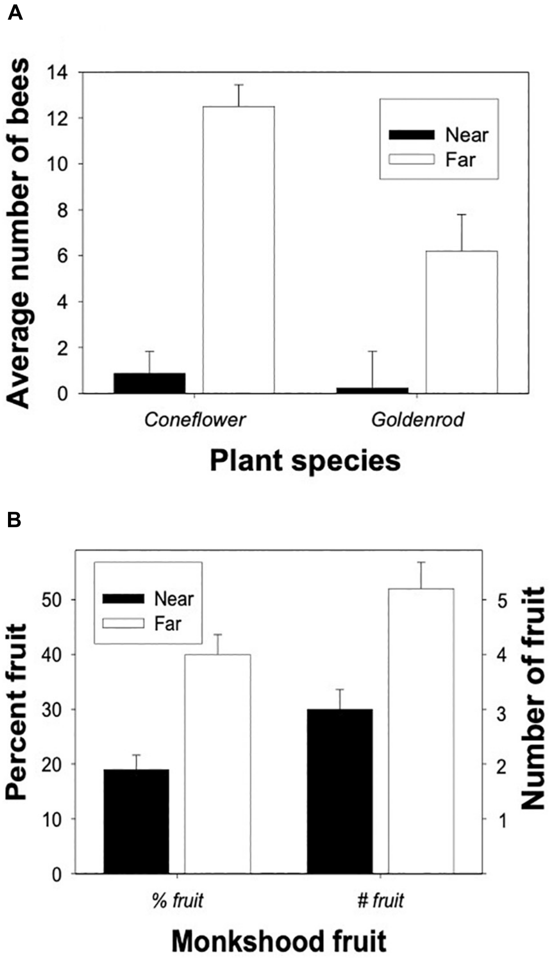

FIGURE 7 | (A) The mean ± SE number of bumble bees observed at six matched pairs of coneflower (*Rudbeckia occidentalis*) and goldenrod (*Solidago* spp.) within 4 km and farther than 5 km from a large bumble bee wolf aggregation. **(B)** Fruit-set in the bumble bee pollinated flower, western monkshood (*Aconitum columbianum*), within 0.5 km and farther than 5 km from a large bumble bee wolf aggregation. Left bars: the percentage (mean ± SE) of marked monkshood flowers that produced fruits. Right bars: the total number (mean ± SE) of fruits on haphazardly chosen monkshood plants. Data from Dukas (2005).

COLLECTIVE NAVIGATION AND SOCIAL LEARNING

Group-living animals balance individually acquired information with social information to make navigational decisions for home range and migratory movement. When individual information is insufficient, social information can reduce uncertainty (Bergman and Donner, 1964; Hamilton, 1967; Grünbaum, 1998; Couzin, 2018). As we discuss below, collective decision-making mechanisms consist of sharing information among group members or following a subset of directed individuals. Concurrently, knowledge regarding movement patterns can propagate within the group, reducing individual learning costs and improving movement efficiency (Mueller et al., 2013; Sasaki and Biro, 2017; Jesmer et al., 2018).

Collective Navigation Using Shared Information

Collective navigational accuracy can be increased by comparing information through social cues (emergent sensing), pooling information (many wrongs), or communicating preferences (voting).

Emergent Sensing

In emergent sensing (**Figure 8A**), group members respond to environmental gradients. This results in collective navigation even if all individuals are naïve (Berdahl et al., 2018; Couzin, 2018). Theoretical models suggest that this is a simple collective decision-making strategy that does not require either memory or complex cognition (Torney et al., 2009; Berdahl et al., 2013; Hein et al., 2015). Individuals within the group respond to environmental information and subsequent social cues. For example, golden shiners (*Notemigonous crysoleucas*) were tested in environments with varying light patches. Golden shiners prefer dark environments and increase swimming speed as a function of light, causing individuals to reduce speed in dark patches, resulting in the group collectively navigating toward dark areas (Berdahl et al., 2013). There is a trade-off between sensitivity to environmental gradients and social information. Greater ability to perceive environmental gradients lessens the need for social interaction, which could decrease group cohesion (Puckett et al., 2018). Therefore, an appropriate balance between

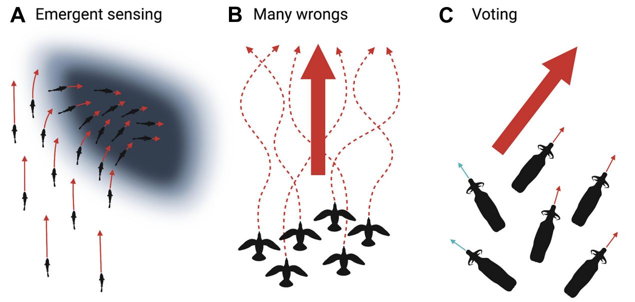

FIGURE 8 | Illustrated examples of collective decision-making strategies. **(A)** Emergent sensing in which individuals respond to environmental gradients (e.g., golden shiners increase swimming speed as a function of light) and social cues (e.g., responding to movement of neighbors). This results in collective navigation toward favorable dark areas. **(B)** Many wrongs in which the collective pooling of estimates suppresses individual error (e.g., indirect homing routes in pigeons; dashed arrows) and increases collective navigational accuracy (large arrow). **(C)** Voting occurs when individuals express their preference for initiation or direction of movement (e.g., African buffalo orienting toward a proposed movement path; small blue and red arrows). Voting prompts the group to choose the majority (large red arrow) or average the proposed paths. Created with BioRender.com.

environmental cues and social information can be achieved by weighing incoming information (Puckett et al., 2018).

Many Wrongs

The many wrongs principle (**Figure 8B**) emerges from individuals pooling each imperfect estimate of direction to improve accuracy, in which group cohesion suppresses individual noise (Bergman and Donner, 1964; Tamm, 1980; Simons, 2004; Biro et al., 2006; Codling and Bode, 2014; Nesterova et al., 2014; Berdahl et al., 2018). For example, homing pigeons released with a small flock flew faster and more direct routes compared to their routes when released alone, even in familiar areas (**Figure 9**; Dell'Ariccia et al., 2008). When individuals are uncertain about navigational decisions, averaging group information reduces error. However, if the difference between individual estimates becomes too large, the group may split or adopt a leader (Biro et al., 2006; Nesterova et al., 2014). For example, homing pigeons with distinct individually established route preferences were released in pairs. When the distance between the two routes was small, pairs typically averaged their paths. But if the distance between each individual's established route grew beyond a threshold, pigeons either followed one of the established routes or split to pursue their own route (Biro et al., 2006). For both emergent sensing and many wrongs, directional accuracy increases as group size increases, notably in groups with few individuals (Bergman and Donner, 1964; Wallraff, 1978; Berdahl et al., 2013). We can expect these strategies to be especially advantageous when knowledge among the group members is low and homogeneous, e.g., a group moving through a novel landscape or consisting of inexperienced juveniles.

Voting

During the voting strategy (**Figure 8C**), individuals advertise their preference and then the group selects the majority or averages the choices (Norton, 1986; Black, 1988; Sueur et al., 2010, 2011; Walker et al., 2017). For example, it has been suggested that adult female African buffalo (*Syncerus caffer*) indicate their preferred foraging patch by orienting themselves toward a certain direction while grazing. The herd then departs in the average direction of individual preferences (Prins, 1996). This widely cited example requires critical tests. Similarly, individuals in troops of olive baboons (*Papio anubis*) propose a movement path. If the difference between the various prospective paths is above a threshold, the group follows the majority. But, when the angle between proposed routes is below the threshold, the group compromises to average the paths (Strandburg-Peshkin et al., 2015). Emergent sensing, many wrongs, and voting are not mutually exclusive. Furthermore, they are frequently combined with leadership and social learning discussed in the next sections.

Leadership

Group members can have varying degrees of influence on navigational decisions. Commonly, animal groups consist of a subset of individuals called "leaders" which guide the remaining group members deemed "followers" (Chance, 1967; Squires and Daws, 1975; Wallraff, 1978; Wilson, 2000; Van Vugt, 2006). Leadership can be distributed among multiple animals or centered around a sole individual (Garland et al., 2018; Strandburg-Peshkin et al., 2018). Leaders may be aware of their status, are recognized by the group as leaders, and can even produce overt signals to lead their group (Raveling, 1969; Poole et al., 1988; Boinski and Campbell, 1995; Lusseau and Conradt, 2009). Alternatively, leaders could be anonymous and unaware of their influence, thus followers rely on passive cues, such as the orientation of neighbors (Couzin et al., 2005; Rosenthal et al., 2015). The terms leader and follower are relative, as a leader in one situation may be a follower in another. For example, leadership may vacillate depending on the area. Homing pigeons can take turns leading during different segments of the same route (Biro et al., 2006). Additionally, leadership status depends on the identity of others in the group. For example, pigeons have leader hierarchies: if individual A leads B, and B leads C, A will also lead C (Biro et al., 2006; Nagy et al., 2010).

In some groups, knowledge or experience determines leadership. Leaders may possess and act on information that followers do not have, such as knowledge of a migratory route (Reebs, 2000; Olsen, 2001a,b; Chernetsov et al., 2004; Jesmer et al., 2018). However, followers are not always naïve. Followers may hold the same knowledge as leaders, but are more agreeable (Arnold, 1977; Smith et al., 2016), have lower route fidelity (Freeman et al., 2011), or are more receptive to social information (Guttal and Couzin, 2010). In homing pigeons, experience increases the chance of becoming a leader, but does not predict it (Flack et al., 2012, 2013; Watts et al., 2016). Factors such as social status (King et al., 2008), sex (Lusseau and Conradt, 2009), or age can also drive leadership. For example, pods of killer whales (*Orcinus orca*) are led by postreproductive females (Brent et al., 2015). Likewise, V-formations in families of greater white-fronted geese (*Anser albifrons*) are primarily led by the father (Kölzsch et al., 2020).

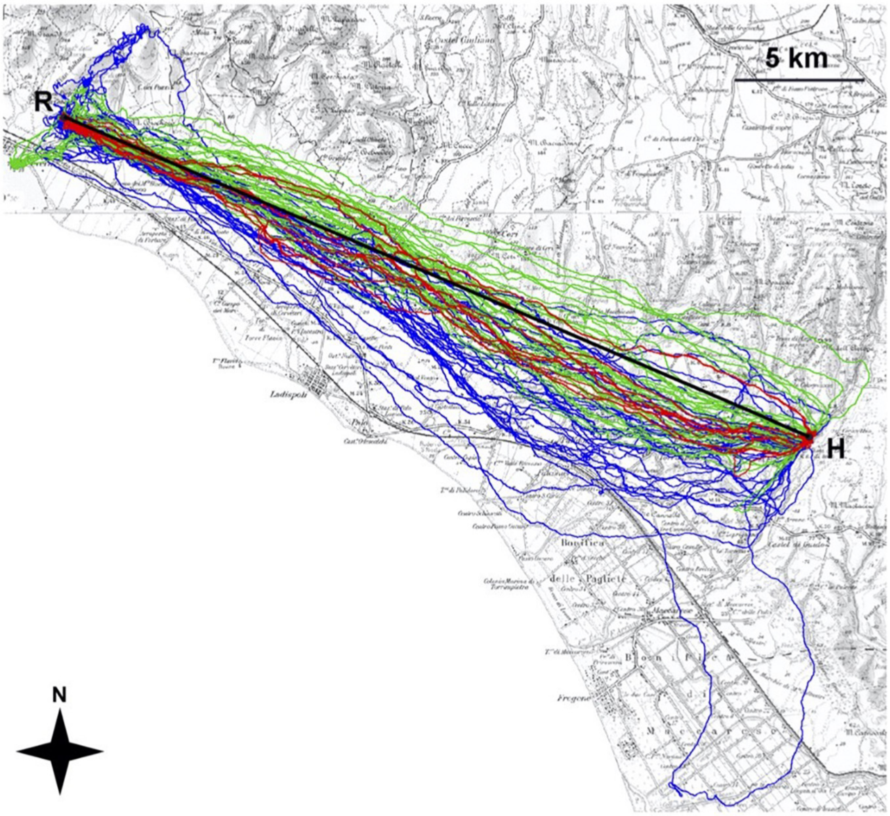

FIGURE 9 | GPS-tracked pigeon routes between a release location (R) and home loft (H). Six pigeons were released six times individually (blue), then six times as a flock (red; one track per flock release), then pigeons were released another six times individually (green). Pigeons released with a small flock flew faster and more direct routes compared to their routes when released alone. Figure from Dell'Ariccia et al. (2008) with permission.

Old individuals may possess information on the most efficient migratory route or the location of a rarely visited site that provides limited resources such as food or water. Such a site may be crucial for the group's success during either a local food shortage or drought. It has been suggested that old elephant matriarchs possess exclusive spatial information crucial to group fitness (Foley et al., 2008; Mutinda et al., 2011). There is indeed evidence for a positive association between matriarch age and her social knowledge, which translates into superior leadership by older matriarchs (McComb et al., 2001, 2011; Mutinda et al., 2011). The role of spatial information in that superior leadership, however, is unknown.

In some cases, leadership is much less systematic. For example, individuals that travel at high speeds (Pettit et al., 2015) or near the front of the group (Pettit et al., 2013b) can emerge as leaders. Further, group members may rotate leadership roles frequently. Alternating leadership roles is fittingly seen in juveniles with similar demographics and experience (Nesterova et al., 2014). For example, flocks of juvenile northern bald ibis (*Geronticus eremita*) take turns leading their V-formation during migration (Voelkl et al., 2015; Voelkl and Fritz, 2017). Additionally, leaders can emerge through simple behavioral rules by followers following the movements of their neighbors (Herbert-Read et al., 2011; King et al., 2011; Rosenthal et al., 2015; Torney et al., 2018; Sankey et al., 2021). Thus, the individuals that initiate movement may have a large influence on group navigation.

Although followers are less influential than leaders, followers can participate in and even initiate decisions. However, the threshold to reach a quorum is higher when followers propose decisions compared to leaders (Kummer, 1968; Bousquet et al., 2011; Walker et al., 2017). For example, families of Canada geese (*Branta canadensis*) perform vocalizations and head-tossing to evoke movement in the group, which ensures cohesion for take-off. If the calls are initiated by a family member other than the father, the number of calls required to elicit movement increases, as well as the period of time before departure (Raveling, 1969).

Cognitive abilities are not identical across group members, leaving some individuals predisposed to become leaders or followers. The shy–bold dimension of animal personality posits that bold individuals have a consistent tendency to explore unfamiliar areas and objects (Gosling and John, 1999; Sih et al., 2004; Réale et al., 2007). Bold individuals are more likely to be leaders than shy individuals (Kurvers et al., 2009; Found and St. Clair, 2016). Compared to shy individuals, leaders are more likely to explore while navigating (Flack et al., 2018), travel at faster speeds, and lead in both familiar and unfamiliar locations (Sasaki et al., 2018). In some cases, leaders may be responsible for immense changes in collective migratory behavior. For example, in elk (*Cervus canadensis*), bold individuals are three time less likely to migrate than shy individuals from the same population (Found and St. Clair, 2016), likely because they better adapt to changing environments (Found and St. Clair, 2019). Another dimension of personality, sociability, can also produce leaders. Chacma baboons (*Papio ursinus*) follow the movements of individuals that they are socially affiliated with (King et al., 2011). Thus, individuals that are highly social are more influential than their less social peers.

Social Learning

Information can diffuse throughout a population and across generations via social learning. Accumulated knowledge can act as a second, non-genetic, inheritance system (Whiten, 2005; Tennie et al., 2009; Jesmer et al., 2018). Many animals learn migratory behavior from their parents or older conspecifics in their population (Olsen, 2001a,b; Agostini, 2004; Chernetsov et al., 2004; Urbanek et al., 2005; Harrison et al., 2010; Palacín et al., 2011). Social influences may even override genetic instructions (Schüz, 1951; Perdeck, 1958; Ferrari et al., 2009; Mellone et al., 2016). Old individuals possess valuable information that has helped them survive thus far. Hence, juveniles profit by learning from old, experienced members of their group, even if juveniles possess adequate migratory information. For example, juvenile whooping cranes (*Grus americana*) migrate using more direct routes when flying with older individuals compared to groups consisting only of young birds (**Figure 10**; Mueller et al., 2013). It is unclear, however, if juveniles deviate from direct routes because of either error or exploration of unfamiliar territory (Mueller et al., 2013; Wolfson et al., 2020). Additionally, learned migratory behaviors are more flexible than genetic instructions, allowing changes in migratory patterns to spread through populations within the lifetimes of individuals. For example, populations containing older whooping cranes were more likely to modify their migratory routes by establishing new wintering grounds closer to their breeding grounds (Teitelbaum et al., 2016).

Individuals can update socially transmitted information to filter out inefficient routes. While homing, pigeon followers actively participate in navigation, learning more direct routes than that of their leader (Pettit et al., 2013a). Additional individuals incorporating their own information into the collective pool of knowledge can further improve group performance. An experiment by Sasaki and Biro (2017) investigated the effects of social learning and cumulative improvement. The experimental group consisted of chains of homing pigeon pairs, beginning with a single pigeon that had developed a homing route after 12 releases. The pigeon was then paired with a naïve individual for another 12 releases. The naïve individual learned the route throughout those trials, becoming experienced, then was paired with a new naïve individual for another 12 releases. This process of pairing a newly experienced pigeon with a naïve pigeon was repeated an additional two times for a total of 60 releases per chain. One control group consisted of solo pigeons and the other control group consisted of fixed pairs of pigeons. Pigeons in both control groups were released 60 times from the same site as the experimental group. By the end of the experiment, the experimental group outperformed both solo and fixed pair controls, which plateaued in efficiency. This suggests that naïve individuals learn route information via social learning and contribute to cumulative improvements in route efficacy, more so than solo or fixed pairs with the same total amount of experience.

Synthesis

Social groups adopt various strategies, typically coinciding, to move within and throughout a landscape. Groups can share information to improve navigational accuracy, during which opinions from some individuals have more influence than others, while valuable information can diffuse throughout the group via social learning. For example, leadership and voting coincide in packs of African wild dogs (*Lycaon pictus*) during pre-departure social rallies. Pack members increase the amount of abrupt nasal exhales (sneezes) prior to departure. Any pack member can propose a departure by initiating sneezing, although individuals other than the highest ranking dominant dogs must have higher signal frequency in order to succeed (Walker et al., 2017). Collective navigation, leadership and social learning are difficult to assess in nature through observation alone. Without controlled experiments, we can only estimate which process is occurring without firm conclusions.

EXPERTISE AND MOVEMENT

Individual learning, social influence and social learning are ubiquitous among animals. Their long term, combined effects lead to expertise, defined as the features that allow individuals with extensive experience on a given complex task to show superior performance on that task compared to novices (Dukas, 2019). While expertise has been studied primarily in humans (Ericsson and Lehmann, 1996; Ericsson et al., 2006; Vaci et al., 2019; Strittmatter et al., 2020), it is highly relevant for other species as it can manifest in many behaviors including movement. Two domains pertinent to movement ecology are first, mastery of an individual's habitat, which may include a vast memory about the identity, location and occurrence of a variety of relevant items, events and individuals. Examples include the location of seasonal food plants, shelters, territorial neighbors, and predators. Second, individuals can improve their movement speed and efficiency with practice. This may be owing to motor learning within a small territory (Stamps, 1995), adopting optimal routes that avoid challenging terrain in a large home range (Green et al., 2020), or learning to better handle a variety of challenges throughout a long travel route. For example, a within individual comparison in black kites (*Milvus migrans*) indicated improvement in migratory performance with age. Part of this improvement was due to birds enhancing their abilities to exploit tailwinds and cope with wind drift (Sergio et al., 2014). Other studies also indicate that birds improve their abilities to handle winds and rising air currents with experience (Harel et al., 2016; Wynn et al., 2020).

Critical research on expertise is currently scarce as it requires comparisons of the same individuals over time while controlling

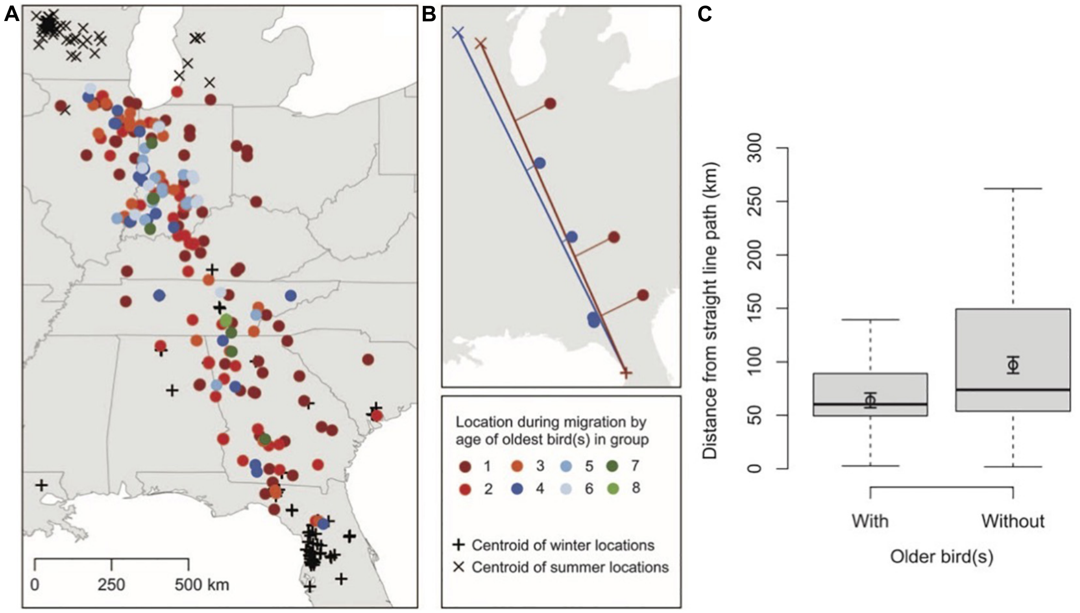

FIGURE 10 | Groups of whooping cranes containing old individuals migrate using more direct paths compared to groups consisting of only juveniles. **(A)** Telemetry and visually observed locations of whooping cranes throughout their migratory journey. **(B)** Examples of migratory routes that juveniles performed with (blue) and without (red) the presence of older individuals. **(C)** Distance from straight line paths during migration of juvenile groups with and without older individuals. Figure from Mueller et al. (2013) with permission.

for relevant alternatives that affect performance. These include correlated changes in anatomy, morphology, physiology and effort (Dukas, 2019). Furthermore, between individual analyses are insufficient as they commit selection bias owing to the likely higher mortality rates of inferior individuals. As far as we know, only a single program, which combined observations and controlled experiments in the field, has considered all factors by quantifying within individual foraging performance in natural settings, muscle physiology, and effort as functions of experience (Dukas and Visscher, 1994; Dukas, 2008b,c; Schippers et al., 2006, 2010). Many other species are amenable for long term research programs that add controlled experiments to information about within individual changes in performance with age (Clutton-Brock, 1988, 2016; Wooler et al., 1990; Sand et al., 2006; Daunt et al., 2007a,b; Leach and Sedinger, 2016).

CONCLUSION AND PROSPECTS

Our three main conclusions are first, that birds and mammals possess good spatial learning and memory, which enable them to find their way while engaging in their daily activities. Second, we have good understanding of the cognitive mechanisms that allow many species to navigate successfully over distances spanning up to thousands of km. Third, the movement ecology of many birds and mammals is heavily determined by social influence and social learning. While there is large variation among animals, researchers initiating work on a lesser studied species may assume that it has good spatial cognitive abilities that are influenced by social observations. Nevertheless, the strength of evidence for our three conclusions is rather mixed. Very few controlled experimental studies assessed spatial learning and memory in birds and mammals over a large area. On the other hand, owing to the conspicuousness and ubiquity of animal migration, we have known for a long time about animals' abilities to orient well between their winter and summer grounds. Some of the mechanisms underlying these navigational skills are mostly understood, at least for a small selection of species, primarily birds. Finally, we know that social information influences some aspects of bird and mammal movement including, for example, philopatry and migration in some species. There are probably, however, many other aspects of movement that are under social influence but understudied. Examples include trails, long-lasting scents, and cues that indicate recent activity or successful reproduction by conspecifics.

While we focused on relatively well studied topics, our review can readily reveal subjects that invite future research. Most notably, we have not critically addressed specific issues of both perception and decisions even though they likely have strong effects on animal movement (Avgar et al., 2013). Some studies have addressed issues of perception relevant to movement ecology. For example, the topic of perceptual range, defined as the maximum distance from which one can detect relevant landscape features, has been recognized for some time (Zollner, 2000; Schooley and Wiens, 2003), but we still know relatively little about it. Similarly, while decisions have been implicitly included within the overall study of animal movement, there has not been a focus on the exact decision rules employed by individuals when considering, for example, when and where to go (Bauer et al., 2011). Finally, our review primarily encompassed issues related to movement either within a home range or during seasonal migration. We have not addressed the two other relevant categories of dispersal and nomadism (Baguette et al., 2014; Teitelbaum and Mueller, 2019) even though they can gain from a synthesis that takes a cognitive ecology approach.

There are various areas that would gain from further integration of methods and insights from cognitive ecology into the study of animal movement. First, there is a strong research bias toward the visual domain. It is thus crucial that we devote more research effort to the effects of understudied sensory domains on animal movement. Such domains include olfaction, electromagnetic radiation beyond the human perceptual range, and night vision. For example, we perceive the landscape primarily in the visual domain, but soundscape (Pijanowski et al., 2011; Van Oosterom et al., 2016) and smellscape (Wallraff and Andreae, 2000; Nevitt, 2008; Gagliardo et al., 2013; Henshaw, 2013; Buehlmann et al., 2015; Ackels et al., 2021) may be as or more important for many species. Particularly promising is the likely possibility that many animals perceive a rich scene of long-lasting olfactory cues, which inform them about the location, condition, age and sex of conspecifics, competitors and predators. Second, enlightening information gathered from GPS-collard animals has inspired increased interest in the spatial information that animals learn about, remember and employ to guide their movement. The GPS data, however, are merely observations on individuals' locations over time. Hence they must be supplemented with controlled field studies that critically test for the spatial learning and memory of species of interest. Such work may modify protocols previously employed for critical tests of spatial memory in the field, such as the one detailed in **Figure 1** (Edwards et al., 1996). Third, a few studies indicate that the large-scale spatial structure of animal movement affects species at other trophic levels through competition, predation, herbivory, pollination and seed dispersal (e.g., Dukas, 2005; Kohl et al., 2018). We think that further research on the effect of the movement patterns of one species on other species can be highly illuminating. Fourth, understandingly, a large share of movement ecology research has been devoted to large mammals. However, we have little experimental data on the mechanisms underlying seasonal migration in these species. For example, do they rely on all three compasses as birds do? Fifth, mechanisms of time keeping both within day and throughout the year have received significant attention in both animal cognition and physiology (Gallistel, 1989; Shettleworth, 2009; Kumar et al., 2010). While we know that animals possess excellent biological clocks that guide their short and long term movement decisions, we know less about how animals time their revisits to familiar places within and between days and years (Janmaat et al., 2013, 2014; Berger-Tal and Bar-David, 2015). Finally, there is growing appreciation that non-humans show long-term improvements in performance similar to those studied in human experts (see Expertise and Movement section above). Mechanisms contributing to the superior performance of experts include greater working and long-term memory, better allocation of attention among co-occurring tasks, and quicker and refined decisions (Dukas, 2019). Decisions regarding movement can benefit from expertise and should be subjected to future research. Similarly, evidence from humans indicates that people working together for a long time develop group expertise primarily owing to enhanced social dynamics (Argote and Epple, 1990; Tindale and Winget, 2017). Similar group expertise likely occurs in animal groups and probably contributes to superior movement performance.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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REVIEW
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Learning and Animal Movement

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Integrating diverse concepts from animal behavior, movement ecology, and machine learning, we develop an overview of the ecology of learning and animal movement. Learning-based movement is clearly relevant to ecological problems, but the subject is rooted firmly in psychology, including a distinct terminology. We contrast this psychological origin of learning with the task-oriented perspective on learning that has emerged from the field of machine learning. We review conceptual frameworks that characterize the role of learning in movement, discuss emerging trends, and summarize recent developments in the analysis of movement data. We also discuss the relative advantages of different modeling approaches for exploring the learning-movement interface. We explore in depth how individual and social modalities of learning can matter to the ecology of animal movement, and highlight how diverse kinds of field studies, ranging from translocation efforts to manipulative experiments, can provide critical insight into the learning process in animal movement.

Keywords: animal cognition, decision-making, migration, reinforcement statistical learning, translocation

INTRODUCTION

Animal movement, in the form of translocation from one locale to another, takes many forms and is critical to ecological processes. This understanding has given rise to the rapidly growing discipline called movement ecology (Nathan, 2008). Concurrently, the subject of learning has been studied from the perspective of animal behavior, both in the context of ecological interactions and in the context of movement itself (**Box 1** and **Table 1**). Animal behavior has a well-established and celebrated history of understanding learning and there has been recent growth in connecting learning and memory to animal movement behavior (e.g., Fagan et al., 2013). At the same time, a recent explosion of ideas about machine learning is now creating new perspectives on understanding animal movement based on algorithms.

Along with these recent developments, the ability of ecologists to track animal movements and behaviors remotely in the wild has been steadily increasing. The collection of massive amounts of data on animal movement, primarily *via* satellite tracking, is now possible at a scale and level of detail previously unimaginable and can be linked with similarly improving remotely sensed or modeled environmental data (e.g., vegetation, anthropogenic disturbance, terrain, NDVI, snow depth) (Kays et al., 2015). Furthermore, more recent advances in bio-logging (e.g., accelerometers, proximity measures, audio-, and video-recording devices) provide direct information on some of the physiological (e.g., jaw movement, heart rate, cortisol, stable isotopes, reproductive status), and social (e.g., interactions with conspecifics), contexts of movements (Wilmers et al., 2015). This coupling of movement patterns with the movement context has created opportunities to infer learning mechanisms and meld ideas from animal behavior, movement ecology, and remote sensing in the context of ecology of learning and animal movement. We develop such a synthesis here.

We start with a focus on learning as a means for acquiring information and making decisions. Employing two related definitions of learning, one from psychology and the other related to computer science, we evaluate the benefits, costs and limitations of learning in the context of animal movement. Next, we address the modality of learning in animal movement, ranging from individual to social. We then develop links to related disciplines: psychology, animal cognition, and machine learning. We close by reviewing approaches to studying the process of learning and animal movement, whether from experimental or observational studies, discussing the role that models can play in this endeavor, and suggesting areas for future developments.

INDIVIDUAL INFORMATION ACQUISITION AND DECISION MAKING

Definition of Learning

We start with a *psychology-based definition* of learning, which states that learning is the information acquisition that occurs *via* an individual's experience that results in a detectable and consistent change in neurophysiology and/or behavior (**Box 1**). Movement intersects with this definition of learning in several key ways. First, movement will give rise to learning if the movement facilitates information acquisition by introducing an animal to a new environment (e.g., information on forage availability) or state (e.g., information from increased vigilance). Second, the learned information can give rise to new movement decisions if the information acquired is used to change movement patterns (e.g., switching to area-restricted search in regions of high forage availability). Lastly, learning can be about movement itself, for example, when an animal learns where and when to migrate by imitating conspecifics (e.g., crane migration). **Figure 1** depicts these connections among movement, information processing, the environment, and the internal states of the animal.

Laboratory studies of learning can be used to seek out direct cellular evidence for neurophysiological changes arising from information acquisition and storage *via* functional magnetic resonance imaging (Marsh et al., 2010). However, these approaches are impractical in studies of wild animals, for which most ecologically relevant evidence for learning comes from observing changes in behavior as a result of experience. Thus, although the psychology-based definition of learning above does not strictly involve decision-making, the ecological implications of learning are often intimately tied to experience and the decision-making process. This emphasis on process means that movement-related learning is more similar to how machine learning is defined: improved performance for a specific task as a result of prior experience. This definition, which we refer to as the *task-based definition*, differs from the psychological definition because it is directly tied to experience-based improvements in performance for a specific task (**Box 1**).

The Learning Process

The process of learning includes all the steps needed for information acquisition based on experiences encountered. Broadly, these steps include attention to relevant information, perception of the information, acquisition of that information, and, finally, storage, retention, and retrieval (memory) of that information. At this point, the information can be acted upon, for example, to make a movement decision (**Figure 1**).

Diverse factors may impede or enhance an animal's attention to information from its environment or from other individuals. For example, animals in unfamiliar environments may be more (or less) observant of environmental cues (Wolfe, 1969) and certain types of social interaction may increase or decrease attentiveness, leading to social learning (Heyes, 1994). Other factors, such as the internal state of an animal (Dorrance and Zentall, 2001) or its risk sensitivity (Bacon et al., 2010) may also play a role in determining attentiveness (**Figure 1**).

The perception and acquisition of information depend on an animal's sensory capacities. For most animals, certain sensory cues will be easier to detect than others, which can lead to different hierarchies of inputs, which may be altered contextually. For example, many aural and olfactory cues may be more important than visual information at night (Zollner and Lima, 1999). Once acquired, information must be committed to memory as part of the learning process. Spatially distributed information may be stored as a cognitive map, sometimes in a network-based non-Euclidean format (Noser and Byrne, 2014). Storage and retrieval of learned information is essential for decision making, which can be based on recent events or information from long ago (Polansky et al., 2015; Abrahms et al., 2019).

A test of successful learning is the ability to make a decision using information from past experiences that discriminates among alternative strategies. For example, in laboratory studies, exposure to spatially distributed food rewards in mazes can affect the movement choices of rats (Leonard and McNaughton, 1990). Similarly, for wolves, memory-related statistical metrics like "time since last visit" to a location may form the basis for movement decision discrimination (Schlägel et al., 2017). Of course, this link between experiences and decision making is both complex and context-dependent, being modulated by layers of complexity regarding habitats, social status, and internal states (**Figure 1**). The so-called *diffusion theory* for learning posits that the brain does not solve decision-making problems exactly but

BOX 1 | Definitions of terms associated with learning.

This box defines terms central to a synthesis of concepts from animal behavior, ecology, psychology, and certain quantitative methods.

Foundational Concepts

Learning:

> *Psychology-based definition:* the cause-effect process leading to information acquisition that occurs as a result of an individual's experience.
>
> *Task-based definition:* improved performance for a specific task, based on experience.

Memory: The storage, retention and retrieval of information.

Spatial memory: The memory for where objects/resources/places are in space. Representation of space. Encodes spatial relationships or configurations.

Supervised machine learning: The process by which the machine is trained to perform a task where some input data are already labeled with the correct output. It can be compared to learning in the presence of a supervisor or teacher.

Statistical learning theory: An unsupervised framework for machine learning that deals with the problem of extracting statistically relevant correlations from data.

Modes of Learning

Associative learning: When an animal makes an association between a stimulus and an outcome. Two forms are:

> *Classical (Pavlovian) conditioning*: an animal associates a biologically relevant stimulus (e.g., food) with a previously irrelevant stimulus. For example, a dog presented the sound of a bell rung alongside the presentation of food, will come to salivate at the sound of the bell in the absence of food. Another example would be that a raccoon learns that garbage cans contain food.
>
> *Operant (instrumental) conditioning*: the behavior of an animal is controlled by the consequences of that behavior. Typically, this behavior develops through sequential reinforcement (e.g., a raccoon learns how to open the garbage can to get food and is rewarded).

Positive reinforcement: Behavior is rewarded and then increases.

Negative reinforcement: Behavior is increased through avoidance of an unpleasant stimulus (also known as instrumental conditioning).

Punishment or Inhibitory learning: Behavior is decreased through avoidance of an unpleasant stimulus. This contrasts with negative reinforcement, where the behavior increases.

Reinforcement learning: *From machine learning*: The learner is not told which actions to take, but instead must discover which actions yield the most reward by trying them. This is synonymous with *trial and error learning*. As in optimal foraging in ecology, the focus is on the balance between exploration (of unfamiliar objects/places) and exploitation (of current knowledge).

Online learning: *From machine learning*: A technique for implementing machine learning based on data becoming available in a sequential order and then being used to update the best predictor for future data at each step.

Habituation: after repeated exposure, an animal decreasingly responds to a stimulus. The stable end state is the animal's level of tolerance of a stimulus and the outcome is higher tolerance.

Sensitization: after repeated exposure, an animal increasingly responds to a stimulus. The stable end state is the animal's level of tolerance of a stimulus, and the outcome is decreased tolerance.

Latent learning: an animal learns by gathering and storing information, without immediate reward.

Pathways of Learning

Social learning: Also called "transmission," this is an umbrella term that includes transfer of skills, concepts, rules and strategies that occur in social contexts and can affect individual behavior. These include:

> *Social facilitation*: An animal has an increased probability of performing a behavior in the presence of a conspecific.
>
> *Local enhancement*: An individual's interest in an object or location is mediated by the interest or movement of others.
>
> *Imitation*: Novel copying of a model behavior through observation that results in a reliably similar outcome.

Cultural transmission: Social transmission leading to the development of traditions that are passed down from generation to generation.

Vertical vs. horizontal learning: Sometimes referred to as parent vs. peer learning, this dichotomy characterizes the generational source of social information.

Information center: Particular locations or events that provide opportunity for information exchange. For example, a community roost may enable individuals to follow well-fed peers to new foraging locations.

Direct information exchange: An animal is provided sender-based, actively communicated information by another individual. For example, honeybees tell their sisters the locations of rewarding flowers.

Optimization-related Terms

Genetic algorithm: A population of candidate solutions to an optimization problem that evolve toward better solutions.

Policy: In machine learning, the mapping of states to actions (e.g., a hungry animal begins to hunt).

Utility function: In machine learning, the assignment of weights or values to agent states. Actions are selected by comparing the values of the predicted states that derive from particular action. For example, a policy involving search vs. sit-and-wait strategies will yield different outcomes for a hungry animal.

Adaptive movement: When animals modify their movement in response to a change. In models, adaptive implies movement behaviors that confer fitness/performance benefits.

uses algorithms that optimize the speed and accuracy of choices (Bogacz, 2007).

Benefits and Costs of Learning

All mobile organisms face a wide variety of spatial challenges that influence individual fitness and present opportunities for decision making shaped by learning. Foraging opportunities and energetic constraints are patchy in space and time, in large part because the underlying physical and biotic processes are also patchy. Optimal foraging theory (McNamara and Houston, 1985; Stephens and Krebs, 1987; Mangel and Clark, 1988) provides a framework for understanding how benefits accrue from foraging in patches that offer the highest returns of energy or nutrient intake per unit time relative to time or energetic costs. Lost opportunities for social interaction, breeding, reproductive care, or shelter, and the risks of mortality due to predation, parasitism, or disease can then be considered.

When the rate of environmental change varies across time and space, as is common along elevation or rainfall gradients, theory suggests an animal may be able to improve its fitness through appropriate patterns of nomadic or migratory movement (e.g., Fryxell and Sinclair, 1988). Field studies support this theory. For example, migratory ungulates can choose patches at a landscape scale that yield appreciable improvement in rates of energy gain, even when such gains are transitory and require continual nomadic repositioning (Fryxell et al., 2004; Holdo et al., 2009). Memory can also influence the choice of movement patterns, such as the balance between range residency and migration (e.g., Shaw and Couzin, 2013). For example, when undergoing seasonal transitions between ranges, migratory ungulates can obtain fitness benefits by remembering previous trajectories (Bracis and Mueller, 2017; Jesmer et al., 2018; Merkle et al., 2019).

Researchers have investigated how learning can influence and confer advantages to moving organisms. Agent-based models of foragers with spatial memory have shown how fitness accrues from moving to acquire reliable information, even when that movement samples sub-optimal patches (Bracis et al., 2015). This is particularly clear when naïve animals are presented with an unfamiliar environment and movement is exploratory. However, even experienced individuals can benefit by spatially sampling a dynamic environment, in particular when resources can be depleted (Boyer and Walsh, 2010) or predation risk can change (Bracis et al., 2018). In this case, movement keeps current the information needed for appropriate decision making.

Given that foraging often results in resource depletion, fitness may also be improved through informed departure criteria based on marginal value leaving rules (Charnov, 1976; Arditi and Dacorogna, 1988; Brown, 1988). The field of "sampling behavior" (Stephens, 1987) extends ideas originally developed within the optimal foraging theory framework, which traditionally assumed that animals are omniscient (Krebs and Inman, 1992; Stephens et al., 2007). One sampling framework considers when animals should visit a patch to assess whether it has changed in value (Green, 1980), whereas another framework focuses on the benefit accrued by tracking a changing environment (Shettleworth et al., 1988). Foragers that sample patches or track changing conditions

TABLE 1 | Case studies of learning and animal movement.

References	Species	Spatial processes involved	Individual learning vs. social learning	Learning in novel or familiar contexts?	Learning linked to memory?	Simple elapsed time?	Juvenile vs. adult compariso?
Barry et al. (2020)	Wolves	1. Natal dispersal 2. Territory formation	Individual	Novel	Y	Y	N
de Grissac et al. (2017)	Wandering Albatross	Foraging	Individual	Novel	N	Y	Y
Grecian et al. (2018)	Gannets	1. Foraging 2. Exploration	Elements of both	Novel	Y	N	Y
Leadbeater and Chittka (2009)	Bumblebees	Foraging	Social	Novel	N	Y	N
Lihoreau et al. (2012)	Bumblebees	Foraging	Individual	Familiar	Y	Y	N
Papastamatiou et al. (2011)	Sharks	1. Orientation 2. Patch use	Individual	Familiar	Y	N	Partly
Scott et al. (2014)	Sea turtles	1. Foraging 2. Migration	Individual	Novel	Y	Y	Partly
Sigaud et al. (2017)	Bison	1. Foraging 2. Patch Use	Social	Novel	Y	Y	N
Teitelbaum et al. (2016)	Whooping Cranes	1. Migration 2. Shortstopping	Elements of both	Familiar	Y	Y	Y
Votier et al. (2017)	Gannets	1. Foraging 2. Exploration	Elements of both	Novel	Y	Y	Y

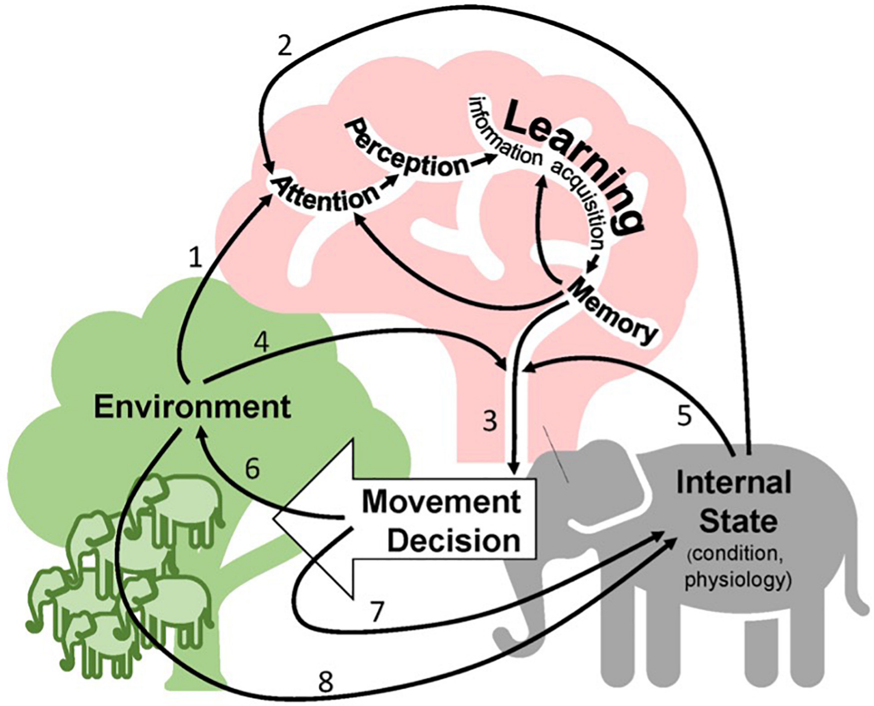

FIGURE 1 | A conceptualization of learning in the context of animal movement. An individual's environment (green, including social context) and its internal state (gray) can both influence the onset of information gathering *via* the attention that an individual pays to landscape features (arrows 1 and 2, respectively). As currently understood by psychologists, the information gathering pathway involving attention, perception, learning, and memory appears inside the animal's brain (pink, unlabeled arrows) ultimately providing input to a movement decision (arrow 3). Both the individual's environment (arrow 4) and its internal state (arrow 5) can then shape and modify the link between memory and movement. The movement decision has ramifications for the environment (arrow 6) and for the internal state (arrow 7). Lastly, the environment can alter an individual's internal state directly (arrow 8) without invoking information gathering and memory, often *via* social interactions.

are learning about the current state of the environment (Stephens, 1987). Informed decision making about which patches to feed in and how long to do so requires reliable expectations regarding resource availability, predation risk, and energetic costs across an individual's home range, as well as the capacity to estimate these same variables at a given spatial location. For example, primates foraging on fruit track the productivity of different trees and possibly fruit ripeness (Janson and Byrne, 2007). Overall, environmental predictability appears to be essential for the origin and success of movements based on learning and the reshaping of movement strategies based on experience more generally (Mueller et al., 2011; Riotte-Lambert and Matthiopoulos, 2020).

Learning can also help improve fitness even when spatial movement processes are not directly tied to foraging (e.g., territorial defense, migration, reproduction) (**Box 2**). For example, learning can provide advantages in dominance interactions (Kokko et al., 2006), efficiency of movement (Stamps, 1995), effective escape from predators (Brown, 2001), and large-scale dispersal decisions (Barry et al., 2020), all of which can translate into fitness benefits (Brown et al., 2008; Patrick and Weimerskirch, 2017). For territorial species, learning can influence how conflicts drive pattern formation (Stamps and Krishnan, 1999, 2001; Sih and Mateo, 2001) and alter strategies for territorial defense (Potts and Lewis, 2014; Schlägel and Lewis, 2014; Schlägel et al., 2017). For migratory species, this includes determining least-cost migration corridors between seasonal ranges (Bischof et al., 2012; Poor et al., 2012).

While learning may have benefits, acquiring information based on experience does not come without costs. For example, information gathering can require substantial investment in time and/or energy, and may heighten risk (Eliassen et al., 2007) or come at the expense of lost opportunities for foraging, social interaction, or search for suitable breeding sites (Dall et al., 2005). The machinery for learning also exacts an energetic cost (Isler and Van Schaik, 2006; Niven, 2016). Furthermore, retained memories may negatively affect the acquisition of new information, and so there may be a trade-of between memory retention and acquiring new memories (Tello-Ramos et al., 2019).

Limitations to Measuring Learning From Animal Movement Patterns

Typical methods for recognizing learning in animal movement patterns do not measure the acquisition of information directly but rather rely on the *task-based definition* of learning, which requires improved performance for a specific task, based on acquired experience (**Box 1**). There are limitations to such methods, which pose challenges to learning from uncontrolled field-derived data. Unambiguously explaining a particular movement is a general challenge in the study of wildlife, where context, perception, internal states, and particular environmental cues all determine an animal's response, but are often unobserved. For example, the "time since last visit" behavior in wolves, mentioned above, may not require memory, but could be explained by information from decaying scent marks (Schlägel and Lewis, 2014).

Obvious and obscure alternative explanations to learning and memory must be carefully considered in uncontrolled field studies. **Table 2** categorizes a number of movement studies according to the level of evidence for learning—from strong to simply consistent with learning. For each we provide other, non-learning interpretations of the data that cannot be definitively excluded (**Table 2**).

PATHWAYS OF LEARNING FOR ANIMAL MOVEMENT

Individuals can experience or gain information about their environment *via* different pathways—individually (i.e., by direct interaction with the environment; Dall et al., 2005) or socially (i.e., by observing others; Bandura and Walters, 1963; Rendell et al., 2010)—with *learning* demonstrated by a change in an individual's behavior due to its experience (**Box 1**).

Individual Learning

Much of an animal's individual learning is associative; that is, the individual learns by making an association between a stimulus and an outcome. Associative learning may arise either from classical (Pavlovian) conditioning, where an animal associates a biologically relevant stimulus (e.g., food) with a previously irrelevant stimulus (e.g., railway tracks), or from operant (instrumental) conditioning, where the behavior of the animal is controlled by the consequences of that behavior (e.g., feeding on grain on tracks leads to a food reward) (Pearce and Bouton, 2001).

These learning processes can make a behavior more likely through positive reinforcement (*via* rewards) or negative reinforcement (*via* unpleasant stimuli), or less likely through punishment or inhibitory learning (again, *via* unpleasant stimuli). For example, a bear foraging on railway tracks (Murray et al., 2017) might be more likely to forage when it finds grain (positive reinforcement) but less likely to forage through negative interactions with moving trains (punishment or inhibitory learning). Additionally, it might increase its vigilance through negative interactions with moving trains (negative reinforcement).

One associative learning mode relevant to animal movement is discrimination learning, where an animal learns to respond differently to distinct stimuli. For example, because homing pigeons can discriminate between the presence and absence of anomalies in magnetic fields, magnetoreception could be used for navigation (Mora et al., 2004).

Two *non-associative* learning modes that are relevant to movement are habituation (decreased response to a stimulus after repeated exposure) and sensitization (increased response to a stimulus after repeated exposure). These modes depend on the strength of association between stimulus and outcome, rather than the association itself. For example, the sensory responsiveness of honey bees declines after bees receive low sucrose sugar solutions (habituation) and increases after offerings of high sugar solutions (sensitization) (Scheiner, 2004). In turn, the sensory responsiveness of honey bees constrains individual foraging plasticity and skews the collective foraging decisions of colonies (Scheiner, 2004).

BOX 2 | Learning and Movement Processes.

Movement is the spatial consequence of a number of different behaviors by animals. For example, a predator searching for predictable but mobile prey must change its location in space to increase the chances it will encounter a prey item. In many situations (e.g., predictable environments or regularly available prey), learning can reduce uncertainty and increase success in such spatial behaviors. We outline a selection of these below:

Search and attack in predation—When prey live in a complex and heterogeneous environment, predators may benefit by adjusting their search and attack behavior over time (Stephens et al., 2007). When predators detect their prey through visual, auditory, or olfactory cues, they can use associative learning to refine their "search image" and improve their ability to detect and attack prey (Ishii and Shimada, 2010). For instance, desert ants (*Cataglyphis fortis*) use associative learning to connect specific odors to food, and then use this food-odor memory to assist their next foraging journey (Huber and Knaden, 2018).

Escape from a predator—Spending time in familiar space allows animals to learn motor programs that enhance efficient movement within that space (Stamps, 1995). For instance, in response to a pursuing human, Eastern Chipmunks (*Tamias striatus*) within their home range (i.e., familiar space) take half as much time and travel half as far to reach a refuge compared to when outside their home range (Clarke et al., 1993).

Foraging bouts—An animal's rate of energy gain while foraging can increase by collecting information about the environment (Stephens and Krebs, 1987), given the environment changes in a (at least somewhat) predictive way. In most of these cases, animals use associative learning to connect the reward of a food source with some aspect (e.g., color, nearby landmark) of that food source. For instance, Rufous Hummingbirds learned the location of flowers that they had emptied in a foraging trial, and in subsequent trials did not waste time visiting them again (Healy and Hurly, 1995).

Navigation and migration—Migratory movements notably occur at spatial scales that greatly exceed perceptual abilities of animals (mammals: Teitelbaum et al., 2015; birds: Alerstam et al., 2003). Thus, it is expected that animal migration is at least partly based on memory of past experience (though some migrations appear to be innate). When migration has a learned component, learning is likely used to improve migratory performance. For instance, social learning of migration helps ungulates improve energy gain (Jesmer et al., 2018) and helps birds reduce costs (Mueller et al., 2013).

Home range or territory selection—The decision process of choosing the size and location of home range or territories can be thought of as a learning process of integrating new information about the distribution of resources of a landscape (Mitchell and Powell, 2004). For instance, home range size is often larger in areas with fewer resources available (e.g., Morellet et al., 2013; Viana et al., 2018). Further, increased exploration events, presumably to sample new locations when others are unavailable, can result in still larger home ranges (Merkle et al., 2015).

Another mode of learning, latent learning, is relevant to animal movement (Franks et al., 2007). Latent learning involves the gathering and storing of information, without immediate reward, such as when animals learn their migration route away from breeding grounds after they are born (e.g., in autumn) and must use that information to return in springtime. **Box 1** provides further details on these modes of learning.

Social Learning

Social learning is an umbrella term for the learning pathway that includes transfer of skills, concepts, rules, and strategies that occur in social contexts and can affect individual behavior. Types of social learning include (i) social facilitation (increased probability of performing a behavior in the presence of a conspecific), (ii) local enhancement (an individual's interest in an object or location mediates interest/movement by others), and (iii) imitation (novel copying of a model behavior through observation that results in a reliably similar outcome) (Visalberghi and Fragaszy, 1990). Note that these are distinct from the transfer of declarative or procedural information *via* direct information exchange, such as in bee dancing, to relay information concerning resource locations (Leadbeater and Chittka, 2007).

Each type of social learning is relevant to movement ecology. For example, social facilitation explains bison movement: individuals are more likely to travel to a given new location when in a group where another animal had knowledge of that location (Sigaud et al., 2017). Following behavior occurs in ants where leaders provide guidance to naïve individuals concerning the location of resources (Franks and Richardson, 2006), and in elephants where matriarchs lead herds to waterholes not known to the rest of the group (Fishlock et al., 2016). Imitation can be

TABLE 2 | Mapping empirical examples of learning to machine learning concepts.

	Machine learning example	**Empirical examples**			
Step	**AlphaGo Zero (Silver et al., 2017)**	**Hummingbird traplining (Tello-Ramos et al., 2015)**	**Crane migration (Mueller et al., 2013)**	**Experimental elk translocation (Frair et al., 2007)**	**Sheep and moose migration (Jesmer et al., 2018)**
Task	Win	Forage efficiently	Migrate efficiently	Exploit environment optimally	Exploit environment optimally
Experience	Repeated play against self	Movement within a controlled array of feeders	Repeated migration journeys across years	Movement away from initial capture/release location	Movement and population persistence over decades
Performance measure	Victories	Path distance per bout	Deviations from straight-line migratory path	Settlement and survival rate	1. Proportion of green wave exploited 2. Percent of population migrating
Demonstrated improvement over time (or in comparison to benchmark)	Increased competitive ranking	Decreased length of movement path	Decreased length of migratory journey	Increased rate of residency	Increased migratory tracking and universal migration
Plausible learning mechanisms	Reinforcement learning	Positive reinforcement	1. Spatial memory 2. Social learning 3. Positive reinforcement	1. Positive reinforcement (forage) 2. Negative reinforcement (predation) 3. Horizontal social transmission	1. Vertical transmission 2. Positive reinforcement (individual moose foraging) 3. Positive reinforcement (social sheep foraging) 4. Cultural transmission
Alternative explanations	Not necessary	Controlled experiment	Tested and rejected wind-mediated movement and ontogeny	Mortality-mediated natural selection	1. Mortality-mediated natural selection 2. Population growth and expansion 3. Kinesis
Evidence of learning?	Yes	Yes	Yes	1. Consistent with learning but not direct evidence. 2. Population-level rather than individual-level metrics impede direct evidence for learning.	

seen in fish, where translocation experiments demonstrate how naïve individuals learn migration routes through association with experienced individuals (Helfman and Schultz, 1984), as well as in replacement experiments where the long-term re-use of resting and mating sites can be socially learned rather than quality-based (Warner, 1988).

Individual learning can interact with social learning. For example, independent exploration allows ants to improve upon the paths they have learned *via* social learning through tandem running (Franklin and Franks, 2012). Here, independent exploration is the basis for improvement of route navigation, which can then be distributed within a colony *via* "information cascades." More generally, individual learning may be modulated by associational acquisition, where options for individual learning are constrained by the individuals with which an animal associates (Fragaszy and Visalberghi, 2004).

Social learning is emphasized though existing social bonds, such as parent-offspring relationships. For example, elephants will learn resource locations in complex landscapes through both vertical and horizontal transmission (Bowell et al., 1996) and maternal-offspring pairs of whales may complete entire migrations together (Hamilton and Cooper, 2010), thus enhancing the potential for social learning.

However, social learning does not always confer a net benefit (Giraldeau et al., 2002), and may result in costly strategies of movement and resource use (Sigaud et al., 2017). For example, tested alone, adult female guppies that had shoaled with trained conspecifics as they swam to food used the same route used by their trained fellows, even if the route taken by the trained shoal was longer and more energetically costly than were alternative routes (Laland and Williams, 1997; Giraldeau et al., 2002).

LEARNING AND SPACE USE: CONNECTIONS TO OTHER DISCIPLINES

We distinguish two fundamental constructs for learning in conjunction with animal movement: *updating the world model* and *building a new world model*. To understand the difference between these, it helps to assume that the animal has a cognitive model of the world ($\hat{Q}$) and a set of "policy rules" (β) for mapping conditions—including the snapshot of that cognitive model and the state or priorities of the animal—into outcomes, in particular movement decisions. The policy rules can be thought of as the coefficients of a function governing outcomes in terms of conditions. Within this construct, *updating the world model* refers to the process of movement through a world, acquiring and storing information about the world, updating the world model $\hat{Q}$, and acting upon that knowledge according to the fixed set of policy rules β. The learning process itself is limited to updating the world model. Note that this kind of learning is only meaningful if the world itself is dynamic, with resources or threats moving, regenerating, or depleting in a way that makes it necessary to update expectations. When confronted with a new world, either *via* dispersal, translocation, or a significant perturbation to the existing world, the very structure of the world model and the policy rules both require adjustment by *building a new world model*. These two fundamental kinds of learning are schematized in **Figure 2** where an elk's movement among three dynamic patches permits constant updating of information (*updating the world model*), a process with relies on moving between those patches. But when a patch is significantly perturbed, or becomes unusable in a novel way, the fundamental structure of the world needs to be altered (*building a new world model*), and novel policy rules to govern interaction with novel elements must be developed.

The main distinction between *updating the world model* and *building a new world model* appears in a slightly different form in the machine-learning literature, where the two kinds of learning are labeled as *base-level* and *meta-level.* Specifically, "*The base-level learning problem is the problem of learning functions, just like regular supervised learning. The meta-level learning problem is the problem of learning properties of functions, i.e., learning entire function spaces*" (Thrun and Pratt, 1998). The function spaces in our analogy comprise $\hat{Q}$, whereas the learning functions are the coefficients β. In the neurosciences, the terms model-based and model-free reinforcement learning are used in analogy with base-level and meta-level learning (Doll et al., 2012).

Cognitive ecologists typically have stringent experimental criteria for identifying learning. For example, experimentation plus control conditions sufficient to rule out alternate explanations are fundamental to confirming the existence of social learning (Reader and Biro, 2010). In this framework, experimentation could involve manipulation of physical aspects of the environment, individual animals *via* translocations or similar means, or the routes governing social transmission of information. Rare cases where a wild population can be experimentally manipulated provide the strongest cases for demonstrating and parameterizing memory-based movements (Ranc et al., 2020).

It is also interesting to note that complex behaviors that appear to involve decision-making can arise from other mechanisms of self-organized behavior. Self-organization occurs when simple rules lead to emergent behavior (Gros, 2015). A prominent theoretical example is cellular automata whereby a specific rule set, such as "the game of life," gives rise to agent-like configurations that may travel, replicate, and combine. Self-organized robots (**Box 3**) can exhibit emergent behavior, such as autonomous direction reversal, which an external observer could mistakenly interpret as decision-making (Kubandt et al., 2019). Because self-organization is not purposeful, an agent solely based on self-organizational principles will not be able to improve, or to "learn" its score in a given task. However, complex, emergent behavior that appears to be adaptable can confound efforts to recognize signals of learning in movement data.

Machine Learning Approaches

Machine learning tasks involve an explicit goal, such as parameter estimation or classification, and require a clear objective function, such as minimizing a cost function or correctly classifying data. To the extent that animals also have clear objective functions (e.g., ultimately: increasing individual fitness; proximally: eating, avoiding being eaten, reproducing), and that these objectives might be satisfied by performing a specific movement-related task

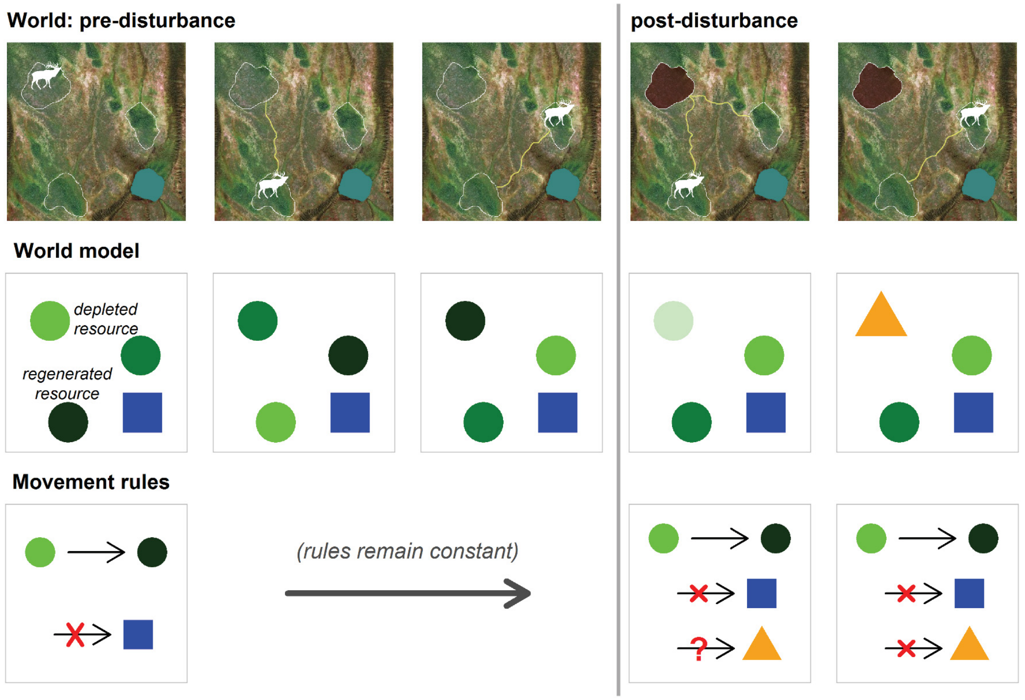

FIGURE 2 | A schematic representation of a forager's movement rules in a heterogeneous landscape, how a stable set of rules might be applied, and how landscape disturbance could force an update to the movement rules *via* learning. In a pre-disturbance world (left three columns), the forager (denoted by the white elk symbol) occupies a landscape with three depletable and renewable resource patches and a water body. The "real world" is represented in the top row, with all of its complexity. The second row represents the forager's model of that world, which distils the complexity to the most relevant information. Shapes indicate different landscape elements, while colors reflect a quantitative score: darker greens are regenerated, paler greens are depleted. The forager has two movement rules in this landscape (bottom row): (1) move from depleted resource patch to a regenerated resource patch and (2) avoid the water body. The pre-disturbance movements rely on a dynamically updated spatial memory, as the forager learns about a changing environment. Post-disturbance, the forager's world model changes after it gains information about the loss of a potential foraging area, e.g., a new oil well destroys one of the patches. Accordingly, the forager's world model is refined to include a novel categorical element (orange triangle), with its own avoidance rule for movement (dynamic learning).

(e.g., selecting appropriate places to forage), it is useful to draw a general analogy between a machine-learning algorithm and an animal that learns. As described above, we use the term *task-based learning* when referring to this type of process.

Types of Machine Learning

Machine learning has three main learning paradigms: supervised, statistical (unsupervised) learning and reinforcement (**Box 1**). Training data for supervised learning is labeled with the correct output (Jordan and Mitchell, 2015). However, statistical and reinforcement machine learning do not require labeled training data and thus may be more directly applicable to animal learning. *Statistical learning* attempts to extract statistically relevant correlations from data (Hastie et al., 2009) whereas *reinforcement learning* attempts to maximize a cumulative reward through a balance between exploitation of current knowledge and exploration of new strategies (Sutton and Barto, 2017; **Box 1**).

A wide range of machine learning approaches emphasizes the importance of improvement through experience (Jordan and Mitchell, 2015), which is close to some definitions of animal learning. Good examples are artificial neural networks (ANN), a class of biologically inspired statistical learning algorithms. The input of an ANN, typically the sensory perception of the agent or animal, is propagated through a network of idealized neurons, which can be readjusted by experience-generated reward signals. The sophistication of the ANN can be increased *via* multiple layers (referred to as *deep learning*). The output of the ANN induces observable behavior, although it may suffer from overfitting the model to the particular data set at hand. Another way to incorporate the effects of improvement through experience is *via* evolutionary computing. This method mimics the trial-and-error process of natural evolution, with inheritance, mutation, and crossing over providing the material upon which selection, *via* reward signals, acts.

The Bayesian probabilistic model for inference provides another perspective on learning. While Bayesian reasoning is most often applied for statistical tasks such as parameter estimation and complex model fitting, it is also a central, probabilistic model for human cognition and learning (Chater et al., 2006; Tenenbaum et al., 2006). In the context of animal movement, prior information represents existing knowledge or existing preference sets (e.g., spatial memory and selection coefficients). Bayesian perspectives readily permit prior knowledge to be updated with new data (experiences) gained by an animal's movement through the environment. For example, Michelot et al. (2019) draw an explicit analogy between stochastic rule-based animal movement and a Gibbs sampler performing Markov chain Monte Carlo sampling. The resulting posterior distributions accurately reflect the animal's resource selection function (RSF).

As introduced above, reinforcement learning is a paradigm involving iterated remapping of situations to actions with the goal of maximizing a numerical reward (Sutton and Barto, 2017). Learners are not provided with rules, but must instead employ repeated trials to discover relationships between actions and rewards. This framework has strong parallels to experience-based frameworks for animal learning. Indeed, the *temporal difference* algorithm from machine learning calculates a reward-prediction error, reflecting how much better the world is than expected (Sutton and Barto, 2017). This algorithm closely resembles the Rescorla-Wagner learning rule (Rescorla and Wagner, 1972), a mainstay from animal learning theory, which posits the change in associative strength during learning is proportional to the difference between the reward received vs. predicted. By way of example, a schematic of the reinforcement optimizer for a computer learning to play the game Go is broadly similar to schematics of animal behavior and learning (**Table 2**). In both frameworks, an agent takes actions (movements) in the environment, and the outcomes of those actions are processed by an interpreter (cognitive model), which either "rewards" or "punishes" the agent, thereby modifying its internal state and modifying its subsequent actions. Additional aspects of realism are that rewards can be short term or delayed, and that the appropriateness of actions is not provided initially but must be learned *via* exploration.

Criteria of machine learning applied to animal learning

The machine learning literature provides concrete criteria for identifying if an algorithm has learned (Thrun and Pratt, 1998). Specifically, given (1) a *task*, (2) *training experience*, and (3) a *performance measure*, if performance at the task improves with experience, the algorithm is said to have learned. This is a useful framework for interpreting observational animal movement data. For example, for the sheep and moose in Jesmer et al. (2018) the *task* was maximizing energy intake and the *training experience* was several years of moving around the landscape. The *performance measure* was whether the animals adopted a migratory movement strategy to track variability in energy availability across space and time. Because of an increase in the proportion of migrants in the population over time (and, thereby, an increase in the proportion of individuals with increased energy intake), the animals likely had "learned". Other instances of mapping empirical examples to machine learning concepts, given in **Table 2**, include hummingbird traplining, crane migration, and experimental elk translocation.

A major challenge to applying machine learning criteria to moving animals involves identifying the *task* and *performance measure* in meaningful ways, given the animals' spatial context and scale of movement. Survival and reproduction are the ultimate tasks, but foraging, resting, finding a mate, and avoiding predation are all proximal tasks. Nonetheless, the framework helpfully and unambiguously associates movement

BOX 3 | Robotics: learning by mobile autonomous agents.

Robots that move and act autonomously, learning as they go, are confronted with tasks that parallel, in some ways, the life needs faced by moving animals. As in living animals, future decisions by a mobile autonomous robot hinge on what the learning robot experiences and encounters. Consequently, it is interesting to investigate how animal decision making about movement (**Figure 1**) may be understood using concepts commonly used in robotics and control theory (Jordan and Mitchell, 2015).

The basic model of an autonomous learner includes the following ingredients:

1) The external *environment* (e.g., spatial locations of forage).
2) An internal *state representation*, sometimes termed a *world representation* (e.g., an individual's location, energy level and knowledge of forage locations).
3) A set of possible *actions* (e.g., foraging strategies).
4) A *policy map* that relates *state representations* to *actions* (e.g., anticipated energy gain from each foraging strategy).
5) *Information acquisition,* which is a consequence of *actions* interacting with the *environment* and the *state representations* (e.g., accumulated information on forage locations).
6) *Value functions that quantify benefits and consequence of actions as represented by the internal states* (e.g., benefits and consequences of choosing a foraging strategy, given an individual's location, energy level and knowledge of forage locations).

A robot's *state representation* simplifies all the information in the environment to a manageable (pruned and stylized) subset of relevant information that can eventually be linked to *actions*. Unsupervised *state representations* (Lesort et al., 2018) in which there are no performance measures, may be particularly relevant as constructs for how learning operates in animals. *State representations* allow the *policy map* to act on a dimensionally reduced decision space (the collection of states), which dramatically simplifies the task of learning individual policies.

A *policy map* structures the relationship of the robot's *state representation* to possible *actions*. A *policy map* may be complete, mapping all possible states to actions, or calculated on the run. Monte Carlo tree search, as used in the Go program AlphaGo from Google Deepmind (Silver et al., 2017), determines the next move *via* an extensive stochastic search. As an additional complication, a robot may possess several *policy maps* and then select among the alternatives in a rule-based fashion. Specified in this way, the basic details of a mobile autonomous robot map quite closely onto a formal conceptualization of the learning process in the context of animal movement (**Figure 1**).

in the environment with *training experience*. **Table 2** cross-references a machine-learning example with field studies that provided experimental evidence of learning.

Machine learning may suggest new avenues for research in learning and animal movement. Active topics include feature extraction, in which derived values are intended to be informative and non-redundant (for example, preference for exploring as yet unvisited locations in mice or composition of feeding groups in jackdaws), and feature selection, which is the choice of a subset of goal-relevant features (for example, availability of resources for mice or foraging efficiency for jackdaws) (Valletta et al., 2017; Maekawa et al., 2020). These subjects must also play a role in the information processing associated with learning and animal movement; developing the connections may provide new insights.

A particularly interesting learning challenge involves *updating the world* (as described above) in a familiar rather than novel landscape. For example, in the foraging models of Bracis et al. (2015, 2018), the task is maximization of instantaneous energy intake, the training *experience* is the movement (together with the acquisition of information for updating the cognitive map), and the *performance measure* is the amount of forage obtained. This challenge can be connected to that of *online statistical machine learning* (**Box 1**), where data become available in a sequential order and are used to update the best predictor for future data at each step.

Could machine learning move beyond an analogy by providing specific hypotheses about the way animals learn to move? It has done so, but the cases are few. By way of example, foraging bumblebees were manipulated in a laboratory environment by presentation with artificial blue and yellow flowers dispensing sucrose solution according to probabilistic reward schedules, and their sampling strategy was compared to the results under the equivalent *two-armed bandit* reinforcement learning decision rules (Keasar et al., 2002). These decision rules describe optimal behavior of gamblers choosing repeatedly between options that differ in reward probability, without any prior information. In this case, the bees' behaviors were generally consistent with the decision rule predictions.

LEARNING ABOUT LEARNING: METHODS AND APPROACHES

Experimental vs. Observational Frameworks for Gathering Evidence of Learning in Movement

Researchers have inferred connections between learning and animal movement *via* classical experiments, observational studies, and translocation/reintroduction efforts. These diverse data types provide distinct insights into how movement can be used to infer learning.

Experimental Studies

Informative experimental studies of learning and movement derive from both field and laboratory settings (Jacobs and Menzel, 2014). Many experimental studies involve insects. Indeed, study of insect navigation propelled much of the early understanding of animal behavior and movement and includes work by Nobel Prize winners Tinbergen and von Frisch. Examples range from moving landmarks to show the effects on navigation to food sources (Wystrach and Graham, 2012) to displacing individuals to show the effects on path integration when returning to an organizing center (Collett and Collett, 2000). Experimental resource manipulations have been used to demonstrate that hummingbirds can learn abstract concepts like spatial position (Henderson et al., 2006) and can encode spatial location on the basis of surrounding landmarks (Flores-Abreu et al., 2012). When applied to roe deer, experimental resource manipulation in a field environment demonstrates that memory, rather than perception, drives foraging decisions (Ranc et al., 2020). Elsewhere, Preisler et al. (2006) tracked elk movements in relation to experimental treatments involving all-terrain vehicles (ATV). They found that elk were more likely to respond to ATVs when on an ATV route, even if the ATV was far away. These data suggest that elk have learned to associate ATV presence with their routes.

In laboratory settings, radial mazes and water mazes (e.g., Leonard and McNaughton, 1990) have been used to study how quickly rodents can learn movement routes and improve their efficiency. Elsewhere, laboratory arenas built for insects have demonstrated that pesticide exposure can impair spatial learning of resource locations by bumblebees (Stanley et al., 2015).

Sometimes field and laboratory experiments can be combined with great benefit, including comparisons among three classic model systems (homing pigeons, bees, and rats; Jacobs and Menzel, 2014). For example, experimental lesioning studies of young homing pigeons, followed by release in unfamiliar areas, demonstrate that immature birds are very good at learning movement routes and that there is a consolidation phase during which experiences (e.g., encounters with landmarks) are neurally encoded (Bingman et al., 2005).

Observational Studies

To assess learning in observational studies, researchers must analyze how an animal behaves at a given time based on local conditions and past experiences. Observational studies typically record the location of animals and thus their experiences over relatively long time-frames (e.g., multiple years, or entire lifetimes). Remotely sensed geographic and climatological data then provide the local conditions the animal is experiencing during movement. Additional information on the behavioral and physiological states of the animal may also be relevant. Fortunately, the ongoing evolution in remote animal tracking and sensing technology means that researchers are increasingly able to infer physiological and behavioral states over long periods of time (Kays et al., 2015).

Data on repeated movement patterns can help differentiate learning hypotheses. For example, data on repeated migration routes have helped distinguish whether animals follow resource gradients, rely on memory to navigate, or learn from experience to shape their movement decisions (Mueller et al., 2013; Merkle et al., 2019). However, long-term tracking data may also be sufficient for analysis. For example, wolf movement data have identified how animals follow resource levels, but that they may also rely on the memory of time since last visit to a location (Schlägel et al., 2017). Augmenting tracking data with information that the animals might gather, for example the location of kill sites (Gurarie et al., 2011) or profitable forage patches (Merkle et al., 2014), can further enhance our understanding of how animals monitor their environment (Gurarie et al., 2011).

Comparative studies can be useful for identifying instances of learning. For example, comparing the movement efficiency of juveniles and adults shows that seabirds start by exploring their landscape and then learn to identify the good foraging areas and cues as adults (de Grissac et al., 2017; Votier et al., 2017; Grecian et al., 2018; Wakefield et al., 2019). Effects of early-life experience can be identified by analyzing the site fidelity of animals to their breeding ground (Weinrich, 1998) and by comparing the migration patterns of offspring to those of their mother's (Colbeck et al., 2013). Finally, comparing the movement of cultural groups, especially if sympatric, can help to assess the effect of culturally transmitted information on animals' space use (Kendal et al., 2018; Owen et al., 2019).

Translocations and Reintroductions

Some management actions involve human-aided displacements of animals, either from captivity (reintroductions) or from wild populations (translocations). Tracking the animals released in such manipulations can provide unique opportunities to understand how the animals adapt to their new environments (He et al., 2019). For example, recurring short displacements (such as when animals are repeatedly taken to the same sampling station for physiological samples), can be used to assess how quickly the animal learns the return route to its home range (Biro et al., 2007).

Translocations of animals into existing populations can aid understanding of learning when movement behaviors of individuals new to the environment can be compared to those of already-resident individuals. For example, quantifying the rate of convergence of movement metrics between new arrivals and residents could help estimate learning rates. In addition, if translocated animals, such as elk, are sourced from areas that differ in predation risk (or other factors) but released in a common space, comparison of the survival and movement patterns could be useful to understanding how previous experience shapes learning (Frair et al., 2007). Translocations of social animals may also create opportunities for newly arrived individuals to learn from resident conspecifics (Dolev et al., 2002).

Overall, comparing movements of animals in novel environments over years or even generations with historical populations can reveal learning and cultural transmission and identify the rate at which animals gain knowledge. For example, Jesmer et al. (2018) found that it took multiple decades for translocated bighorn sheep and moose to regain the capacity to identify and follow the optimal forage gradients that existed in their landscapes as they migrated. Likewise, tracking the movement of prey species before and after the introduction of predators into a landscape affords unique opportunities for investigating how animals learn to avoid predators (Ford et al., 2015).

Uncontrolled Experiments

Beyond intentional displacements, other management actions can serve as uncontrolled experiments for learning. For example, aversive conditioning, which is routinely used in wildlife conflict management, could provide guidance on the mode of learning (Bejder et al., 2009) and may provide contrast the efficacy of different deterrence systems. For example, Ronconi and Clair (2006) showed that presence-activated deterrent systems were more useful than were randomly activated systems for limiting the landing of waterfowl on tailing ponds from oil extraction. Likewise, fences involving bee hives were more likely to turn away elephants than were bush fences (King et al., 2011) and problem elk repeatedly chased by humans and dogs stayed further from town (Kloppers et al., 2005).

Rapid changes in habitat can also serve as uncontrolled experiments. For example, because ungulates will select recently burned areas (Allred et al., 2011), monitoring animal movement in fire-prone systems could help understand how these animals learn about and navigate to novel habitats. Studying movement in the vicinity of new obstacles (e.g., pipelines and roads) and passageways (e.g., road-crossing structures) could help to understand how animals change their spatial patterns as they learn to circumvent barriers and make use of new structures (McDonald and Clair, 2004; Ford and Clevenger, 2018).

Identifying and Characterizing Learning

Analytical and computational tools have a special role to play in the context of learning and animal movement. They can be used both to develop new theory, and in inference regarding actual movement behaviors.

Modeling Frameworks for Exploring How Learning Operates

Dynamical systems models are often used to investigate learning and animal movement in a purely theoretical context (**Table 3**). The most common purpose is to investigate possible emergent patterns, which arise from the inclusion of learning in movement models. Here spatial location and spatial memory are given by variables that change in time and space, and dynamical rules postulate how these variables could change through the interplay of movement and learning. The actual form of the dynamical systems ranges from difference equations used to analyze home ranges (van Moorter et al., 2009), to "record-keeping" models of cognitive maps based on incremental experiences (Spencer, 2012), to partial differential equations used to analyze searching ability (Berbert and Lewis, 2018) to stochastic processes used to investigate patrolling ability (Schlägel and Lewis, 2014). Agent-based simulations have also been used to track the development of complex spatial movement behaviors *via* learning (Tang and Bennett, 2010; Avgar et al., 2013). A review of the ways in which decisions can be integrated into agent-based models is given in DeAngelis and Diaz (2018). Often a balance is required between current perceptual information vs. memories of long-term averages and between random exploration vs.

determinism when exploiting resources (see Boyer and Walsh, 2010; Bracis and Mueller, 2017). When it comes to the sharing of information between individuals, ephemeral public information about resource locations can lead to permanent aggregations of memory-based foragers that move *via* circuits (traplines) (Riotte-Lambert and Matthiopoulos, 2019), and sometimes the rules for near-optimal traplines can be developed based on simple heuristics (Lihoreau et al., 2013). Theoretical studies can investigate relationships or feedbacks between movement and learning that generate patterns similar those seen in nature. They can also be used to explore the environments in which learning might confer benefits. Intriguingly, in the face of an uncertain heterogeneous environment, it may be better for individuals to overestimate environmental quality, as optimistic animals can learn the true value of the environment faster, allowing for a higher rate of exploration (Berger-Tal and Avgar, 2012). Theoretical explorations are particularly useful for studying the *updating the world model* type of learning, where it is more difficult to make a clear distinction between precipitating events of experiences and movement outcomes in observational data.

Machine learning is emerging as a powerful paradigm for the analysis of many biological systems. In the context of learning and animal movement, these approaches can map environmental conditions to movement behavior outcomes without necessarily investigating the learning process itself (see, for example, Mueller et al., 2011; Wijeyakulasuriya et al., 2020). Furthermore, as described earlier, machine learning can serve as prototype models for the process of animal learning itself.

Testing for Change Over Time in Key Movement Metrics

Across diverse data types, a key indicator of learning is a change quantified as a function of "time in the environment" (**Figure 3**). While not sufficient to say confidently that learning has occurred, a strong signal that an animal's movement behavior has changed with experience suggests that it is learning. For example, the range occupied by a group of newly translocated animals would be expected to stay very close to their point of release as they focus on learning attributes of their new environment, but wander more widely as time since release increases as they start to exploit their new environment more widely (e.g., total daily displacement, He et al., 2019). It has been proposed that Lévy walks may arise from a learning process wherein animals attempt to learn optimally from their environment (Namboodiri et al., 2016). In this situation the change from simple random (Brownian) motion to a Lévy walk pattern of movement could be interpreted as learning (but see, for example, Benhamou and Collet, 2015 for a critique of this type of formalism).

Decreases in the rate of range expansion over time indicates that translocated individuals may have learned to favor certain parts of the landscape. In this case, exploration shifts to an exploitation phase (Berger-Tal et al., 2014) as translocated animals exhibit a greater probability of revisiting previously visited areas in a goal-directed manner (**Figure 3**, top row), and may ultimately establish home-ranges (Moorcroft and Lewis, 2006). Similarly, exposure to a hostile landscape element (e.g., human habitation) may condition wild animals to avoid such elements, altering their spatial distribution to favor locations far from habitation (**Figure 3**, middle row). This issue has been particularly well-investigated with elephants (Hoare and Du Toit, 1999; Cheptou et al., 2017).

Animals that "sample" different landscapes during exploratory movements may ultimately settle in landscapes featuring the kinds of elements they encountered and exploited during the exploration phase. This can occur during dispersal, during which animals effectively sample and make decisions in an environment about which they are completely naïve. Wolves have been shown to show less avoidance of human

TABLE 3 | Models for learning and animal movement.

Step	Bracis et al., 2015	Merkle et al., 2017	Avgar et al., 2016	Schlägel et al., 2017
Task	1. Maximize consumption 2. Reduce predation	Forage efficiently	Forage efficiently and survive	Patrol
Experience	Movement	Movement among patches	Movement	Movement
Model prediction	Consumption and predator encounter rate	Patch selection	Redistribution kernel	Entire movement path
Null model	Context-dependent behavioral switching	Connectivity, size, and quality of patch	Forage quality, predation risk, competitors, and snow	1. Movement in response to prey density 2. Distance to territory boundary
Information updated	Location and quality of forage and encounters	1. Location and quality of patches 2. Memory of past patch quality	Location and quality of habitat	Time since last visit to territorial locations
Improvement *via* learning	Learning forager outperforms null model	Learning forager is more efficient	Yes	Yes
Plausible connections to fitness	1. Foraging efficiency 2. Reducing encounters with predators	Past experience leads to foraging in higher quality patches	Past experience leads to better habitat use	Territorial maintenance and defense
Plausible learning mechanism	Sampling and trial-and-error plus reinforcement	Positive reinforcement	Positive reinforcement	Positive reinforcement

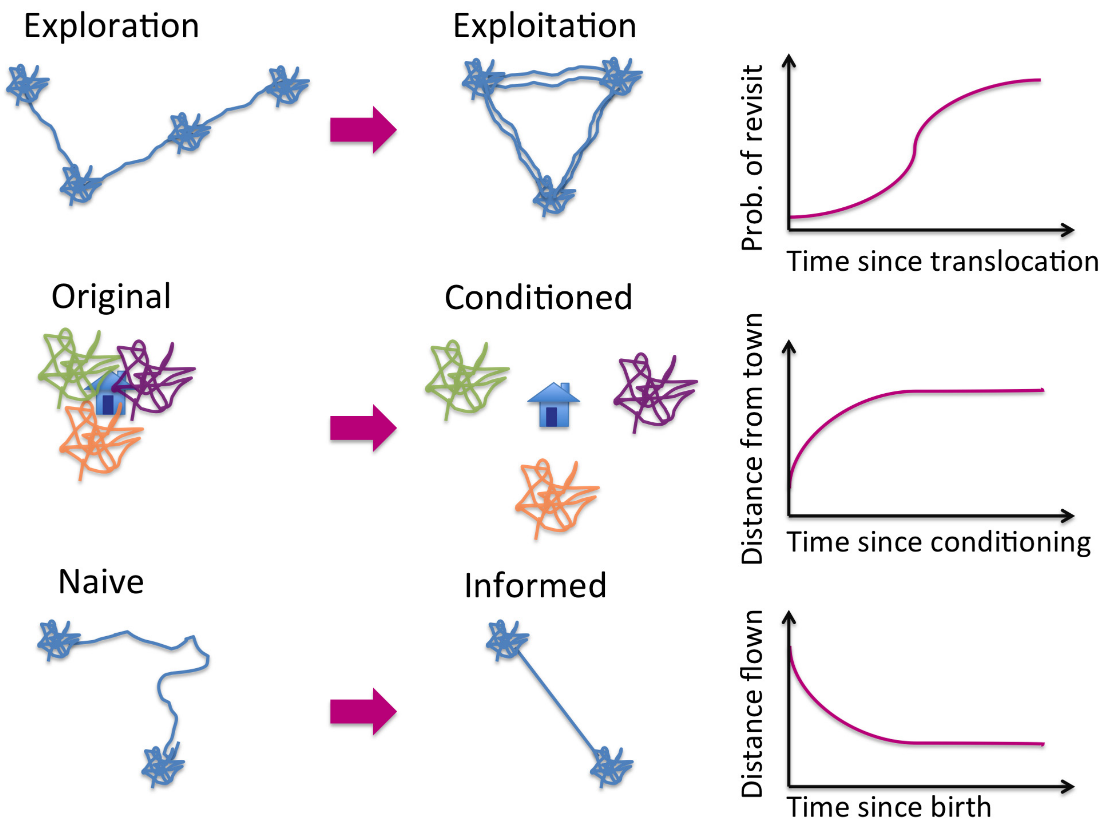

FIGURE 3 | Exemplar movement patterns associated with learning. We represent clusters of movement activity as squiggles and range displacement events as periods of directed motion. In each of the three examples, the process of learning alters the pattern of movement in a statistically detectable manner. Exploration becomes exploitation through repeated visitation (top row). Conditioned responses to habitat elements may manifest as before / after displacement events (middle row). Information gathering during a juvenile (or otherwise naïve) phase may yield improved efficiency of travel. In all three examples, one or more key metrics will exhibit time-dependence (right column).

BOX 4 | Grand challenges in the study of animals learning to move.

How animals learn to move in novel environments. As a key form of experimental manipulation on animals in the wild, translocations and reintroductions have provided unique insights into the role of social learning of migration and the time-lags required to re-establish migration routes (Mueller et al., 2013; Jesmer et al., 2018). By designing efforts to collect pre-translocation movement that could be compared with post-release data would allow insight into the ways animals learn to move in novel environments.

Social learning. Social learning is particularly hard to study in the context of animal movement because it requires simultaneous information on the location of multiple individuals (Fragaszy and Visalberghi, 2004; Sigaud et al., 2017). One promising approach for studies in this area involves the deployment of animal tracking collars with proximity detectors that can be used to characterize and quantify how known individuals spend their time near or far from other known individuals.

Near-term prediction of movement. Successful prediction of movement, even over modest time horizons of one or a few days, requires a strong, probabilistic representation of animals' decision-making process. With such a representation in hand it would become possible to gauge how novel experiences shape subsequent movements.

Understanding fitness consequences of learning on population interactions. Learning about movement affects interactions with other individuals (conspecifics, predator, prey and so forth), as well as with the environment. While much has been done to connect individual learning to the environment *via* optimal foraging (Stephens and Krebs, 1987) there is not yet a comprehensive theory for the influence of learning about movement on population level interactions and the subsequent impacts of these interactions on individual fitness. A natural place to start investigating these feedbacks would be social insects.

Machine learning as a source for new testable hypotheses regarding animal learning and movement. This contrasts with simply providing an interesting analogy for the learning process. While the multi-armed bandit problem has been applied as a model for insect foraging (e.g., Keasar et al., 2002), there are few other cases. However, ML algorithms (for example, K nearest neighbors, decision trees) provide intriguing hypotheses for how learning could proceed. A good place to start would be to build on connections between the theory of ML and the theory of learning, such as the similarity of the reward-prediction error rules in the *temporal difference* algorithm from machine learning calculates (Sutton and Barto, 2017) and the Rescorla-Wagner learning rule in cognitive science (Rescorla and Wagner, 1972). To date, little has been done on applying machine learning as a source for new testable hypotheses regarding animal learning and movement, but this is an intriguing area for future research.

elements, in particular relatively little-used forest roads, in new territories after a greater level of exposure and use during a dispersal phase, suggesting that they might have learned that the benefits of using those human elements outweigh the risks (Barry et al., 2020). Translocation, which can be considered an artificial and more abrupt dispersal, also requires decision making in novel environments. Changes in movement behavior (and improved survival) were recorded following translocation of naïve elk from a savannah landscape in Alberta to a forested landscape in eastern Canada (Fryxell et al., 2008).

Migration can also feature time-dependence in characteristics of movement (**Figure 3**, bottom row). For example, both Mueller et al. (2013) and Jesmer et al. (2018) report changes in migration performance as a function of animals' time in a landscape (**Table 2**). On smaller scales, foraging journeys from a central place and other kinds of daily activity patterns can show the same kind of performance gains (e.g., reduced tortuosity) as a function of experience or age (Franklin and Franks, 2012; de Grissac et al., 2017; Votier et al., 2017; Wakefield et al., 2019; **Table 1**). Resulting spatial patterns of movement can be complex, exhibiting increased speed and goal-directedness (Noser and Byrne, 2014) and even providing evidence of future-oriented cognitive mechanisms (Janmaat et al., 2014). Emerging patterns may include periodic recursions (Riotte-Lambert et al., 2013) as well as sequential movements, where locations are revisited in a regular order (Ayers et al., 2015, 2018; De Groeve et al., 2016; Riotte-Lambert et al., 2017).

Statistical Inference to Identify Learning in Movement Processes

Analytical and computational tools may also be used to infer learning processes from data. For example, the step-selection function (SSF, Fortin et al., 2005) is of particular utility when it is connected to regular samples of location data and allows for inference of movement parameters that depend on different habitat types. Computationally efficient approaches such as integrated step selection analysis (iSSA) (Avgar et al., 2016), provide practitioners a straightforward way to evaluate movement decisions against actual observations. A generalized form of the SSF, termed the coupled SSF (Potts et al., 2014), allows for the inclusion of memory and past social interactions. Here memory and past interactions can be included into the model, as one or more spatio-temporal maps, sometimes referred to as cognitive maps. Although superficially similar to a changing habitat layer, the contents of the cognitive maps are particular to each individual as they are populated by information gleaned from the individual's past experiences (Fagan et al., 2013). With such an SSF, one can test how the individual's movement behavior is governed by cognitive maps whose contents arise from different types of memories or social interactions. Coupled SSFs have been used to test for evidence of memory (Polansky et al., 2015; Oliveira-Santos et al., 2016; Schlägel et al., 2017) and learning (Merkle et al., 2014) in animal movement patterns.

Analysis *via* SSF assumes that animals' location data are known without error. If error is significant, as it can be for marine systems, a different class of model, known as state space models, are needed. State space models are hierarchical and feature separate models for the movement process and the measurement error process. These models can be modified to include a hidden Markov process, whose latent state is determined by physiological status (e.g., searching or traveling) or by learning (Avgar et al., 2016). Such models, while flexible, may suffer from parameter estimability issues (Auger-Méthé et al., 2016) and must be implemented with care.

CONCLUSION AND NEW HORIZONS

Traditionally, studies of animal learning and movement have taken place in controlled laboratory environments or small-scale field studies. Thanks to animal tracking technologies, increasingly detailed observations of how free-ranging animals move and interact are possible, leading to opportunities to formulate and test new ideas about learning and movement. We summarize a variety of outstanding new opportunities as grand challenges in **Box 4**. However, potential pitfalls accompany this exciting development. Alternative explanations to learning must be considered, and if these alternatives cannot be ruled out, then we can only infer that observations are consistent with learning (**Table 2**).

There are two possible approaches to solving this problem. First, field observations can be transformed into controlled experiments *via* manipulations, as in the hummingbird example in **Table 2**. While allowing for incisive analysis, this approach limits the scientific questions to those where such experiments can be set up. A second possible solution is to collect more direct data on the individual experiences over a life-time, including the environmental features of locations animals visit, physiological measurements, and sensory data as made possible by daylight sensors and collar cameras.

Exciting approaches to studying learning and animal movement arise from "uncontrolled" experiments, specifically translocations, reintroductions, aversive conditioning, and rapid environmental change. Understanding learning in the context of relocations and environmental change may ultimately help with understanding how animals can adapt to an increasingly complex world, driven by elevated levels of anthropogenic impacts.

The emergence of machine learning as a dominant paradigm for solving human problems provides fertile ground for modeling and understanding learning from animal movement patterns. Here, processes such as reinforcement learning have close natural ties to animals learning to move to maximize fitness (e.g., optimal foraging). As machine learning algorithms are currently improving and evolving, we expect this field to shed light on further possible models for learning and animal movement. However, as described in the fifth Grand Challenge of **Box 4**, machine learning has yet to meet its full promise as a reliable source for new testable hypotheses regarding animal learning and movement. This is despite the recognition that animal cognition and communication can be closely tied to computational models (Ma, 2015) and that behavioral decisions can often be best formulated by simple algorithmic models (heuristics) (Hutchinson and Gigerenzer, 2005).

Overall, the subject of learning and animal movement is at a crucial point in development and a host of new possibilities are on the horizon. Our goal in this review has been to set the context for these new possibilities and point out some future directions.

AUTHOR CONTRIBUTIONS

ML and WF designed and organized the review, secured the funding, and led writing of the manuscript. MA-M, JF, JMF, CG, EG, SH, and JM contributed to the review and helped writing the manuscript. All authors contributed to the article and approved the submitted version.

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Exploring the Evolution of Perception: An Agent-Based Approach

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Perception is central to the survival of an individual for many reasons, especially as it affects the ability to gather resources. Consequently, costs associated with perception are partially shaped by resource availability. Understanding the interplay of environmental factors (such as the density and distribution of resources) with species-specific factors (such as growth rate, mutation, and metabolic costs) allows the exploration of possible trajectories by which perception may evolve. Here, we used an agent-based foraging model with a context-dependent movement strategy in which each agent switches between undirected and directed movement based on its perception of resources. This switching behavior is central to our goal of exploring how environmental and species-specific factors determine the evolution and maintenance of perception in an ecological system. We observed a non-linear response in the evolved perceptual ranges as a function of parameters in our model. Overall, we identified two groups of parameters, one of which promotes evolution of perception and another group that restricts it. We found that resource density, basal energy cost, perceptual cost and mutation rate were the best predictors of the resultant perceptual range distribution, but detailed exploration indicated that individual parameters affect different parts of the distribution in different ways.

Keywords: perceptual evolution, agent-based model, resource-dependent movement, perceptual range, perception

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INTRODUCTION

Locating resources and gathering information about immediate surroundings are crucial for the survival of an individual, and this makes perception an important nexus for behavior, ecology and evolution. What an individual can detect and respond to is dictated by its perceptual or sensory systems and how these systems are constructed and constrained over species-specific evolution (Stevens, 2013). This evolution of the perceptual apparatus is regulated by interactions of the species with its immediate environment and via inter and intra-specific interactions. Such evolution can sometimes completely redefine the ecological dynamics of a system. This is particularly apparent in the evolution of sensory systems, in tandem with major evolutionary transitions and species radiations (Plotnick et al., 2010). For example, a marked increase in spatial heterogeneity of resources and evolution of mobile organisms as well as new ecological lifestyles changed the information landscape of the Cambrian period. This ushered in a major sensory transition, along with major changes in feeding and predation modes (Dzik, 2005; Plotnick et al., 2010).

Possessing greater sensory input is always valuable as it gives a better model of the surrounding world. However, the sensory apparatus is not without its context and costs: changes in habitat and surrounding environmental conditions can force organisms to adapt their perceptual apparatus due to inherent biological costs (Laughlin, 2001; Niven and Laughlin, 2008; Stevens, 2013). Loss of eyes in animals dwelling in caves or other light-limited habitats has been widely documented, especially various forms of cavefish (Jeffery, 2009; Protas and Jeffery, 2012; Wilkens and Strecker, 2017). A similar loss of visual acuity has been studied in *Drosophila* across multiple generations in captivity (Tan et al., 2005). Likewise, researchers have investigated the weakening of electric organ discharges in electric fish in oxygen-stressed habitats (Salazar and Stoddard, 2008; Stoddard and Salazar, 2011), which may represent an adaptation for saving energy under adverse conditions. Clearly, interactions between species-specific and environmental factors mold the sensory systems of organisms and how they relate to movement and behavior. A theoretical framework that facilitates systematic exploration of these costs and benefits would help clarify the process of perceptual evolution.

Extensive theoretical and empirical work has been undertaken to explore the interplay of movement and perception at various spatio-temporal scales, especially in the context of foraging (Hastings, 1983; Johnson and Gaines, 1990; McPeek and Holt, 1992; Perry and Pianka, 1997; Farnsworth and Beecham, 1999; Beecham, 2001; Cressman and Křivan, 2006; Cantrell et al., 2010; Averill et al., 2012; Bracis et al., 2015). Among the theoretical approaches, there is a great amount of variation in the assumptions regarding information gathering capabilities of individuals based on the mathematical frameworks that the researchers decide to use (Fagan et al., 2017; O'Dwyer, 2020; Martinez-Garcia et al., 2020). Patch models generally assume omniscience about the environment (Fretwell, 1969; Pyke, 1984; Pleasants, 1989; Houston and McNamara, 1999) whereas other modeling frameworks allow for complete environmental information to be learned through sampling (Cressman and Křivan, 2006). In contrast, many partial differential equation (PDE) (Okubo, 1980; Cosner, 2005; Cantrell et al., 2006) models typically make foragers follow a resource gradient, with movement dependent on purely local information from their immediate vicinity. Certain integrodifference/integrodifferential equation (IDE) frameworks, although permitting for extensive non-local movement (through longer-tailed dispersal kernels), allow for the perception of strictly local information, while some other IDE models use patch-level knowledge or full-omniscience (Cosner et al., 2012). The same is true for many agent-based models where agents get information on a strictly local scale (either spatially, temporally or spatio-temporally; i.e., information only about where they currently exist in a model scenario) and do not have access to any form of non-local knowledge in the context of foraging and decision-making (Ranta et al., 2000; Matsumura et al., 2010; Fraker and Luttbeg, 2012; Nabe-Nielsen et al., 2013; Swain and Fagan, 2019). Between these extremes, only a few formalisms exploit the concept of limited but possibly non-local information (Berec, 2000; Hillen et al., 2007; Barnett and Moorcroft, 2008; Martínez-García et al., 2013; Fagan et al., 2017). Using these frameworks, past research has described information gathering and resource tracking in static landscapes (Viswanathan et al., 1999; Edwards et al., 2007; Vergassola et al., 2007; Bartumeus and Levin, 2008; Hein and McKinley, 2012), but equivalent questions in dynamic landscapes remain less explored (but see Torney et al., 2011; Berdahl et al., 2013).

The limits of information gathering and perception lead to alterations in behavior and movement strategies over different spatio-temporal scales, as outlined by previous research (Zollner and Lima, 1999; Zollner, 2000; Gehring and Swihart, 2003; Calabrese and Fagan, 2004; Olden et al., 2004; Prevedello et al., 2011; Fletcher et al., 2013; Fagan et al., 2019). This limit—the maximum distance at which landscape elements can be identified by an organism—is often called its perceptual range (Fagan et al., 2017). The spatial size of the perceptual range varies widely, with magnitudes depending on species, individual state, sensory mode, and spatial context (Zollner and Lima, 1997; Zollner, 2000; Mech and Zollner, 2002; Fletcher et al., 2013). Encoding and exploration of perceptual ranges in ecological systems has been done more through agent-based models (Ranta et al., 2000; Matsumura et al., 2010; Fraker and Luttbeg, 2012) than through equation-based frameworks (Skalski and Gilliam, 2003; Tyson et al., 2011; Martinez-Garcia et al., 2020) due to the complexity of incorporating them in the latter (Fagan et al., 2019). Both modeling frameworks have provided important clues about the interplay among resource detection, movement patterns, swarming dynamics and other phenomena (Grünbaum and Okubo, 1994; Berec, 2000; Barnett and Moorcroft, 2008; Martínez-García et al., 2013; Fagan et al., 2017, 2019), but most of these previous models have focused primarily on changes in perceptual range and how it affects population-level performance. In this work, our objective is instead to explore what environmental and species-specific factors might result in the emergence, evolution, and maintenance of perception in a species. In other words, we are more interested in the evolutionary timescale, rather than the near-term ecology of the system.

We use a simple agent-based model in a semi-dynamic resource system to understand how the interplay of environmental factors with species-specific factors can allow for population trajectories by which perception may evolve. Environmental factors such as the availability and heterogeneity of resources help regulate the range of perception in organisms as well as its usage and efficacy (Plotnick et al., 2010; Stevens, 2013). Metabolic costs to maintain sensory apparatus as well as basal energy requirement and reproductive costs can affect the perceptual range and its evolution in organisms (Laughlin, 2001; Niven and Laughlin, 2008; Stevens, 2013; Tan et al., 2005). We introduce a basic set of parameters in our model that represent these environmental and species-specific factors, but we avoid bringing in too many details to balance biological realism with breadth of applicability to a variety of organisms with different sensory modalities. More such details can be added above the current model in further explorations of the work.

We incorporate a context-dependent movement strategy for each agent where it switches between undirected (random walk) and directed (advective) movement based on its perception of resources. Behavioral switching has been demonstrated in a wide range of species at different spatial scales of foraging, such as opossums (Prevedello et al., 2011), woodpeckers (Vergara et al., 2019), tuna (Newlands et al., 2004), and even mosquitoes (Raji and DeGennaro, 2017). Such a switching pattern has been shown to better describe empirical behavioral patterns in bees and caribou than a more straightforward blending of movement strategies (Tyson et al., 2011). We also opted to use a movement model that involves switching between random walk and advective motion because models with such switching have already identified a clear role for non-zero perceptual ranges to enhance foraging success (Fagan et al., 2019). Alternative models of movement exist certainly, such as ballistic movement for agents with no information and increased tortuosity when near resources (see Gurarie and Ovaskainen, 2013; Bartumeus et al., 2016), but these and other foraging models are frequently couched in terms of what is optimal (i.e., what strategy or combination of strategies will yield the greatest uptake of resources), which provides a poor baseline for consideration of issues hypothesized to occur early in evolutionary history. To supply additional biological realism, we investigated evolution in a reproductive context, imposing limits on the amount of resource an individual can gather and store and exploring a wide range of initial conditions and parametric scenarios.

Focusing on the evolved distribution of perceptual range, we assigned the parameters in the model to two categories based on their effects: activation and deactivation parameters (i.e., parameters which generally promote evolution of perception and that restrict it, respectively, in a simulated population). We observed a non-linear, non-monotonic response as a function of resource density, which interacts with other parameters. Resources play a major role in determining the stability of equilibria of the system, controlling whether or not perceptual ranges emerge at all. In addition, we found that the system's behavior mirrored some biological aspects, with the evolution of perceptual abilities depending on their costs.

MATERIALS AND METHODS

Model Description

We model the dynamics of the system using an agent-based approach (see **Figure 1**). The computational spatial domain is a 100 unit by 100 unit continuous square with parallel sides identified (toroidal boundary conditions). Each simulation starts with all individuals having zero perceptual range. Through selection (enforced by environmental and species-specific parameters) and neutral processes (brought about by mutation) (**Table 1**), we observe the shape of the perceptual range distribution in the population over time. Before the simulation begins, a constant amount of total resource is specified according to two parameters: *resource density* and *resource quality*.

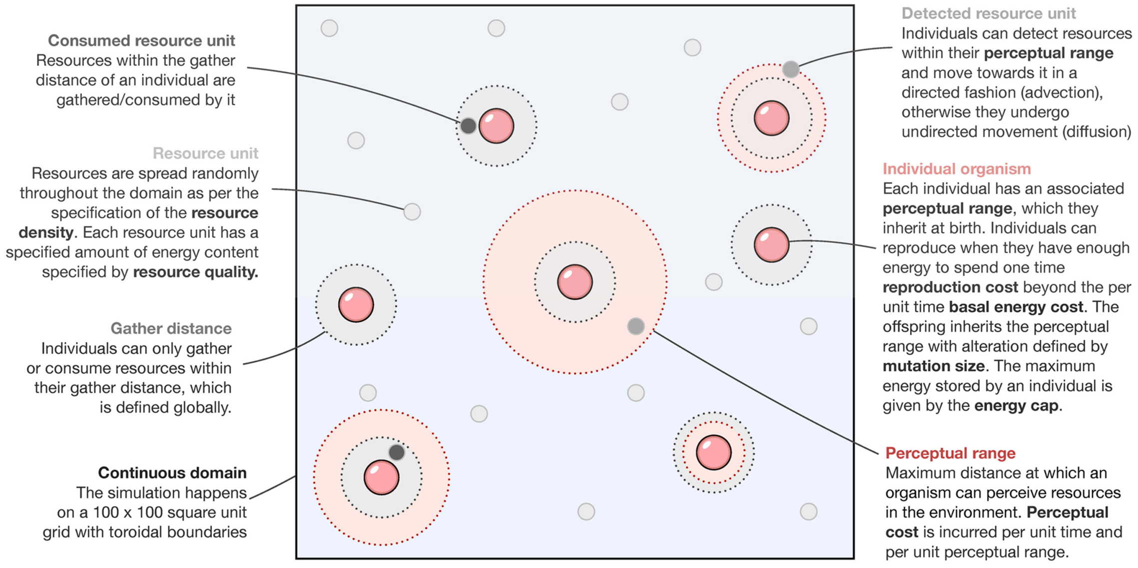
Resource density is defined as the amount of resource patches per unit area in the domain; thus, the number of patches where resources are present is equal to the *resource density* times the area of the domain. The resource patches are then distributed randomly on the domain with each patch containing an amount of resource equal to the *resource quality* (or the energy quantity per resource), ensuring a spatial heterogeneity in resource availability to mimic natural scenarios. At every time step, the code checks the resource distribution and adds more resource patches with the same *resource quality* if the total amount of resources is less than the initial amount. This way, the total amount of resources is held constant over time for simplicity.

Individual agents (foragers) default to undirected movement (a random walk) until resources enter their perceptual range, at which point they switch movement modes and move along a straight line (advective movement) to the nearest resource patch and gather resources from it (see **Figure 1**). All foragers have the same constant movement speed of one spatial unit per time step. This simulates the mode of movement observed in organisms in natural settings during foraging (Tyson et al., 2011). Foragers having a non-zero perceptual range incur an additional cost every timestep per unit perceptual range, termed as the *perceptual cost*. We assume the relation between perceptual range and its cost to be linear for simplicity: increased perception translated directly into higher costs (Protas et al., 2007; Moran et al., 2015). This cost is above the *basal metabolic cost* incurred per timestep for survival, irrespective of the perceptual range. A forager can gather an amount of resources equal to the *gather amount* parameter only if the resources are within its *gather distance* (irrespective of its perceptual range) and the forager is not exceeding its *energy cap*, which defines the maximum amount of resource that an individual can consume. A special case arises when the *gather distance* is lesser than an agent's perceptual range, and in such a case, the gathering action can be understood as a rudimentary detection, which we assume, can occur irrespective of complex perceptual systems.

Once a forager has sufficient resources, it can randomly reproduce asexually according to a threshold *growth rate* parameter. Should an individual reproduce, it incurs a one-time cost associated with reproduction (*reproduction cost*) and transfers that energy/resources to the offspring (new individual). The offspring also undergoes a mutation in its perceptual range, changing its parent's perceptual range by an amount randomly drawn from a uniform distribution on the interval $[-m,\ m]$ where m is the *maximum mutationsize* parameter. In implementation, we ensured that perceptual ranges were always non-negative. Death only occurs when the foragers run out of energy. From our numerical experiments, we found that this causes the population size to be regulated by the resource availability (similar to the idea of carrying capacity), although the exact values can depend upon other parameters such as metabolic costs.

Model Implementation and Analysis

We implemented the model in the Go programming language using its standard libraries (see the code and data availability section for details). A detailed account of all parameters appears



Consumed resource unit
Resources within the gather distance of an individual are gathered/consumed by it

Resource unit
Resources are spread randomly throughout the domain as per the specification of the **resource density**. Each resource unit has a specified amount of energy content specified by **resource quality.**

Gather distance
Individuals can only gather or consume resources within their gather distance, which is defined globally.

Continuous domain
The simulation happens on a 100 x 100 square unit grid with toroidal boundaries

Detected resource unit
Individuals can detect resources within their **perceptual range** and move towards it in a directed fashion (advection), otherwise they undergo undirected movement (diffusion)

Individual organism
Each individual has an associated **perceptual range**, which they inherit at birth. Individuals can reproduce when they have enough energy to spend one time **reproduction cost** beyond the per unit time **basal energy cost**. The offspring inherits the perceptual range with alteration defined by **mutation size**. The maximum energy stored by an individual is given by the **energy cap**.

Perceptual range
Maximum distance at which an organism can perceive resources in the environment. **Perceptual cost** is incurred per unit time and per unit perceptual range.

FIGURE 1 | Conceptual figure of the model.

TABLE 1 | Summary of various parameters used in the model, their definitions and their effects on the perceptual range distribution.

Parameter	Definition	Observed effect
Resource quality	Amount of energy per resource patch	Activation parameter; Affects higher percentiles slightly more
Resource density	Total energy per unit area	Activation parameter; Major predictor of perceptual range distribution; Affects lower percentiles more
Growth rate	Probability to reproduce per timestep	Activation parameter; Affects lower percentiles more
Max. mutation size	Maximum perceptual mutation per reproduction	Activation parameter; Major predictor of perceptual range distribution; Affects higher percentiles more; influences the variance of the perceptual range distribution.
Reproduction cost	Energy cost to reproduce	Weak deactivation parameter; Affects all percentiles almost uniformly
Basal energy cost	Energy cost to continue living	Deactivation parameter; Major predictor of perceptual range distribution; Affects higher percentiles more; Increases perceptual ranges until a cutoff
Perceptual cost	Additional energy cost per unit perceptual radius per timestep for having a perceptual range	Deactivation parameter; Major predictor of perceptual range distribution; Affects higher percentiles more
Gather amount	The amount of energy an agent can gather at once (in a given time-step)	Weak deactivation parameter; Affects higher percentiles more
Gather distance	The distance within which an agent can gather resources, irrespective of the perceptual range	Activation parameter; Affects higher percentiles slightly more
Energy cap	Maximum amount of energy an agent/forager can store at any given time	Weak activation parameter; Affects lower percentiles more

The first two rows, resource quality and resource density, control the quality and quantity of resources. The next two, growth rate and maximum mutation size, control the reproductive and mutation processes. The next three rows are the energy requirements imposed on foragers due to various conditions. The last three rows depict the limitations on the collection of resources from the environment.

in **Supplementary Table 1**. To obtain a representative behavior in the ensemble of simulations, we performed 10 million runs, involving parameter combinations chosen using a Latin hypercube sampling (LHS) procedure. Each simulation was run for 150 time-steps and had a starting population of 100 zero-perceptual range individuals. From a set of preliminary simulations over a wide variety of parameters, we found that simulations stabilized to almost a constant distribution (less than 5 percent difference) in under 150 timesteps and remained stable afterward (see **Supplementary Figure 1** and **Supplementary Video**).

Each simulation begins by randomly placing 100 foragers on the computational domain and initializing their energy levels to 1.0. At each time step, a sequence of events occur: (1) all individuals check their perceptual radii for resources; (2) foragers move in a random manner (if they cannot perceive any resources) or a directed manner to the closest resource (if they can perceive one or more resources); (3) If possible, foragers gather resources from the locations harboring resources; (5) All foragers pay their cost penalties; (6) if they have sufficient resources, foragers reproduce with a probability prescribed by the *growth rate* parameter with their offspring placed at a random location adjacent to their parents (randomly within a distance of 5 units), and lastly, (7)resources are replenished according to the parameters in the code.

Each parameter combination was replicated 10 times and then the end time perceptual ranges were aggregated (for each combination) to obtain an averaged, statistically robust distribution of perceptual ranges (i.e., 10 replicates times 100 randomly placed individuals at the start of each simulation) from which we could calculate percentiles of interest (2.5, 25, 50, 75, and 97.5). We focus on these percentiles rather than a simple mean because we anticipate that different factors may influence the structure of the perceptual range distribution in different ways. For example, the degrees to which the parameters affect the lowest perceptual range values would be different from how they affect the highest perceptual ranges in the system. After accumulating all the data, we performed further analysis in Python and R. Preliminary analyses justified our choice of 10 replicates per parameter combination. To do this we ran 100 replicates for 100 randomly selected parameter combinations and then calculated the Bhattacharyya distance among replicates for various subsets from 1 to 100, discovering that 10 was an optimal number with respect to computational time and statistical robustness (see **Supplementary Figure 2** for details). Bhattacharyya distance is a standard statistical metric for quantifying the similarity of two probability distributions; it reflects the amount of overlap between two statistical samples or populations (see Bhattacharyya, 1943), and is measured between 0 and 1, where 1 denotes complete similarity.

One might argue that assuming the probability of mutation to be 1 on reproduction, irrespective of mutation size, is not a biologically relevant scenario, and instead the probability of mutation should vary depending upon environmental conditions and species-specific factors. However, we found that a mutation probability of 1 was appropriate for our purposes, by conducting a series of numerical experiments in which we considered 1,000 parameter combinations at each of ten mutation probabilities. These simulations show that the probability of mutations (independent of the mutation size) only affects the timescale of the simulations. It does not affect the final distribution of perceptual ranges (see **Supplementary Figure 3** for details). Therefore, to be computationally efficient we assume mutation probability to be 1 and focus our analyses of mutational dynamics on *maximum mutation size*.

To obtain a simplified dependence structure of various parameters on the evolution of the perceptual range distribution, we determined the partial rank correlation coefficient (PRCC) of various parameters with respect to the 2.5, 25, 50, 75, and 97.5 percentiles of the distribution, using the *sensitivity* package (Iooss et al., 2020) in R. We also performed a Random Forest (RF) regression, using the *random Forest* package (Liaw and Wiener, 2002) in R, to identify which parameters are the strongest predictors of the patterns in different percentiles of the perceptual distribution. We optimized the number of parameters available for splitting at each tree node in the RF using out-of-bag error (OOB) (Liaw and Wiener, 2002). We use the IncNodePurity statistic (another standard statistical metric defined as the total decrease in node impurities from splitting on a given parameter, averaged over all trees; Impurity is measured by residual sum of squares and is calculated only at the node at which a given parameter is used for a split; see Liaw and Wiener, 2002) for comparing variable importance scores in RF models. Higher values of IncNodePurity denote higher importance of a parameter in predicting a given variable.

To further analyze the details in the patterns of perceptual evolution and identify how perceptual evolution depended on resource availability, we fixed a standard set of parameters (see **Supplementary Table 1** for details) and plotted the distributions by altering one parameter at a time in three different resource regimes (low, medium, and high; see **Supplementary Table 1**).

RESULTS

Classifying Parameters and Their Impact

Figure 2A summarizes results from the PRCC analysis investigating how model parameters affect the percentiles of the distributions of perceptual ranges. To understand the impact of various parameters, we categorized all parameters into two groups: *activating*, which are the ones with PRCC greater than 0.0 (i.e., a positive effect on the distribution of perceptual ranges) and *deactivating*, with PRCC less than 0.0 (i.e., a negative effect). This categorization groups *resource quality, growth rate, maximum mutation size, resource density, gather distance*, and *energy cap* as activating parameters because these parameters positively affect and/or aid the evolution of non-zero perceptual ranges. On the other hand, *basal energy cost, perceptual cost, reproduction cost* and *gather amount* fall into our deactivating category and affect the evolution of non-zero perceptual ranges negatively.

Although this broad classification is helpful, the impact of each parameter within the categories differs substantially, and for some parameters (e.g., *maximum mutation size*) the impact differs across the parts of the perceptual distribution (**Figure 2A**). To further elucidate parameter impacts on perceptual range, we can examine the variable impact scores from RF regression models and quantify how individual parameters affect perceptual ranges when all others are held constant.

Parameters as Predictors of the Perceptual Distribution

We plot the variable importance scores through the IncNodePurity statistic from the RF regression models, with all parameters as predictor variables and percentiles of the perceptual range distribution as the outcome variable (**Figures 2B–F**). See **Supplementary Figure 4** for RF optimization. These results echo the findings from the PRCC plot (**Figure 2A**) and describe more than 70% of the variance in each of the five perceptual percentile levels. Specifically, RF could explain 74.84, 70.03, 70.25, 70.16, and 72.92% of the variance for the 2.5, 25, 50, 75, and 97.5 percentiles, respectively).

Perceptual cost, basal energy cost, maximum mutation size, and *resource density*, which have the highest PRCC values for almost all the percentile perceptual values, are consistently the

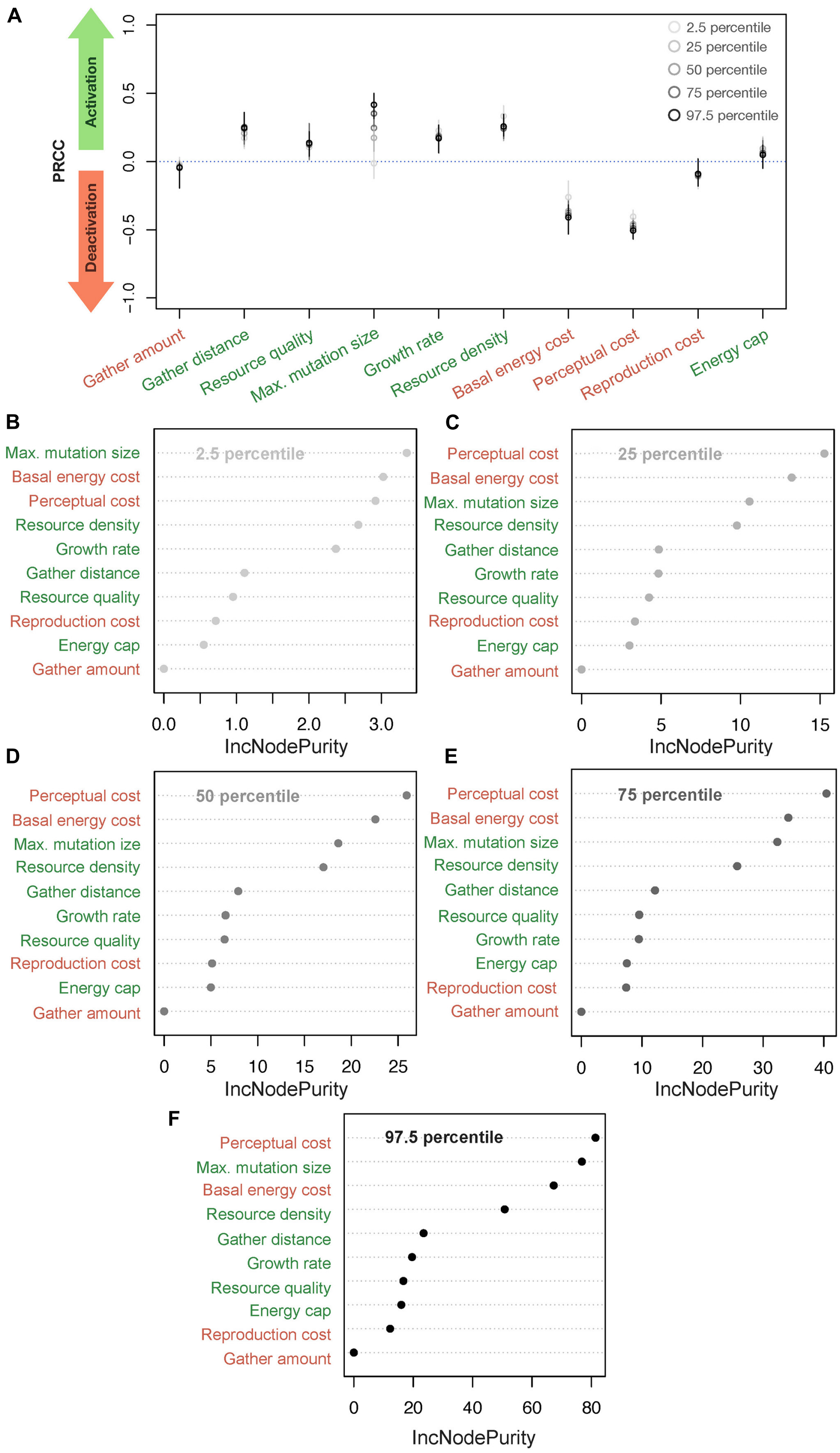


FIGURE 2 | Finding critical parameters. **(A)** Classifying parameters into activating and deactivating groups using partial rank correlation coefficient (PRCC); parameters where the mean PRCC is above 0.0 are activating and those with mean PRCC below 0.0 are termed deactivating. **(B–F)** Represent a Random Forest (RF) Regression of different parts of the resultant perceptual range distribution from the parameter values where **(B–F)** represent the results for 2.5, 25, 50, 75, and 97.5 percentiles, respectively (and percentage of variance explained: 74.84, 70.03, 70.25, 70.16 and 72.92%, respectively). The labels in green are activating parameters and those in red are deactivating. The *x*-axis in **(B–F)**, IncNodePurity, refers to the total decrease in node impurities from splitting on a given parameter, averaged over all trees. Higher IncNodePurity means higher variable importance.

best predictors of evolved perceptual range. Only the relative ranking of the importance of these four parameters changes in the RF regression across the percentile levels. In the case of the 2.5 percentiles, growth rate approaches a similar range as the top four parameters listed above, but in all other cases, growth rate's PRCC value remains low. Although gather distance positively affects the perceptual evolution and affects its variation as evident in PRCC values (**Figure 1**), it is not a good predictor of the percentile perceptual values.

Detailed Discussion About Parameters

To gain more insights into the model's evolutionary dynamics, we plotted the mean perceptual radius of simulations where we tuned one parameter and kept the others constant at standard values (**Supplementary Table 1**). We did this for each of three resource regimes in **Figure 3** to uncover broad scale patterns associated with changing *resource density*. For a more detailed structure of the distribution, please refer to **Supplementary Figures 5, 6**.

Activation Parameters

Activation parameters allow perceptual ranges to evolve and persist in the population. *Resource quality, growth rate, maximum mutation size, resource density, gather distance,* and *energy cap* are activating parameters. Each of these parameters has a threshold value such that when the parameter is below the threshold, conditions are sufficiently harsh that no perceptual range evolution is possible. Once above the threshold, however, the parameter creates a setting that activates perceptual range evolution (see **Figure 3B** and **Supplementary Figure 5**).

Threshold values vary among the activation parameters, and across the parameter space. Regimes where positive perceptual ranges reliably exist are usually characterized by a *resource density* of around 0.5 or more, showing an important dependence on resource availability. In the low resource case (resource density is 0.25), we see interesting patterns: populations with non-zero perception exist only sporadically and by chance; but when they do exist, they create higher mean perceptual ranges than higher resource density cases for similar parameter values (**Figure 3**). The *maximum mutation size* parameter is unique among the activation parameters, as it allows populations to thrive more reliably in low resource regimes than other parameters (**Figure 3**). The perceptual range distribution exhibits high variation in harsh or low resource environments for all parameters as compared to those in medium and high resource environments (**Supplementary Figure 5**).

Deactivation Parameters

Deactivation parameters, such as *basal energy cost, perceptual cost, reproduction cost,* and *gather amount*, make it more difficult for perceptual ranges to evolve and persist in a population. Instead of having thresholds, these parameters have cutoffs after which no non-zero perceptual ranges generally evolve (**Figure 3** and **Supplementary Figure 6**).

The perceptual range distribution is very sensitive to changes in *perceptual cost* (**Figures 2**, **3A2**). We see a quick decrease in perceptual ranges as perceptual costs go up, but greater perceptual costs are tolerated in high resource scenarios (**Figure 3A2**). For *basal energy cost*, which is another strong predictor of perceptual range (**Figure 2**), we see an increase in perceptual range until the cutoff is reached (**Figure 3A3**). Although *reproduction cost* reduces the distribution of perceptual ranges, its impacts are relatively small (**Figures 2**, **3A1**). *Gather amount* behaves like an activation parameter, in having a threshold rather than a cutoff, and has a small negative impact on perceptual evolution (**Figure 3A4**).

DISCUSSION

Understanding the evolution of perception in a given ecological setting sheds light on the interplay between environmental and species-specific factors in structuring the sensory spaces of organisms. Using our simple agent-based model, with assumptions pertaining to biological scenarios, we can predict possible effects of various environmental and biological factors on perceptual evolution. Moreover, our simulations include both neutral and adaptive processes of change (i.e., through mutation size and selective pressure to survive and reproduce), which allows for exploration of how such evolutionary changes may take place.

The simulations draw a stage where the foragers try to maximize their temporal energy gain while trying to minimize the risk of running out of energy, under various starting conditions and a spatially heterogeneous (but controlled) environment. Although it would be interesting to understand conditions and evolutionary strategies through which one can view the emergence and maintenance of various perceptual range distributions, the complex form of density dependence and continuous space of possible pathways or strategies present in our model mean that such investigation is not at all straightforward. Therefore, we focus here on a higher-level correlative view of the emergent patterns of perceptual range distributions.

Results from the simulations suggest a few major patterns. From the RF analysis and PRCC estimation, we found the four major predictors of perceptual range evolution to be *resource density, maximum mutation size, perceptual cost,* and *basal energy cost,* with *resource density* providing the uniformly strongest effects (**Figure 2A**). From basic ecological principles, one expects factors akin to *resource density* to affect the evolution of perception, either directly or indirectly. A good example involves the reduction of sensory apparatus in a variety of organisms in resource-limited environments in both natural settings and in well-controlled experimental systems (Stevens, 2013; Brandon and Dudycha, 2014; Brandon et al., 2015). For example, caves have resource-limited conditions, and the reduction in visual organs of cavefish, as compared to their above-ground relatives (Jeffery, 2009; Borowsky, 2008), may be driven by the relatively high energetic costs of the visual system coupled with minimal benefit of vision (Niven and Laughlin, 2008), in addition to other developmental constraints. Likewise, in benthic decapods, eye size increases with increasing depth, as expected from the fact that larger eye size improves vision in dimmer environments

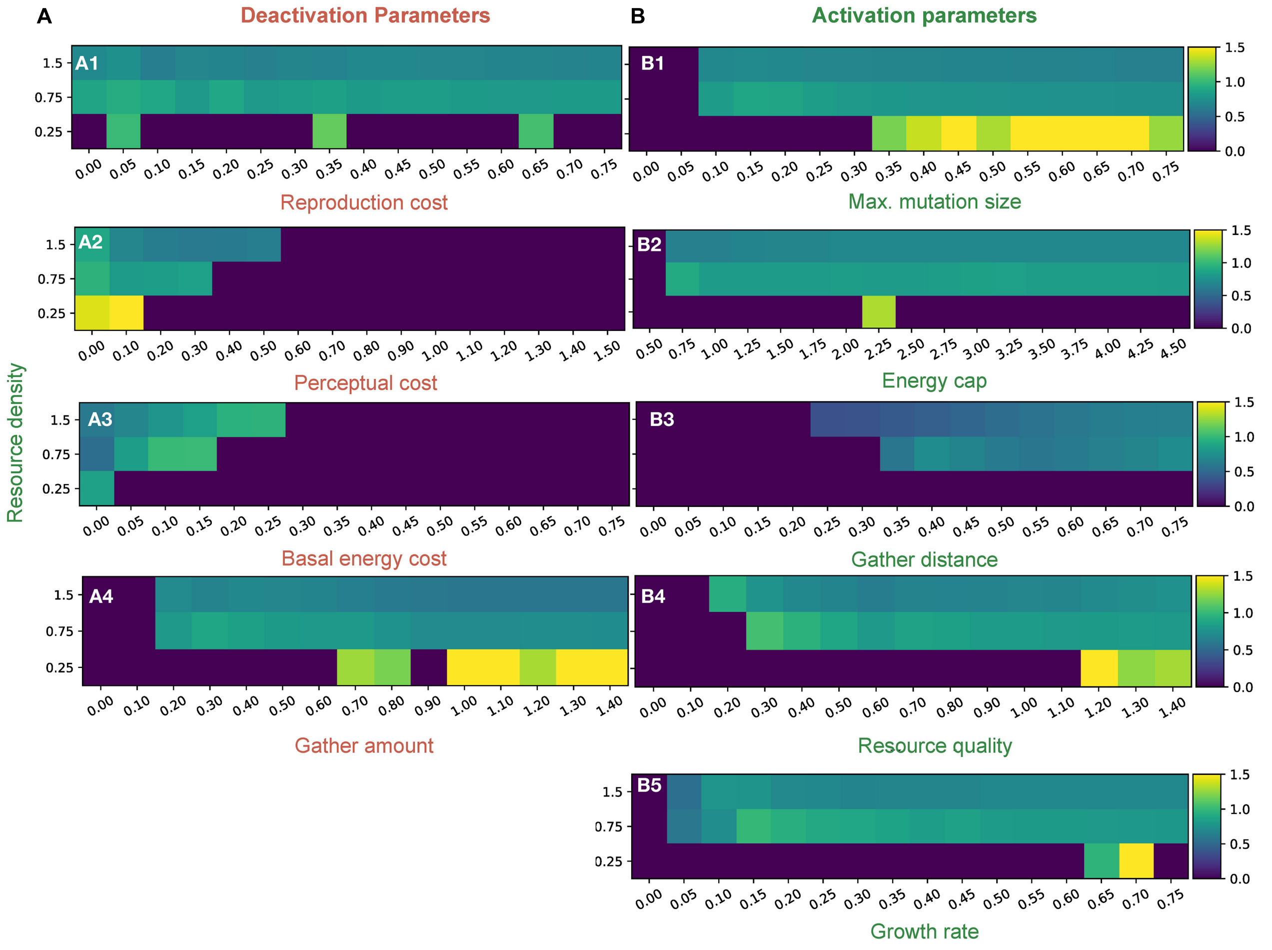


FIGURE 3 | Mean distribution values of perceptual range for different parameters in three different *resource density* regimes. **Column A (A1–4**) represents deactivation parameters and **column B (B1–5)** represents activation parameters (The labels in red are deactivation parameters and those in green are activation). Resource densities of 0.25, 0.75, and 1.5 correspond to the "low," "medium," and "high" resource conditions, respectively. Detailed distributions of the perceptual ranges and how they are affected by various parameters can be found in **Supplementary Figures 5, 6**.

(Hiller-Adams and Case, 1985). However, the opposite trend was observed in pelagic crustaceans (Hiller-Adams and Case, 1984, 1988), indicating that large eyes are an energetic burden in the resource-limited pelagic zone. These comparative examples suggest the evolution (or loss) of visual apparatus depends not only on the perceptual environment but may also (directly or indirectly) depend on resource availability (although a strong mechanistic link is still lacking). Evolutionary effects and generational plasticity in perceptual apparatus investment due to limited resources and allocation to other body parts have also been observed in a number of organisms including *Daphnia* (Brandon and Dudycha, 2014; Brandon et al., 2015), beetles (Nijhout and Emlen, 1998), and butterflies (Merry et al., 2011). Although resource availability has been implicated or hypothesized in perceptual loss or gain in these systems, the mechanistic link is still missing, and the observed effects might be due to other secondary factors.

Naively, one might expect that the strongest selection on perceptual ranges would happen under intermediate resource densities, because at high densities, there might be little to no benefit of increased ranges as resources are likely to be encountered under random movement patterns and at low resource densities, the benefits of findings resources may not necessarily offset the costs of the systems necessary to detect them. Interestingly, in our model lower resource density environments sometimes produced noticeably larger perceptual ranges than those of higher resource density environments, even though the threshold for attaining non-zero perception in the latter environments was lower (**Figure 2** and **Supplementary Figures 5, 6**). This effect was, however, sporadic and depended on chance: low resource environments can also lead to smaller perceptual ranges. This diversity of successful strategies seems to be true for some low resource environments like the deep-sea, where certain organisms have exceptionally well-developed sensory capabilities whereas others feature extensive reductions in sensory systems (Drazen and Sutton, 2017). Moreover, although *resource density* had an overall positive impact on the whole perceptual distribution, it had a higher impact in increasing the lower percentiles of the perceptual range distribution (**Figure 2A**), and therefore might play a critical role in early stages of perception evolution.

Maximum mutation size facilitated evolution of more diverse perceptual ranges in all scenarios. The notion that large mutations might aid in the formation of complex morphological features, such as sensory systems, is well-developed both experimentally (Weng, 2014) and theoretically (Lenski et al., 2003). For example, mutation rate affects the time required for eye evolution (Nilsson and Pelger, 1994). In addition, we observed that *maximum mutation size* allowed for a more stable persistence of perception in low resource environments and led to the evolution of larger perceptual ranges (**Figure 3B1** and **Supplementary Figure 5**). Such an observation may be related to the fact that there is bistability in the system (here, bistability corresponds to situations where the equilibrium distribution of perceptual ranges included both zero and non-zero values; **Supplementary Figures 5A2–A4, 6A3–A4**). Bistability would be expected to emerge only when sufficient temporal and spatial conditions are met, and near such points, we would expect to see a transition to situations in which a portion of the population has non-zero perceptual ranges. For example, under standard conditions of our model and low resources, *mutation size* was the major parameter that led to apparent bistable states. In this case, sufficiently high mutation size helps create larger perceptual ranges, which can aid survival under low resource conditions while also meeting the *perceptual costs.* Otherwise, zero-perceptual range is the stable state where random walk foraging and low energetic costs can sustain the population. In other scenarios, we might have such bistability as a complex function of many parameters. As this work provides a path for thinking about evolution of perceptual ranges and the parameters that affect their stable distributions under various conditions, future work, using non-agent-based approaches, should investigate bistability more fully.

Maximum mutation size affected various parts of the perceptual distribution differentially (**Figure 2A**). In particular, the effect of this parameter increased with increasing percentiles of the perceptual range distribution, meaning that higher *maximum mutation sizes* allowed for higher upper bounds on the possible perceptual ranges but did not affect the lower bounds as much.

As expected, an increase in *perceptual cost* decreased the prevalence of non-zero perceptual ranges (**Figures 2A, 3A2**) as the foragers became unable to afford the energy loss incurred by increasing their perceptual range. Such a phenomenon is known from a wide range of species in both natural and captive settings and from physiological experiments (Niven et al., 2007; Niven and Laughlin, 2008; Stevens, 2013). For example, the production of electric organ discharges (EODs) (in weakly electric fish) is metabolically expensive (Salazar and Stoddard, 2008; Stoddard and Salazar, 2011). Fish living in waters with sufficient oxygen show no correlation between metabolic rate and EOD, but those in oxygen depleted waters show reduced EOD (Reardon et al., 2011). In sticklebacks, where divergence into two forms occurs during lake habitat acclimatation—benthic (bottom dwelling, invertivorous) individuals, which live in lower light conditions and have higher perceptual costs, possess diminished eyes, whereas limnetic (open water dwelling, zooplanktivorous) individuals have larger eyes (Willacker et al., 2010). In ray-finned fish, eye size decreases as a function of turbidity of waters they inhabit—pointing to increased perceptual cost in more turbid waters (i.e., reduced visibility) affecting eye size and acuity (Caves et al., 2017). We also note that *perceptual cost* had the strongest effect on the higher percentiles of the perceptual range distribution (**Figure 2A**).

Basal energy cost also had an overall intuitive trend. At low levels, it is easier for foragers to evolve perceptual range, while at higher levels the foragers are unable to meet the cost; this cutoff increased with increasing resources (**Figure 3A3**). But on a finer scale, we observed an increase in perceptual ranges with increasing *basal energy cost*, until the cutoff value, where it abruptly crashed (**Supplementary Figure 5**). Increases in *basal energy cost* forced foragers to find a better way to gather resources and thus, perceptual ranges increased (**Supplementary Figure 5**). This process continued, in increasing strength, until the point where foragers cannot sustain themselves due to a high metabolic cost—which results in the cutoff. Predation and competitive interactions both increase basal energy costs (Hawlena and Schmitz, 2010; DeLong et al., 2014), and larger sensory apparatus can occur in situations featuring greater predation and competition (Beston and Walsh, 2019). But beyond a certain threshold rate of predation, reduced visual apparatus might happen due to higher costs as documented in Eurasian perch (Svanbäck and Johansson, 2019), similar to our results (see **Figure 3A3** and **Supplementary Figure 5**). Another intriguing example of the phenomena involves cylindroleberidid ostracods, in which species with eyes living in the photic zone have larger carapaces (and therefore higher basal energy costs) and may possess a larger number of ommatidia when living at greater depths were resources are fewer (Juarez et al., 2019). In the same group, neither body size nor absolute metabolic rate changes as depth increases in the disphotic zone. However, food availability does decrease with depth (and therefore, relative metabolic rate increases) and eyes have more ommatidia (Juarez et al., 2019). In other words, evolution of better perceptual apparatus is possible over a range of conditions, even with increasing relative metabolic costs.

Beyond these four major predictors, the remaining parameters had smaller or more restricted effects. For example, *growth rate* played an important role in determining the lower bound of the perceptual distribution (**Figures 2A,B**), although it did not impact other parts of the distribution as much (**Figures 2C–F**). Previous works have reported enhanced growth rate being correlated with larger eyes in Trinidadian killifish (Beston and Walsh, 2019) and in amblyopsid fishes (Poulson, 1963).

Reproduction cost negatively affected all percentiles uniformly, although the impact was weak (**Figure 2A**). Although we only modeled asexual reproduction, we take this result as a weak indicator of reproductive investment affecting perception. An example of this can be seen in scarab beetles where there is a strong trade-off between anatomical investments that help in reproduction, such as horns, and eye size (Nijhout and Emlen, 1998).

The rest of the parameters that we introduced to make our model more biologically realistic gave us important insights about perceptual evolution but have limited experimental and observational evidence for validation. For example, *resource quality* was a weak activation parameter, which affected the higher percentiles of perceptual range distribution slightly more than the lower percentiles (**Figure 2A**). *Energy cap* is another parameter of weak influence, but it impacted perceptual evolution in a positive way, and had greater impacts on the lower percentiles of the distribution (**Figure 2A**).

Gather amount is an intriguing parameter, it behaved like an activation parameter (in the sense of having a threshold), but it had a deactivating influence on the perceptual range distribution (**Figure 2A**). When *gather amount* increased beyond a certain value, larger perceptual ranges were possible as the foragers were able to meet biological costs. At the same time, however, foragers with lower perception ranges obtained an advantage by not having to spend much energy on perception, leading to a net weak decrease in perceptual ranges (**Figure 2A**). This could be evidence that *gather amount* is leading to increased greediness among the foragers, resulting in a more equal spreading of resources and decreased efficacy of the evolutionary process.

Gather distance improved the foraging ability of larger perceptual ranges, and therefore affected the higher percentiles of the perceptual range distribution in a more positive way than the lower percentiles (**Figure 2A**). Foragers with small or zero perceptual ranges also would be able to collect resources easily with increasing gather distance, but they would do so in a diffusive movement pattern. This means they would consume more energy per timestep—making them less competitive than foragers able to employ advective movement on the basis of their perceptual ranges. *Gather distance* is especially useful at lower resource densities (beyond a threshold which will allow for survival; **Figure 3B3** and **Supplementary Figure 5**).

Exploring the effects of parameters in our model facilitates understanding of the evolution of perception by identifying how environmental and species-specific attributes (and their interactions) influence the development and maintenance of perceptual range. Such investigations are also beneficial because they suggest patterns of perceptual evolution that might have occurred under various circumstances in the past. In particular, this work suggests the existence of certain "minimal conditions" that are necessary for the evolution and persistence of perception. These conditions, in the form of cut-offs in the case of deactivation parameters and thresholds in activation ones, give us a basic framework to hypothesize about evolutionary trajectories of perception and perceptual ranges. Moreover, given the general nature of this simple model, it is relevant to the evolution of perception for organisms of any size and sensory perception of any modality. Even though we focus on only one type of perception in our model, it can be easily expanded in a future work to involve multiple sensory inputs and their relative trade-offs to better understand the evolutionary trajectories of multiple sensory modalities (Howarth and Moldovan, 2018; Keesey et al., 2019).

In addition, we have not explored the ways in which "dispersal distance" or "mobility" during the reproductive process might affect the system dynamics in the current set of simulations. This topic is a complex one and exceeds the scope of the current paper, but we are able to draw a few conclusions based on pilot results and extrapolations. Small "dispersal distance" leads to agents with similar phenotypes being spatially localized. This does not, however, have a direct impact on the phenotypic distribution because reproduction is purely asexual in the current model. In contrast, dispersal distance could have an impact via resource consumption. Specifically, because agents with higher perceptual range are more effective at removing resources from the environment, spatial clustering resulting from "dispersal distance" can indirectly result in subregions in the simulation space that are less resource-dense because they are inhabited by clusters of highly perceptive agents.

In its current form, our work has provided one way of exploring the evolution of perception in a spatially explicit agent-based model, something that has not been done in the past. Instead, past work on the evolution of perception has used different approaches and considered different themes. For example, researchers have investigated the evolution of perception from a Bayesian perspective to explore the formal link between the statistics of the environment and species-specific characteristics through the lens of genetics (see Geisler and Diehl, 2002, 2003). Those authors used the concept of a maximum fitness ideal observer (a standard Bayesian ideal observer with a utility function) appropriate for natural selection (with a utility function for fitness) and a formal version of natural selection based upon Bayesian statistical decision theory, to explore perceptual systems (Geisler and Diehl, 2003). Others have approached the evolution of perception from a sensory ecology perspective – through the interplay of signals, signaling behaviors and sensory drives (Endler, 1992), where the focus in on how the environment influences the production, propagation, and detection of signals. Our work is complementary to both of these frameworks, as we created a system incorporating important paradigms from movement ecology (foraging, perceptual ranges, and switching between random search and directional movements) to answer the same questions, but with biologically inspired and tunable parameters. Our model is very simple in terms of its treatment of perception and its properties and provides only a crude representation of forager-resource interactions. Nevertheless, it is a first step in the direction of building more sophisticated models of the evolution of perception. Limitations of the current study include (1) our binary treatment of perceptual acuity (we model acuity simply as 1 inside the perceptual range and 0 otherwise, such that a forager isomniscient about resources inside its perceptual range); (2) our lack of attention to sexual reproduction (we assume only asexual reproduction for simplicity because consideration of sexual reproduction would require attention to a great deal behavioral complexity and many further assumptions); (3) our lack of a role for memory; and (4) rudimentary treatment of perception that does differentiates among different modalities.

In the future, we plan to investigate speciation as a function of changing perceptual range. Such inquiry is not possible here because aggregated data obscures our ability to distinguish fine patterns that might indicate "perceptual speciation" and bistability in our scenarios. Understanding such phenomena might be important in exploring patterns of sympatric speciation seen in many subterranean habitats (Segherloo et al., 2018), and perhaps in *Drosophila* (Keesey et al., 2019) and hypogean spiders (Mammola and Isaia, 2017). Moreover, due to our focus on foraging in this model, we did not consider mating signals and interactions, which also play a major role in perceptual evolution (Endler, 1992). Perception of sexual signaling would be a new direction in which our model could be remodeled and explored in the future.

To make this line of modeling more biologically realistic and explore prey-predator interactions (see Hein and Martin, 2020), future studies will include moving resource (or prey) items, different foraging strategies and scale of movement (see Farnsworth and Beecham, 1999; Beecham, 2001). Such a model can also account for co-evolution of perception in multiple interacting species such as the coevolution of hearing in bat-moth systems (Fullard, 1998), and evolution of alternative "cognitive" strategies for movement and foraging (Farnsworth and Beecham, 1999; Beecham, 2001). We also would like to explore more than one type of sensory perception (and its associated range) and incentivize the development of perceptual modalities with different resources. Future work could also explore other properties of perception, such as acuity and memory to increase the model's biological realism. Taken together, such a system of models can help us understand the evolution of perception and the interplay between sensory modalities (Howarth and Moldovan, 2018; Keesey et al., 2019), allowing investigation of the biological and environmental factors that facilitate or hinder such evolutionary changes.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: github.com/anshuman21111/vision-evo.

AUTHOR CONTRIBUTIONS

AS, KL, and WF conceptualized the project. KL and TH wrote the model code. AS and TH performed statistical analyses. AS and WF performed the interpretation of the results and data. AS, TH, and WF wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.698041/full#supplementary-material

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Memories of Migrations Past: Sociality and Cognition in Dynamic, Seasonal Environments

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Seasonal migrations are a widespread and broadly successful strategy for animals to exploit periodic and localized resources over large spatial scales. It remains an open and largely case-specific question whether long-distance migrations are resilient to environmental disruptions. High levels of mobility suggest an ability to shift ranges that can confer resilience. On the other hand, a conservative, hard-wired commitment to a risky behavior can be costly if conditions change. Mechanisms that contribute to migration include identification and responsiveness to resources, sociality, and cognitive processes such as spatial memory and learning. Our goal was to explore the extent to which these factors interact not only to maintain a migratory behavior but also to provide resilience against environmental changes. We develop a diffusion-advection model of animal movement in which an endogenous migratory behavior is modified by recent experiences via a memory process, and animals have a social swarming-like behavior over a range of spatial scales. We found that this relatively simple framework was able to adapt to a stable, seasonal resource dynamic under a broad range of parameter values. Furthermore, the model was able to acquire an adaptive migration behavior with time. However, the resilience of the process depended on all the parameters under consideration, with many complex trade-offs. For example, the spatial scale of sociality needed to be large enough to capture changes in the resource, but not so large that the acquired collective information was overly diluted. A long-term reference memory was important for hedging against a highly stochastic process, but a higher weighting of more recent memory was needed for adapting to directional changes in resource phenology. Our model provides a general and versatile framework for exploring the interaction of memory, movement, social and resource dynamics, even as environmental conditions globally are undergoing rapid change.

Keywords: PDE model, social learning, climate change resilience, seasonal migration, memory

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1. INTRODUCTION

Seasonal migrations are widespread among terrestrial, aquatic, avian and invertebrate species (Dingle, 2014). For many species, migration is an extremely successful strategy, allowing a far greater number of individuals to inhabit landscapes which might not otherwise be able to support large numbers year round (Fryxell et al., 1988). The evolutionary stability of a migratory strategy essentially relies on the fitness benefits of accessing seasonal resources, whether for energetic gain, predator avoidance, or a suitable environment for reproduction, outweighing the energetic and survival related costs of migration (Avgar et al., 2014).

Proximate causes, drivers and mechanisms for migration vary widely across and even within species (Berthold, 1999; Shaw, 2016). Some migrants follow a "green wave" of spring vegetation as it flowers across altitudinal or latitudinal gradients (Bischof et al., 2012; Kölzsch et al., 2015; Merkle et al., 2016). These migrations can be considered "tactical," as they can occur—as an extreme simplification—purely as response to local conditions. Other migrants perform long-distance migrations in anticipation that critical resources will be available at the time of arrival at the end point of migration (Abrahms et al., 2019). This second behavior involves the greatest trade-off between the costs and benefits of accessing those highly seasonal and localized resources. This approach can be considered "strategic" in the sense that it is driven not by immediate cues but by an anticipation based on prior experience (Bracis and Mueller, 2017; Merkle et al., 2019; Bauer et al., 2020).

Migration can be a very successful strategy, with migratory ecotypes of the same species often outnumbering non-migratory conspecifics. Migratory caribou and reindeer *Rangifer tarandus*, for example, are several orders of magnitude more abundant than non-migratory woodland, mountain and forest ecotypes (Festa-Bianchet et al., 2011; Uboni et al., 2016). However, the question of whether migratory animals are more or less resilient to environmental disruptions in the environment remains open and largely case-specific (Moore and Huntington, 2008; Hardesty-Moore et al., 2018; Xu et al., 2021). On the one hand, migratory species may be more vulnerable as disruptions in either of the seasonal ranges or along a migratory corridor can have significant negative impacts (Wilcove and Wikelski, 2008; Seebacher and Post, 2015; Kauffman et al., 2021). On the other hand, migratory species might be more resilient due to their general wide-ranging mobility (Robinson et al., 2009). The resilience of a migratory population depends on the plasticity and adaptability of the population, which can take multiple forms, reflecting variation in *where*, *when* and *whether* the migration occurs (Gurarie et al., 2017; Xu et al., 2021).

Cognitive processes, in particular spatial memory, have been shown to be important mechanisms for the reinforcement and maintenance of migration (Merkle et al., 2019; Bauer et al., 2020). Similarly, sociality and social learning are likely essential to maintaining migration (Guttal and Couzin, 2010; Fagan et al., 2011; Berdahl et al., 2018; Jesmer et al., 2018). However, the interacting role of sociality and spatial memory for the plasticity of migration and the resilience of the behavior when faced with a changing environment are generally unknown, though it has been hypothesized that the importance of these cognitive processes depend on the predictability of these resources (Riotte-Lambert and Matthiopoulos, 2020). Because the scenarios underlying migration are manifold and complex, mathematical modeling may provide some insights and help clarify where, when, and under what conditions we might expect migration behavior to emerge, to be adaptive, to be maladaptive, or to collapse.

Here, we develop a diffusion-advection model with sociality and memory to explore the resilience of a migratory population under various dynamic, seasonal resource distributions. In formulating the model, our goal was to identify the minimum set of movement and memory parameters required to generate an adaptive, migratory behavior. This includes the ability to learn to migrate from non-migratory initial conditions, simulating the release of naive animals in a seasonal environment (Jesmer et al., 2018); to lose the propensity to migrate if the resource distribution does not require it, also a commonly observed phenomenon (Wilcove and Wikelski, 2008); and to assess the resilience or fragility of a migratory population against changing resource distribution dynamics, including both stochasticity and trends in spatial and temporal distributions, mirroring the effects of climate change (Park et al., 2020).

We anticipated that under many conditions a blending of *tactical* (i.e., direct response to resource availability or perception) and *strategic* (i.e., memory-driven and forward-thinking) behavior will help foragers navigate dynamic, seasonal environments. Over-reliance on either strategy should be maladaptive. We further anticipated that a shorter-term memory updating is needed to navigate trends in resource spatial distribution and temporal distribution (phenology), but that a longer-term reference memory is needed to navigate resource distributions that are stochastic (Lin et al., 2021). Similarly, we anticipated that a balance between very low sociality and extreme sociality would lead to the most resilient migratory process.

2. METHODS

2.1. Memory Movement Model

In designing our study, our goal was to develop a minimal heuristic in which the following processes were explicitly modeled: (1) Random or exploratory movement, (2) attraction to resources, (3) sociality in the movements, (4) a long-term (or *reference*) memory of large-scale movement behavior, and (5) a short-term (or *working*) memory that updates movement behavior based on recent experience.

A diffusion-advection equation provided a computationally efficient and versatile framework for examining just such a system. We consider a population moving in one dimension in a constrained domain D and distributing itself according to the following equation:

$$-\frac{\partial u}{\partial t} = -\varepsilon \frac{\partial^2 u}{\partial x^2} + \alpha \frac{\partial}{\partial x}\left(u \frac{\partial h}{\partial x}\right) + \beta \frac{\partial}{\partial x}\left(\nu_s(u)\right) + \frac{\partial}{\partial x}\left(u\, \nu_m(t)\right) \tag{1}$$

where u represents the population distributed in time and space. The first term is the diffusion term, capturing the fast time-scale exploration and "random" movements of individuals, with ε is the diffusion rate.

The second term represents the attraction to a dynamic resource h, with the proportionality of the advection to the gradient of the resource given by the parameter α (note, the population and resource distributions are functions of both space and time $u(x,t)$ and $h(x,t)$ - we omit the dependent variables in the notation for brevity). This is the well-studied standard chemotaxic resource-following behavior. We borrow the general notation from earlier related work expanding diffusion-advection models to incorporate non-local information (Fagan et al., 2017) and behavioral switching (Fagan et al., 2019).

The third term captures the collective or social advection term of the population via a non-local, density dependent function $v_s(u,x)$. If this function takes the form of a convolution around a non-local kernel k, i.e., $v_s(u) = k(x) * u(x)$, and if that kernel is odd, an attractive or "swarming" behavior can be generated (Mogilner and Edelstein-Keshet, 1999). We use the kernel analyzed by Mogilner and Edelstein-Keshet (1999):

$$k(x) = \frac{x}{2\lambda^2}\exp(-x^2/2\lambda^2).$$

The convolution of u with this kernel has the property of pushing the population in a positive direction when $x < \langle u \rangle$, and in a negative direction when $x > \langle u \rangle$, where $\langle u \rangle$ is the mean location of the population. The parameter λ is a length scale of sociality, roughly one-half the size of the swarm, and β is a parameter that quantifies the overall strength of sociality.

Finally, the last term captures the direct advection that emerges from a memory-driven migratory behavior. This term evolves with a set of parameters θ_y that slowly change each year $y \in \{0,1,2,...\}$, i.e., the count of periods τ: $y = \lfloor t/\tau \rfloor$. The migration is specified by six parameters θ: the timing of the start and duration of two anticipated seasons (e.g., summer and winter) t_1, Δt_1, t_2, Δt_2, and the spatial coordinates of the population centroid for each season x_1 and x_2. The remembered migratory speed term is a simple step function given by:

$$v_m(t,\theta_y) = \begin{cases} 0; & t > t_1 \text{ and } t \le t_1 + \Delta t_1 \\ s_{12}; & t > t_1 + \Delta t_1 \text{ and } t \le t_2 \\ 0; & t > t_2 \text{ and } t \le t_2 + \Delta t_2 \\ s_{21}; & t > t_2 + \Delta t_2 \text{ or } t \le t_1 \end{cases} \tag{2}$$

where the migration speeds s_{12} and s_{21} from the respective ranges are set such that they arrive at x_1 at t_1, depart at $t = t_1 + \Delta t_1$, arrive at x_2 at $t = t_2$, and depart at $t_2 + \Delta t_2$. Thus, $s_{12} = (x_2 - x_1)/(t_2 - (t_1 + \Delta t_1))$ and $s_{21} = (x_1 - x_2)/(t_1 - (t_2 - \tau + \Delta t_2))$. This step-like migration function is a one-dimensional version of the migration parameters estimated for individuals (Gurarie et al., 2017) and populations (Gurarie et al., 2019) in empirical studies.

We consider these six parameters to be the known or remembered determinants of the migratory behavior, with an initial set θ_0 determining the reference migration behavior. This reference migration is updated each year by the experience of the population. To perform this updating, we estimate a new set of parameters $\widehat{\theta_y}$ after each year, and combine these new parameters with the reference parameters according to the following weighted mean:

$$\theta_{y+1} = \kappa^y \theta_o + \left(1 - \kappa^y\right) \widehat{\theta_y} \tag{3}$$

where each of the six parameters is updated according to Equation 3 identically. The estimates $\widehat{\theta_y}$ are obtained via a least-squares minimization of the migration track ($m(t,\theta) = \int_0^t v_m(t',\theta_y)\,dt'$) against the spatial mean of the population process in year y (i.e., $\widehat{u}(t) = \int_X u_y(t,x)dx$). The parameter $\kappa \in (0,1)$ captures the reliance on that long-term memory. When $\kappa = 0$, all of the actionable memory is from the preceding year. When $\kappa = 1$, the actionable memory is entirely the reference memory.

The model is confined to a one-dimensional bounded domain $[-\chi, \chi]$, with no flux outside of the boundaries. Formally, this no-flux condition means the following conditions must be met

$$\begin{cases} \varepsilon \frac{\partial u}{\partial x} - \alpha\left(u\frac{\partial h}{\partial x}\right) - \beta(v_x(u)) - (uv_m(t)) = 0 & \text{where } x = \chi \\ -\varepsilon \frac{\partial u}{\partial x} - \alpha\left(u\frac{\partial h}{\partial x}\right) - \beta(v_x(u)) - (uv_m(t)) = 0 & \text{where } x = -\chi \end{cases}$$

In practice, the design of our resource space (see below) and other parameterization lead to 0 or near 0 values of both $h(x)$ and $u(x)$, and the simpler $\partial u(-\chi,t)/\partial t = \partial u(\chi,t)/\partial t = 0$ boundary condition provides a good approximation.

As there are no birth or death processes, the total population remains fixed and constant, for convenience integrating to 1. Furthermore, the parameters remain constant throughout time, with no adaptation or mutation-selection process. Our interest is in the ability of a fixed set of movement and memory parameters to navigate an intra- and interannually dynamic, seasonal environment.

2.2. Seasonal Resource

We ran this model on a spatial domain $x \in [-100, 100]$, and a periodicity $\tau = 100$ (i.e., 100 day years). We were interested in an approximately periodic resource dynamic, i.e., one in which $h(x,t) \approx h(x, t-\tau)$). We generated two types of resource distributions. A "non-surfable" resource (*island resource*), and weakly surfable resource (*drifting resource*). Both are characterized by a peak in time and space centered at m_x at m_t, and $-m_x$ at $\tau - m_t$ (for example, locations 30 and -30 at times 25 and 75, respectively). These pulses have a shared time scale of duration s_t and a spatial scale of extent s_x, the standard deviation in the time and space dimension, respectively. The island resource is simply two uncorrelated bivariate normal distributions

$$h(x,t) = K\left(\Phi(m_x, m_t, s_x, s_t) + \Phi(-m_x, \tau - m_t, s_x, s_t)\right)$$

where Φ is the bivariate Gaussian distribution function, and the normalizing constant K is selected such that the average total amount of resource throughout the year is 1, i.e., $\frac{1}{\tau}\int_T \int_X h(x,t)dx\,dt = 1$.

The drifting resource differs from the island resource in that the total amount of resource at any given time $\int_X h(x,t)dx = 1$. This property is attained by distributing the resource as a re-scaled beta distribution, where the shape and scale parameters vary sinusoidally in such a way as to make the standard deviations and means match the desired values of m_x, m_t, s_x, s_t (see

Supplementary Materials for details). Both types of resources are illustrated in **Figure 1**.

Within a given year, the resource is entirely symmetric: $h_y(x, t) = h_y(-x, \tau - t)$. However, in scenarios exploring climate change we allow the peaks to vary with directional trend and stochasticity according to: $m_x(y) \sim N(\mu_x + \gamma_x y, \sigma_x)$ and $m_t(y) \sim N(\mu_t + \gamma_t y, \sigma_t)$, where the μ, γ and σ terms are the mean, slope and variance, respectively, for the location and time duration of the pulse. Thus, if $\gamma = 0$ and $\sigma = 0$, the conditions are constant across years and if $\gamma_x > 0$ there is a shift of the resource toward the extremes of the domain. While we did not explore phenological shifts in timing, those can readily be modeled as well. These trends model the pole-ward shift of peak resources and the earlier spring phenology occurring with a warming global climate (Renner and Zohner, 2018). The spatial and temporal scales of the resource peak (s_x and s_t) remain constant in all of our simulations.

2.3. Metrics

The main metrics we were interested in are *migration mismatch*, *foraging efficiency* and *adaptation to directional trends*.

Migration mismatch captures the combined difference between the migration phenology and the resource phenology in time and space. Spatial mismatch MM_x is the absolute difference between the migration targets and the resource peaks: $\mathrm{MM}_x = |x_1 - m_x| + |x_2 + m_x|$. Temporal mismatch is the difference between the arrival time and the peak of the resource if arrival is post-peak, the difference between the departure time and the peak of the resource if departure is pre-peak, and 0 if the seasonal duration spans the peak, i.e., $\mathrm{MM}_t = max\{t_1 - m_1, m_1 - (t_1 + \Delta t_1), 0\} + max\{t_2 - m_2, m_2 - (t_2 + \Delta t_2), 0\}$. Thus, the total mismatch is the sum of these: $\mathrm{TM} = \mathrm{MM}_x + \mathrm{MM}_t$. A mismatch of less than 1 is essentially perfect, a mismatch of 1–5 we consider excellent, and beyond 50 the system can be said to have failed to keep track of the resource dynamics.

To quantify the foraging efficiency, i.e., the organisms' ability to track the distribution of the resources over space and time, we use a continuous form of the Bhattacharyya coefficient (Bhattacharyya, 1943) which quantifies the similarity between two distributions. We compute this coefficient at every time point in a given year, and take the mean across the equilibrium year to determine foraging efficiency (FE). Thus, the foraging efficiency index is:

$$\mathrm{FE} = \frac{1}{\tau} \int_0^\tau \int_{-\chi}^{\chi} \sqrt{u(x,t)\, h(x,t)}\; dx\, dt$$

where the spatial integral is taken over the domain. This metric is constrained to be between 0 and 1.

For simulations with a constant resource, we ran the model until a quasi-equilibrium (stationary) state was achieved, i.e., where the Bhattacharya index of the population distribution across subsequent years reached a value of 0.99999. Once stationarity was attained, we computed the migration mismatch and foraging efficiency metrics, as well as the number of years required to reach stationarity.

For numerical runs with climate change, we first run a simulation with a given parameter set until stationarity, as above, and then begin shifting the location of the resource poleward with a slow, moderate or rapid trend ($\gamma_x = 0.25, 0.5$, and 1,

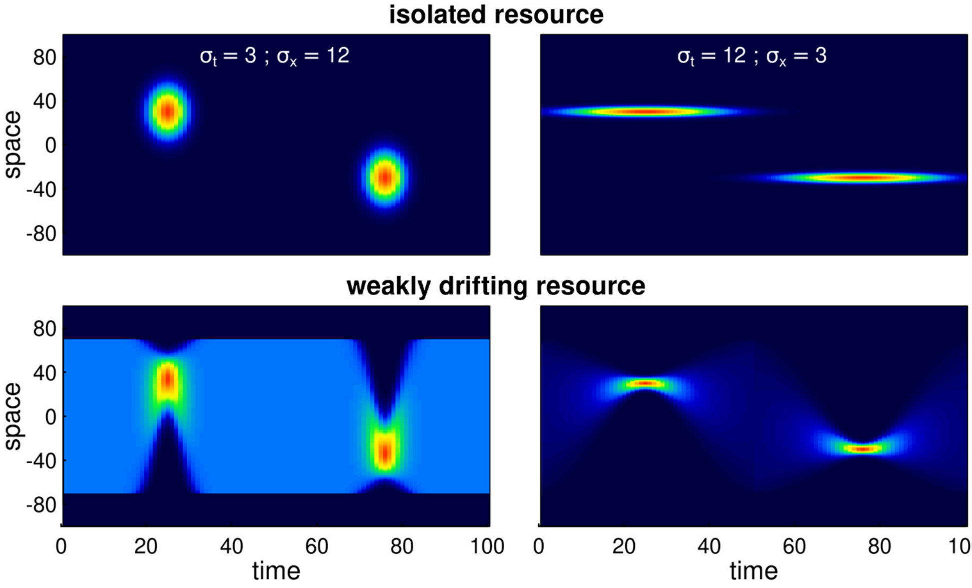

FIGURE 1 | Examples of various seasonal resource distribution functions, contrasting short duration, but wide pulses ($\sigma_t = 3, \sigma_x = 12$; left panels), long duration but spatially concentrated pulses ($\sigma_t = 12, \sigma_x = 3$; right panels), and isolated resource pulses (upper panels) from the weakly drifting resource (lower panels). The total amount of resource is identical across all scenarios. In the weakly drifting resources, the total amount is constant at all times, and uniform in the middle of the phase (time = 0, 50, and 100).

respectively), and/or by adding stochasticity (spatial standard deviation 3, 6, 9, or 12). For stochasticity analyses, we compare foraging efficiency across a range of the reference memory parameter κ. For analyses that included directional trends, with or without stochasticity, we quantified the ability of the system to keep track of climate change with a *spatial adaptation* (SA) index. This index is the ratio of the slope of the memory-based migration location over time, i.e., SA $= \widehat{\gamma}/\gamma_x$ where the adaptation slope estimate is the regression coefficient of the spatial coordinate of the migration against time (i.e., $m_{x,i} = \widehat{\gamma_x} i + m_{x,0}$, where i is the year), and γ_x is the rate of drift of the resource peak (**Table 1**). An SA equal to 1 suggests that the process is keeping up with climate change, an SA of 0 indicates that the process is not responding at all to climate change. Values greater than 1 (super-adaptation) are possible, as are values less than 1, which correspond to a loss of migration behavior. All movement model parameters, resource parameters, and metrics are summarized in **Table 1**.

TABLE 1 | Table of parameters, variables and metrics.

MEMORY MIGRATION MODEL	
ε	Diffusion
α	Strength of resource following
β	Strength of sociality
λ	Spatial scale of sociality
κ	Initial weighting of reference vs. working memory
x_1, x_2	location of population centroids in summer and winter
t_1, Δt_1	start and duration of summer season
t_2, Δt_2	start and duration of winter season
	(long-term) memory vs. working (short-term) memory
RESOURCE DYNAMICS	
τ	duration of period (year)
m_x, $-m_x$	spatial coordinate of resource peak for summer and winter
m_t, $\tau - m_t$	timing of resource peak for the summer and winter
σ_x, σ_t	time duration and spatial scale of resource pulse
γ_x, γ_t	rate of change of peak location and timing of resource
ψ_x, ψ_t	standard deviation of peak location and timing
METRICS	
MM_x	spatial migration mismatch
MM_t	temporal migration mismatch
TM	total mismatch
FE	foraging efficiency
SA	spatial adaptation index

2.4. Simulation Studies

We explored this model using numerical differencing of a system of ordinary differential equations (ODE's) approximating the PDE in Equation (1) with the Runge-Kutte algorithm using the `deSolve` (Soetaert et al., 2010) and `ReacTran` (Soetaert and Meysman, 2012) packages in R. We additionally used the `nlsLM` function in package `minpack.LM` (Elzhov et al., 2016) for robust and fast annual estimation of the migration parameters. The complete code is available as an R package (`memorymigration`) available on GitHub at https://github.com/EliGurarie/memorymigration and as an interactive Shiny application at https://spot3512.shinyapps.io/memorymigrationshinyapp/.

We assessed a wide range of parameter values and resource geometries and dynamics with the goal of answering the four main questions: (1) Can this model adapt to a discrete shift in peak resource location and timing? What is the relative role of memory and sociality for adaptation? (2) Can this model acquire a migratory behavior from a non-migratory initial condition? (3) What is the role of a reference memory for dealing with stochastic resource dynamics? (4) Can this model adapt when the resource peaks shifts in space? Details of parameter combinations and reported metrics are provided in respective results sections.

3. RESULTS

3.1. Adaptation to Resource Phenology

The ability of this system to attain a stable, migratory state that matches the dynamics of the resource is illustrated in **Figure 2**. In the illustrated scenario, it takes nearly 40 years to attain an equilibrium, and the eventual steady state is one where the centroid of the migration lines up exactly with the centroid of the resource, and the arrival timing coincides with the *peak* of resource availability. Notably, the path to this equilibrium is somewhat indirect, with the later winter range taking more time to stabilize than the earlier summer range. The eventual steady state is one where the foraging efficiency is relatively high, near 0.6 compared to an initial value of 0.3. However, the increase in the foraging efficiency was not entirely monotonic, as the system moved through some slightly sub-optimal stages in adjusting its migration behavior.

We ran this process for 8,100 parameter combinations crossing different values of the movement process (α, β and λ) and resource characteristics (σ_x and σ_t), and present the total mismatch (TM) against all those combinations in **Figure 3**. In all of these simulations, memory was entirely recent ($\kappa = 0$), since there can be no benefit to relying on a sub-optimal reference memory. We compared a set of diffusion rates ε between 1 and 8, but only illustrate results for $\varepsilon = 4$.

A well-matched migration phenology (TM < 5) occurred under very many combinations of parameter values, but all parameters play interacting roles. Among the more intuitive results are that greater values of α (resource following) lead to an improved ability to match the migration. Resource peaks with larger spatial extent (higher σ_x) are generally better for migration matching.

Less intuitive was the high importance of the sociality parameters, in particular the spatial scale of the swarming. Higher levels of social attraction (β) led to improved migration matching except in those cases where the sociality scale λ was high. Thus, for example, at $\lambda = 20$, no simulations at $\beta \geq 200$ managed to acquire or maintain a matched migration. However, at $\lambda = 50$ or 100, the migration was slightly better matched at high values of β (**Figure 3**). The spatial extent of the swarm was a remarkably significant variable. Smaller swarms were able to match migration only at low values of social attraction ($\beta = 200$), and relatively high values of resource attraction ($\alpha \geq 600$).

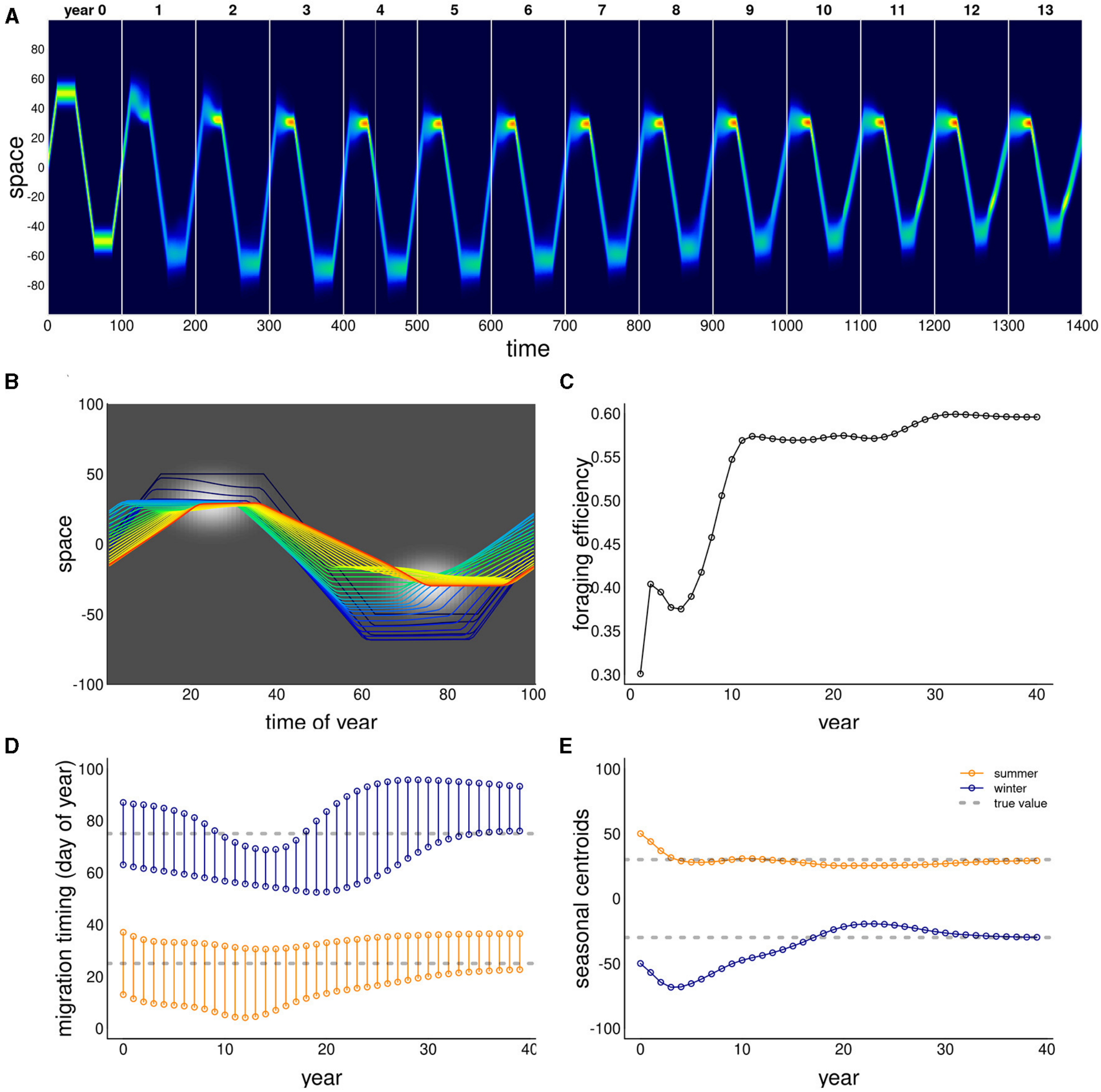

FIGURE 2 | Example of adaptation to a shift in resource peak. The initial (year 0) behavior migrates to locations 50 and –50 at days 15 and 60, whereas the resource peak is at 30 and –30, peaking at times 25 and 75. The panels show **(A)** the first 14 years of the simulation; **(B)** the centroid of the annual movement of the population is shown in panel b, with dark blue to red colors indicating 0–40 year; **(C)** annual foraging efficiency across years; **(D)** migration timing parameters for each year, with orange segments indicating arrival and departure from the summering (northern) grounds, and the blue segments indicating timing of arrival and departure at the wintering grounds; **(E)** migration arrival and departure location across years, with blue and orange indicating winter (southern) and summer (northern) locations.

Random forest analyses, whether on the log of total mismatch or on the classification of a perfect match, uniformly show that the most important variables (Breiman, 2001) were α and λ (4.14 and 4.02 proportional increase in MSE), and the least important was σ_t, with a 0.5 proportional increase.

Overall, foraging efficiency was strongly correlated with migration matching, as expected. At high mismatch ($>$ 50), foraging efficiency was low (mean 0.29, s.d. 0.16) compared to the near-perfect matching migrations (mean 0.58, s.d. 0.14). However, somewhat higher mismatch (1 to 5) showed an even higher overall foraging efficiency (mean 0.62, s.d. 0.18–see also **Figure 4**).

3.2. Learning to Migrate

Figure 5 illustrates the ability of the model animals to learn to migrate in a weakly drifting resource environment with a narrow pulse of resource peaking at 30 and −30 (at days 25 and 75), but a uniform distribution of resource at times 0 and 50. In order to learn to migrate, the system needed to have a higher exploratory impulse (higher diffusion constant ε), a stronger resource advection (higher α) and somewhat weaker sociality (lower β). The qualitative behavior of this process was to start drifting toward the summer resource, while slowly developing a weak pulse toward the winter resource as well. After first locking in on the summer resource, the winter migration, driven both by

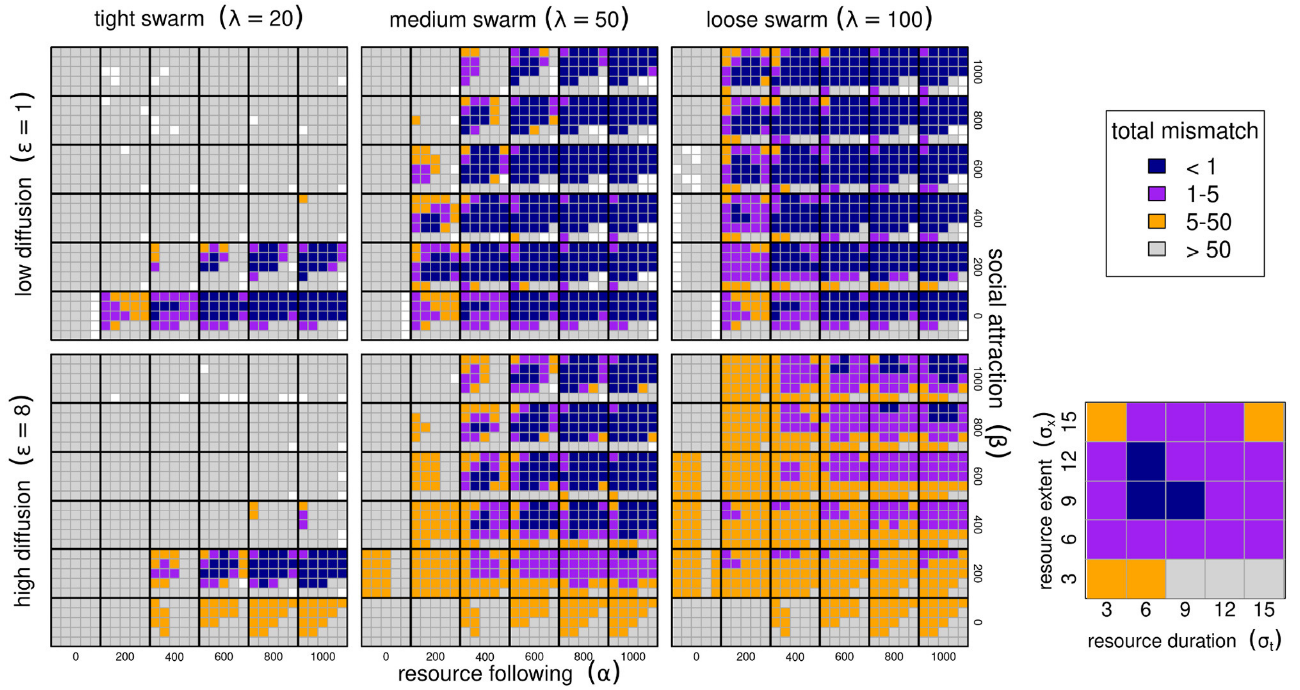

FIGURE 3 | Migration phenology matching across six model parameters. Low and high diffusion ($\varepsilon = 1$ and 8 in upper and lower panel blocks), tight, medium and loose swarms ($\lambda = 20, 50, 100$) left to right panels. Within each of these blocks, high values of the resource following parmaeters α from 0 to 1,000 are left to right, and higher values of the sociality parameter β are bottom to top. Within each of the combinations of $\varepsilon, \lambda, \alpha, \beta$, we show results ranging across 5 values of resource duration (σ_t, 3–15 left to right), and 6 values of resource extent (σ_x, 3–15 bottom to top), as in the zoomed-in panel (bottom right; drawn from $\alpha = 200$, $\beta = 200$, $\lambda = 100$). The color scheme reflects the total mismatch, i.e., the sum of the absolute differences between the migration timing and locations from the resource peak. The white squares represents parameter combinations where the PDE could not be solved for artifactual numerical reasons, that all correspond to a failed adaptation (high mismatch).

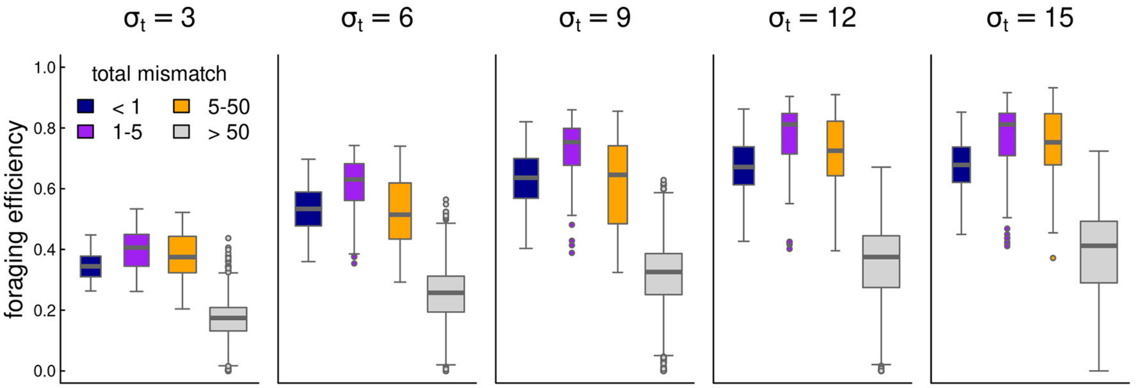

FIGURE 4 | Box-plots of foraging efficiency against mismatch across several values of foraging patch duration.

high diffusion and high resource following, slowly extended itself until both narrow peaks of resource were consistently reached.

The model had, in general, a difficult time learning migration from a non-migratory initial condition. Out of 4,047 successful runs, only four attained mismatch below 1, and 130 below 5. Conditions that were more conducive to learning migration were pulses of *longer* duration (high σ_t), but *smaller* in scope (low σ_x), suggesting that the feedback that encourages migration needs to be compact in space but long enough in duration to lock in to the memory.

3.3. Directional Climate Change

To assess the ability of the system to adapt to a trending climate, we generated scenarios with slow, moderate and fast outward directional shifts in the resource peak (0.25, 0.5, and 1 units/year, respectively). We then assessed 40 parameter combinations for

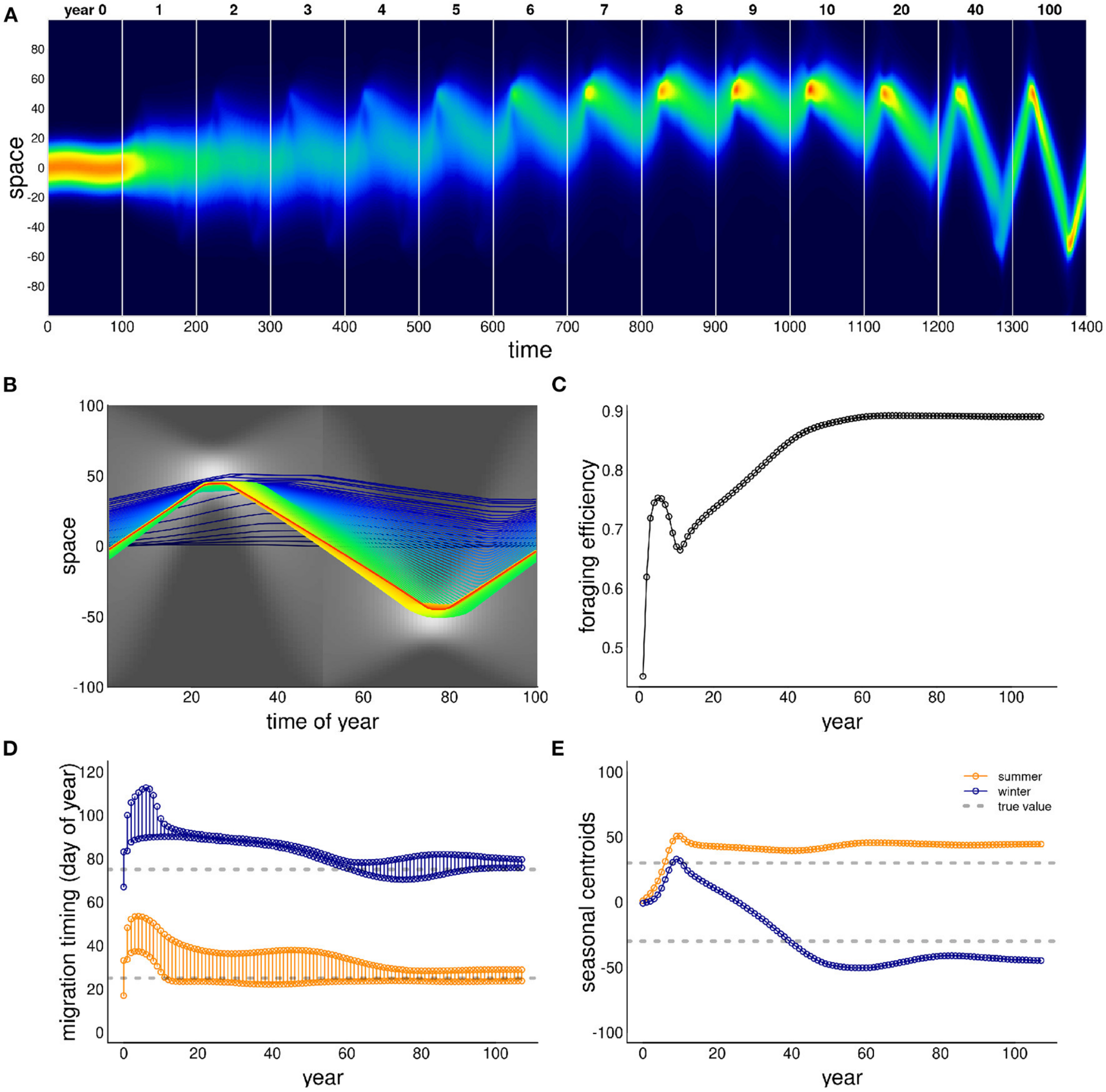

FIGURE 5 | Example of model learning to migrate. The resource is a "weakly drifting" resource and the initial (year 0) condition is non-migratory. The simulation was run for 100 years, and a sampling of those years (labeled) are presented in **(A)**: all years from 0 to 10, followed by 20, 40 and 100. Otherwise, panels are as in **Figure 2**. Additional parameter values were $\varepsilon = 5$, $\alpha = 500$, $\beta = 50$ and $\lambda = 40$.

each of those scenarios, high and low values of resource following ($\alpha = 400$ and 100), high and low values of sociality ($\beta = 400$ and 100) and 10 values of the spatial scale of sociality ($\lambda = 20$ to 200). The spatial and temporal scale of the resource pulses were fixed to $\sigma_x = 12$ and $\sigma_t = 6$, a combination which analyses in section 3.1 showed were generally "easy" to adapt to. We computed the adaptation index and foraging efficiency for each of the 120 runs (**Figure 6**). We were interested in the dynamics against λ due to the consistently high importance of this parameter for matching migration in steady states. Our main index of interest was the spatial adaptation (SA) to trends.

As **Figure 6** shows, higher values of resource following ($\alpha = 400$; orange circles) are nearly universally better for keeping up with climate change (SA values near 1). Furthermore, when combined with high sociality ($\beta = 400$; right panels), nearly all parameter combinations do a good job keeping up with climate change (SA values ranging between 0.53 and 0.85 for a swarm size greater than 50). However, that maximum value is still less than 1, suggesting that truly matching a steadily drifting trend is very difficult. Smaller social spatial scales ($\lambda < 50$) have a very hard time adapting when the social attraction is high, but do fairly well when social attraction is low. Larger sized swarms do progressively worse across more parameterizations, e.g., in the most rapid climate change scenario, the SA drops from 0.83 to –0.13 as the swarm increases in size from 40 to 200 (encompassing, essentially, the entire spatial domain).

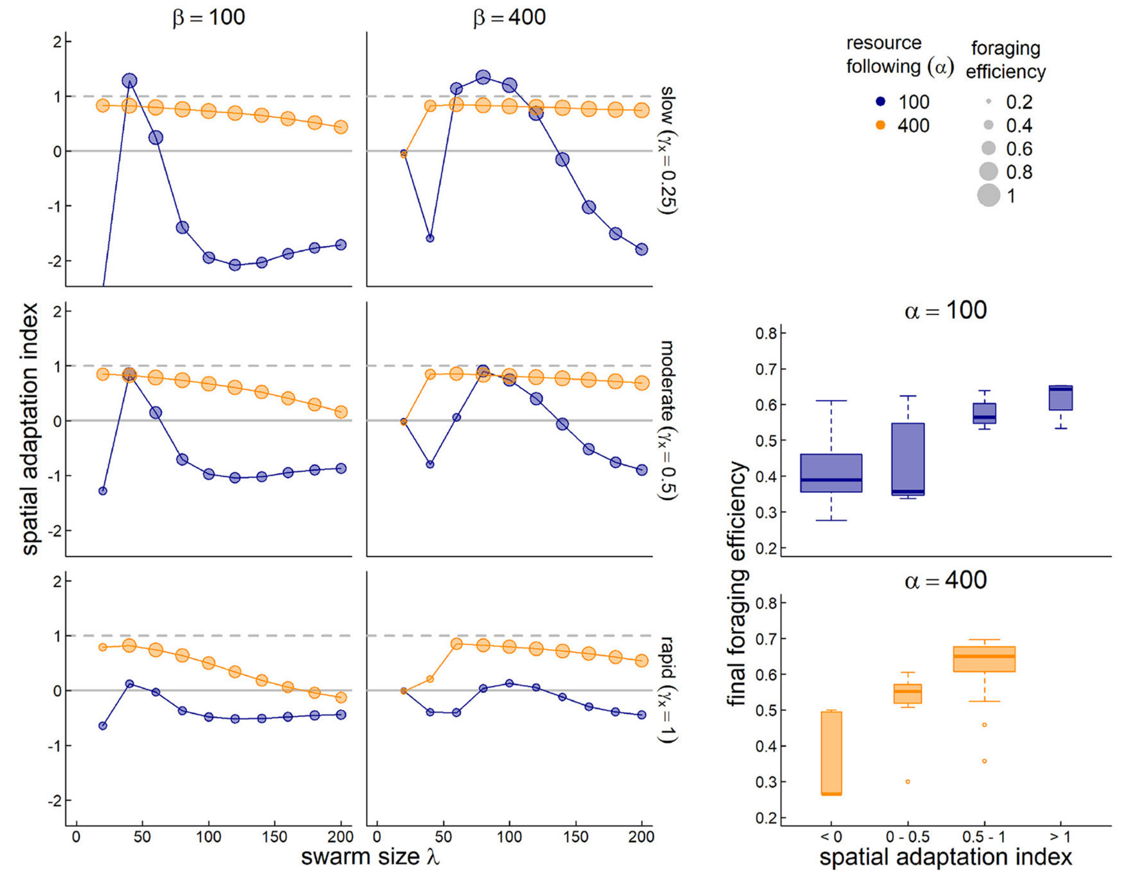

FIGURE 6 | Adaptation to a steadily drifting resource. In three scenarios, the spatial coordinates of the resource drift by 0.25, 0.5, and 1 unit per year (top to bottom, respectively). The *y*-axis is the spatial adaptation index (SA), i.e., the trend of the memory-driven migration divided by the resource drift trend. Values near 1 indicate a behavior that keeps up with climate change, values near 0 indicate no change in migration behavior, and negative values indicate a trend that is opposite to the climate trend. We compare across spatial scales of sociality (λ–*x*-axis), for low and high values resource following ($\alpha = 400$ and 100–orange and blue dots) and low and high values of sociality ($\beta = 100$ and 400, left and right panels). The size of the circles is proportional to the foraging efficiency of the resulting parameter combinations. The bottom-right boxplots indicate the final year foraging efficiency against SA; purple and blue boxes indicate the highest values, orange and gray lower values.

A rather more dramatic pattern is visible for the lower foraging attraction scenario ($\alpha = 100$; blue circles). Notably, no parameter combination at this value comes close to keeping up with the rapid climate change (SA range –0.64 to 0.13). For slower climate change, however, there is a window of values for the swarm size between 40 and 80, where the SA *exceeds* 1, but then crashes quite rapidly to negative values of SA as that swarm size increases. These "super-adaptive" processes indicate a unique sweet spot where a swarm is large enough to capture and adapt to the drifting resource, but not so large that the information gathered in a given year is too weak to adjust the migratory behavior in a following year.

As anticipated, better adaptation to the drifting resource correlated strongly with higher foraging efficiency (inset boxplots).

3.4. Reference Memory and Stochasticity

While recent memory can be helpful for adapting to a single novelty or a smoothly changing conditions, we hypothesized that a more conservative approach that relies on a reference memory may be beneficial when conditions change stochastically. We tested this hypothesis by solving a set of models across a range of κ values fom 0 (all recent memory) to 1 (all reference memory). In these scenarios, we ran the system for as many years as needed with no stochasticity to acquire a stationary state (i.e., similarity index greater than 1-1e-6). We then used the stationary state as the reference memory, and then ran the process for an additional 50 years with a stochasticity (i.e., standard deviation in peak location of the resource) ranging from 0 to 12, and present the resulting average foraging efficiency (**Figure 7**).

Overall, as expected, the greater the stochasticity, the lower the foraging efficiency. Further, as we predicted, highest level of κ can significantly help foraging efficiency, with some variation across the spatial scale of sociality, especially in more highly stochastic scenarios. When that scale of sociality is high enough ($\lambda = 120$, blue colors) there is greater probability of overlap with a stochastic resource, and a conservative, stable migratory regime is much more beneficial in the long run.

3.5. Stochasticity and Trends

We added 30 years of directional trends to the variously stochastic process described above, and assessed the adaptation index against the reference memory parameter κ (**Figure 8**). Over-reliance on reference memory ($\kappa = 1$) by definition does not allow the system to keep up with climate change, leading to an adaptation index of 0. However, in many cases a balancing of recent and reference memory (κ value between 0.6 and 0.8) in many cases was slightly but significantly better than relying entirely on recent memory. The smaller spatial scale (in the selected parameter space) does a generally better job than the larger spatial scale at lower stochasticity. At higher level of stochasticity, however, the larger spatial scale outperforms the smaller spatial scale, which completely loses track of the climate change.

4. DISCUSSION

Animals navigate complex, dynamic and patchy environments. When there is a strongly localized and seasonal component to the resource dynamics, movement strategies limited to straightforward resource-following taxis necessarily fail to efficiently exploit available resources. It is in these cases, quite common in the natural world, that seasonal migration

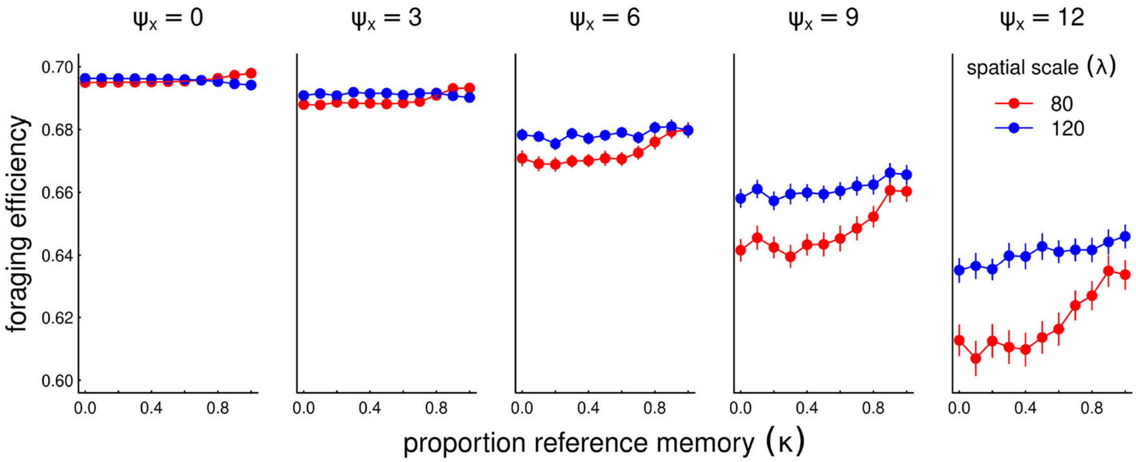

FIGURE 7 | Foraging efficiency (FE) across various values of reference memory κ (*x*-axis) for increasing amounts of interannual stochasticity (ψ_x, panels left to right), and two values of sociality spatial scale $\lambda = 80$ and 120. For the processes with non-zero stochasticity ($\psi_x > 0$), the process was run 90 times for values of κ. Points represent the average of the FE's across all 50 years and 90 replicates. In these scenarios, the resource following parameter $\alpha = 100$, the social attraction $\beta = 400$ and diffusion $\varepsilon = 4$. Note that the *y*-axis scale is constrained over a relatively narrow range (0.6–0.7).

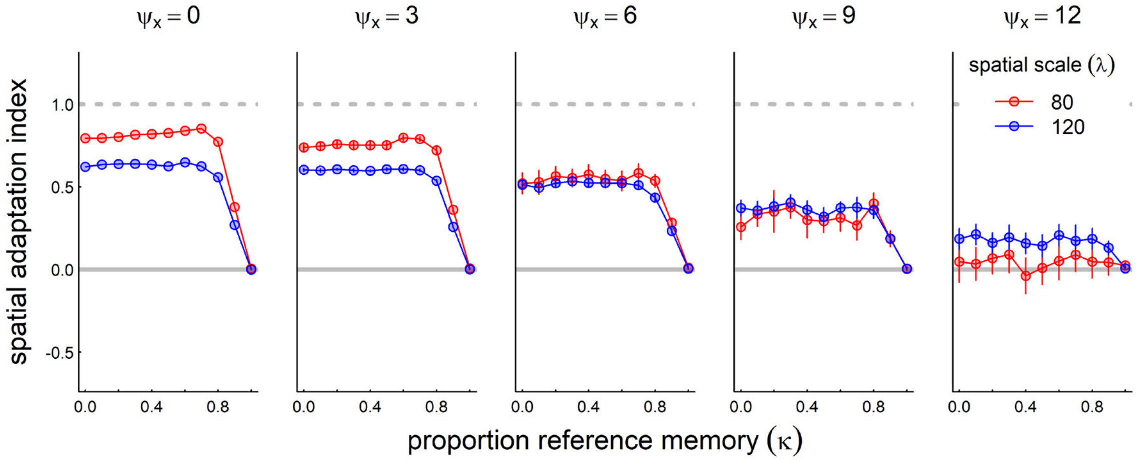

FIGURE 8 | Role of reference memory in adapting to climate change for increasingly stochastic resource dynamics. We ran the model with a moderate rate of climate change (mean shift: 0.5/year) at five increasing levels of stochasticity (inter-annual standard deviation of resource peak 0, 3, 6, and 12, left to right panels). For non-zero stochasticity, we ran the process 30 times and present the mean and standard error of the spatial adaptation index across various values of the reference memory parameter κ: where $\kappa = 0$, the system modifies its migration based entirely on recent experiences; at $\kappa = 1$, the memory never changes from the reference memory. Other parameter values are resource following $\alpha = 100$, social attraction $\beta = 400$, and diffusion $\varepsilon = 4$.

becomes a viable, even necessary, strategy. However, when resources start shifting in space and time—as is occurring at an accelerated pace with recent global climate change—the migration phenology itself must exhibit some plasticity. It is our conjecture that this plasticity is facilitated by a memory-driven process in which recent experiences inform strategic behaviors in subsequent years.

By allowing a population to adjust its migratory behavior based on recent experiences with the resource location, the model we presented here emulated (a) the successful navigation of an environment with temporally and spatially isolated seasonal resource patches, (b) the emergence of a migratory behavior from an essentially resident or naive initial condition, and (c) some intrinsic robustness to changes in those environmental resources, whether steadily shifting trends or inter-annual stochasticity. The relatively simple, social and memory-driven mechanism was able to adapt to long-term changes in resource dynamics, even with inter-annual stochasticity, and may thereby provide a framework with which the interaction of memory, movement, social and resource dynamics can be further explored.

Importantly, our model was in no ways evolutionary, as it contained no birth-death processes or selection pressures. Thus, we used foraging efficiency as a convenient metric of the utility of migration, though this was not a measure explicitly maximized by the model. Other metrics, such as foraging efficiency in a given season, or probability of survival or reproduction relative to resource availability (Bauer et al., 2020) may respond differently across model parameters and could be useful in understanding the relative success of alternative migratory strategies in different contexts. However, the overall annually averaged foraging efficiency metric provided the broadest linkage between resource dynamics and animals' locations and was consistent with the minimal biological assumptions and generality of our framework.

4.1. Adaptation and Resiliency

Our goal was to understand the combinations of factors that lead to a resilient migration behavior. The model we describe was a final iteration of a sequence of models which failed to develop or maintain social migration behavior. For example, in earlier versions memory was modeled as an attractive advection mathematically identical to the resource attraction, but with the attractor being the location of the population in previous years. These models proved to be inefficient at generating a consistent social migratory behavior, i.e., only under very specific parameter combinations and "easy" conditions was a migratory equilibrium attained, and that equilibrium was highly unstable to perturbations. Only a clear, directed advective process with an explicit seasonal signal (i.e., the remembered migration timing, rates, and targets which were remembered in our model) could generate the patterns we aimed to capture. This suggests, somewhat indirectly, that migration behavior is unique as a fundamental, long-term, and risky strategy, profoundly different from the kind of tactical resource response which governs shorter-scaled animal redistributions.

Similarly, iterations of the model that did not have some amount of social cohesion tended to diffuse away without establishing a consistent, migratory stationary state. In fact, sociality parameters—in particular, the spatial scale λ—were, unexpectedly among the most important parameters for determining the resiliency of the process. Populations with small spatial scales tended to have a more difficult time locking in to an adaptive migratory pattern, and only when social attraction was relatively weak. On the other hand, overly large spatial scales compromised the ability of the process to track climate change, due to a dilution of the population's ability to concentrate over available resource patches and remember the corresponding benefits.

The ability to adapt a migration also depended strongly on properties of the resource dynamics. In particular, the reinforcement of memory and foraging is strongest when patches are concentrated in time, but relatively large in space. Interestingly, in most stable patterns, the eventual targeted migration arrival time coincided with the *peak*, rather than the beginning, of the resource dynamic. This indicates that the long-distance social migration behavior may be particularly reinforced when the targeted resource is very sudden. This is the case for the rapid green-up that occurs in high latitudes as snow recedes in tandem with extended day lengths leading to an intense green-up period (Park et al., 2020) or, for example, when resources are linked to the short-duration early blooming phenology of very particular plants (Post and Forchhammer, 2007; Renner and Zohner, 2018).

Even with no strong intrinsic propensity to migrate and a weak phenological resource pulse to follow, our model captured the ability to acquire a strong and adaptive migration behavior (**Figure 5**). Learning migration, however, requires a very strong resource attraction, higher levels of exploratory behavior (e.g., diffusion, and larger spatial scale of sociliaty), and—often—many more years, findings that echo empirical observations (Jesmer et al., 2018).

Despite the ability of the process to adapt under many stable conditions, our migration model (and, perhaps, migration behaviors in general) can also be considered somewhat fragile. Under many shifting conditions, e.g., increasing stochasticity, rapidly shifting resources, a shift in some of the system parameters, or even a shift in the spatial and temporal extent of resources, migration can collapse and turn into a non-migratory, residential behavior (**Figure 3**). This sensitivity may explain why partially migratory populations are so common and, apparently, evolutionary stable (Berthold, 1999; Chapman et al., 2011), as well as the wide range of migration plasticity shown in wild populations, even within a species (Xu et al., 2021).

4.2. Biological Interpretation of Parameters

Diffusion-advection models of animal movement and redistribution are grounded in the general idea that animal movements, somewhat like movements of physical particles, combine random (diffusive) components with directed (advective) components (Skellam, 1951; Turchin, 1998; Okubo and Levin, 2001). While direct relationships between diffusion models and movement data are somewhat tenuous (Gurarie and Ovaskainen, 2011; Potts and Schlägel, 2020), as a theoretical tool for exploring processes they are invaluable for their versatility and the relative ease of numeric computation of the partial differential equations (PDEs) that describe them mathematically.

Despite its evident abstraction, our goal was to develop a model where all parameters have well-defined biological interpretations. The diffusion (ε) captures short time-scaled randomness of movement, reflecting exploratory and short-term dispersive behavior. The foraging advection strength (α) captures the attraction of the population to better quality resources at a relatively large scale. These two parameters, the basic ingredients in diffusion-advection models of animal movement, have direct parallels to empirically estimated properties of animal behavior: diffusion is closely related to families of random walk models (Gurarie and Ovaskainen, 2011) while the advective taxis is related to the step and resource selection functions that are routinely estimated from movement data (Potts and Schlägel, 2020). The spatial scale of the social group (λ) captures the spatial extent of the population, i.e., a population-level home range (Noonan et al., 2019). Diffusion-advection models can also be interpreted as a probabilistic description of a single individual's movement. In this case, λ would correspond to an individual home-range and β would be an individual's tendency to be drawn to the center of that home range, akin to an individual migratory Ornstein-Uhlenbeck process (Gurarie et al., 2017).

The sociality parameter (β) quantifies the strength of an individual's desire to approach the center of the social group. While this parameter is not typically measured, it may in principle be possible to estimate in a manner analogous to a step-selection function by replacing environmental variables with presence of conspecifics as a covariate. The ratio between α and β can be interpreted as the relative importance of foraging to social cohesion, which appears to be important in predicting the resilience of migration.

Migration timing, rate, and seasonal range location parameters can be straightforwardly estimated from movement data (Cagnacci et al., 2015; Gurarie et al., 2019) and synchrony of migration timing and site fidelity are well-documented for many migratory species (Joly et al., 2021). Thus, for example, Gurarie et al. (2019) explicitly estimated the ranging area, timing, and seasonal range locations for migratory caribou, identifying the kind of inter-annual variation that is reflected in the stochastic scenarios explored here, as well as trends in timing.

The reference memory parameter κ is, of course, impossible to observe directly. Our model does, however, allow us to explore in an heuristic way the conditions under which a strong cultural tendency to migrate with certain fixed patterns can help a population hedge against stochasticity (Abrahms et al., 2019; Fagan, 2019). An extremely conservative behavior is the best way to hedge against stochasticity with no directional changes (high κ values in **Figure 7**), as there is no benefit to change behavior based on recent experiences if they provide no information about future conditions. However, this extreme conservatism is, by definition, incapable of adapting when there is a consistent shift in resource distribution (**Figure 8**). In cases where both processes are occurring, we did see a slight improvement in adaptability when long-term reference memory was balanced against a strong response to recent experience (see peaks in **Figure 8**).

Clearly, our exploration of the model was not exhaustive. We did not explore, for example, the resilience of the migration process to changes in resource timing, which would correspond to the widely observed earlier onset of spring as measured by green-up and flowering phenology (Cleland et al., 2007). We hope that making the model available, including via the interactive interface, will facilitate further independent exploration of these processes.

4.3. Social Learning and Collective Knowledge

Models have shown that collective knowledge is important, if not essential, to the evolution and process of migration (Guttal and Couzin, 2010; Shaw and Couzin, 2013; Berdahl et al., 2018). Many migratory organisms are social, and social learning is an acknowledged, non-genetic method for transmitting information (Kashetsky et al., 2021). Furthermore, the general role of social learning for improving a population's ability to track resources has been studied not just in animal systems, but in synthetic systems inspired by social behavior of animals such as optimization heuristics algorithms and the study of swarm robotics (Şahin, 2005; Brambilla et al., 2013). Because our model is not individual-based, we can not identify any specific mechanism (e.g., leader-follower) of social information transfer. But, in a generic way, our model assumes that migration is driven by a collective decision for the timing and locations of seasonal ranges, consistent with the known social and exogenous (e.g., daylength related) triggers for migration. Further, the underlying assumption of the migration "urge" is consistent with the strong endogenous programs to migrate, e.g., the seasonal restlessness known as *Zugunruhe* exhibited by many birds (Berthold, 1999; Helm, 2006). However, in its generic diffusion-based approach to randomness, our model indirectly captures individual-level variation in migration parameters, an inevitable property of any population-level process (Gurarie et al., 2019).

In contrast to the many individual-based models of the evolution of migration (e.g., Guttal and Couzin, 2010; Anderson et al., 2013; Shaw and Couzin, 2013), our model did not include any selection, inheritance or birth or death processes. For example, Anderson et al. (2013) explored the resilience of a population under selective pressure under persistent trends and increased stochasticity of a drifting optimal resource window, showing that a certain amount of heritable phenotypic plasticity is necessary to adapt successfully to climate change even at the cost of efficiency. Our model underscores the fact that some level of resilience and adaptability can be attained with a purely cognitive process that balances sociality with long and short term collective memory. Importantly, this knowledge can be transmitted through social and cultural, rather than genetic, pathways. The high level of sociality among migratory animals, as well as multi-annual parent offspring bonds, are an evident pathway for that kind of transmission. As with those evolutionary models, however, it is clear that when changes are too rapid, no amount of cognition can help entirely mitigate against adverse outcomes. Furthermore, if behaviors are not sufficiently plastic (i.e., if κ is too close to 1), then adaptation is very difficult.

Given the slow scale of fitness selection and the constant change in environmental conditions, it is possible that certain inherent properties of populations, for example the "conservatism" captured by the κ parameter, are themselves selected for to maximize resilience over a long time scale in stochastic environments. The structure of the reference memory in our model was a rather simplistic approach to introduce conservatism or lag to the shifting migration parameters. In our model that reference memory is eventually entirely forgotten, whereas a more sophisticated approach would separate a slowly varying cultural memory, perhaps that is transmitted genetically or culturally, i.e., on the scale of generations, against shorter-scaled responses. In an evolutionary model, we might hypothesize that the overall rates of long- and short-term memory shifts would be related both to the scales of short and long-term fluctuation of the resource, i.e., the auto-correlation scale, strength of trends, and stochasticity of the resource dynamics.

4.4. Summary

Rapid environmental change, both global warming and increased anthropogenic development, is causing severe and dramatic impacts to the widespread and generally successful strategy of seasonal migration for many taxa, and the fate of many animal migrations is a topic of increasing concern (Wilcove and Wikelski, 2008; Kauffman et al., 2021). The ability of animals to respond to these changes depends deeply on their behavioral plasticity and cognitive abilities. The importance of those abilities is in direct proportion to the difficulty in studying them directly. By quantitatively exploring the properties of a heuristic model that distill many of the main properties of wild populations in dynamic and seasonal environments, we hope to have identified some broad patterns that might guide further empirical exploration of the cognitive underpinnings of adaptability and resilience.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

EG and WFF provided the original idea. EG and SP developed and ran models and analysis. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

APPENDIX

A. SUPPLEMENTARY MATERIAL

A.1. Drifting Resource

The drifting resource function has the following properties:

1. The total amount of resource across space is constant throughout the year.
2. At the beginning, middle, and end of the year the resource is uniformly distributed.
3. At some peak time $\mu_t < \tau/2$, the resource concentrates at a location $\mu_x < \chi$ with a spatial deviation σ_x and a temporal deviation σ_t (where τ is the length of the year and χ is the extent of the spatial domain).
4. The resource peaks exactly symmetrically at time $\tau - \mu_t$ and location $-\mu_x$ with the same variances.

To generate a resource with these properties, we allocated the resource in space as a beta distribution, where the two shape and scale parameters vary sinusoidally in such a way as to fulfill the criteria above. Thus:

$$h(x, t, \theta) = \chi B(x/\chi, a(t, \theta), b(t, \theta))$$

where χ is the maximum value (domain) of x, $B(x, a, b)$ is the beta distribution, θ represents the set of parameters $t_r, x_r, \sigma_t, \sigma_x$, and the two shape parameters are given by:

$$a(t) = \frac{m}{s^2}(s^2 + m - m^2)$$

$$b(t, x', \sigma') = (m - 1)\left(1 + \frac{m}{s}(m - 1)\right)$$

where $m(t)$ and $s(t)$ describe the dynamic mean and variance of the resource peak. These equations are solutions to the mean and variance of the beta distribution, $\mu = \alpha/(\alpha + \beta)$, $\sigma^2 = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}$.

The means and variances themselves are Gaussian pulses, with the mean peaking at μ_x at time μ_t with standard deviation σ_t and at $-\mu_x$ at time $\tau - \mu_t$ and the standard deviation pulsing from $2\chi/\sqrt{12}$ (corresponding to a uniform distribution over the domain $-\chi$ to χ) at times 0, $\tau/2$ and τ down to σ_x at t_r and $\tau - t_r$, with standard deviation (in time) σ_t.

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Biased Learning as a Simple Adaptive Foraging Mechanism

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Adaptive cognitive biases, such as "optimism," may have evolved as heuristic rules for computationally efficient decision-making, or as error-management tools when error payoff is asymmetrical. Ecologists typically use the term "optimism" to describe unrealistically positive expectations from the future that are driven by positively biased initial belief. Cognitive psychologists on the other hand, focus on valence-dependent optimism bias, an asymmetric learning process where information about undesirable outcomes is discounted (sometimes also termed "positivity biased learning"). These two perspectives are not mutually exclusive, and both may lead to similar emerging space-use patterns, such as increased exploration. The distinction between these two biases may becomes important, however, when considering the adaptive value of balancing the exploitation of known resources with the exploration of an ever-changing environment. Deepening our theoretical understanding of the adaptive value of valence-dependent learning, as well as its emerging space-use and foraging patterns, may be crucial for understanding whether, when and where might species withstand rapid environmental change. We present the results of an optimal-foraging model implemented as an individual-based simulation in continuous time and discrete space. Our forager, equipped with partial knowledge of average patch quality and inter-patch travel time, iteratively decides whether to stay in the current patch, return to previously exploited patches, or explore new ones. Every time the forager explores a new patch, it updates its prior belief using a simple single-parameter model of valence-dependent learning. We find that valence-dependent optimism results in the maintenance of positively biased expectations (prior-based optimism), which, depending on the spatiotemporal variability of the environment, often leads to greater fitness gains. These results provide insights into the potential ecological and evolutionary significance of valence-dependent optimism and its interplay with prior-based optimism.

Keywords: movement ecology, giving-up density, marginal-value theorem, optimal foraging, cognition, risk allocation, landscape of fear, exploration - exploitation

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INTRODUCTION

Cognitive biases are "consistent deviations from an accurate perception or judgment of the world" (Fawcett et al., 2014). Such biases, as well as their associated costs and benefits, are increasingly studied by biologists, psychologists and neuroscientists (Marshall et al., 2013). The general consensus is that some cognitive biases may be beneficial under ecologically relevant conditions and incomplete information, suggesting they are an adaptive product of natural selection. Adaptive cognitive biases may have evolved as either heuristic rules for computationally efficient decision making, i.e., as computational "shortcuts" to avoid information-processing limitations (Haselton et al., 2015; Trimmer, 2016), or as error-management tools when error payoff is asymmetrical (Tversky and Kahneman, 1974; Haselton et al., 2015; Bateson, 2016; Trimmer, 2016; Jefferson, 2017; Trimmer et al., 2017).

The disposition to expect a favorable outcome when faced with uncertainty is a well-studied cognitive bias, often termed "optimism". A behavioral decision can be defined as optimistic if it is consistent with having a positively biased expectation of reward, or a negatively biased expectation of punishment (Bateson, 2016). Ecologists typically use the term "optimism" to describe a positively biased innate or initial belief (McNamara et al., 2011; Berger-Tal and Avgar, 2012; Houston et al., 2012; Marshall et al., 2015; Krakenberg et al., 2019), which we will refer to hereafter as "prior-based" optimism. Consequently, ecological research on optimism mostly focuses on the role of prior knowledge in creating cognitive biases, leading to circumstances in which animals treat resources that are seemingly identical as strikingly different, depending on their past experiences (Stroeymeyt et al., 2011; Berger-Tal et al., 2014a). Notably, the acquisition of this prior knowledge may range from the immediate time scale (Bateson et al., 2011; Hui and Williams, 2017), to experiences acquired through the individual's life, development or maternal effects, or even evolutionary history (Murphy et al., 2014; Bateson et al., 2015).

Unlike ecologists, human cognitive psychologists often focus on valence-dependent learning as the basis for optimism (sometimes also termed "positivity bias"). Healthy human subjects are known to display unrealistically positive expectations about the future that are driven by an asymmetric learning process, where information about undesirable outcomes is discounted while information about desirable outcomes in amplified (Weinstein, 1980; Sharot, 2011; Kuzmanovic et al., 2015; Gesiarz et al., 2019; Garrett and Daw, 2020). Interestingly, subjects suffering from depression display valence-dependent pessimism – due to an overemphasis on information about undesirable outcomes, their expectations about what the future holds are typically grimmer than what they should be based on the information they have (Strunk et al., 2006; Sharot et al., 2007). The proximate mechanisms underlying this phenomenon have been extensively studied in humans, as well as its consequences (Sharot et al., 2007, 2012; Sharot, 2011; Lefebvre et al., 2017; Dundon et al., 2019). These consequences may range from positive effects of mild optimism on various aspects of human wellbeing, to negative effects of extreme optimism that may extend as far as global financial collapse (Johnson and Fowler, 2011; Sharot, 2011; Jefferson, 2017). Optimism bias is thus considered the only form of misbelief in humans that may have evolved as an adaptive trait (McKay and Dennett, 2009; Johnson and Fowler, 2011; Marshall et al., 2015). To sum, whereas the ecological perspective on optimism translates into a biased belief that erodes toward the truth with the accumulation of experience (a rigid learning process; Berger-Tal and Avgar, 2012), the psychological perspective translates into a dynamic learning process, where biased beliefs do not erode but instead continuously update at a rate that is proportional to the magnitude of environmental changes (Stankevicius et al., 2014; Kuzmanovic et al., 2015; Bateson, 2016). Importantly, valence-dependent optimism (or pessimism) is a plausible mechanism for the emergence of temporally dynamic prior-based optimism (or pessimism), even in the absence of environmental change.

The study of optimism may be particularly relevant to the well-known trade-off between exploration and exploitation (Berger-Tal et al., 2014b; Mehlhorn et al., 2015; Addicott et al., 2017). Consumers, whether they are foraging animals, capital investment firms, or fishing vessels, are constantly balancing known resource exploitation with the time and energy devoted to exploring new resources in order to reduce uncertainty and broaden their portfolio (Cohen et al., 2007; Berger-Tal et al., 2014b; Bartumeus et al., 2016; Votier et al., 2017; Kembro et al., 2019; O'Farrell et al., 2019). The trade-off stems from the fact that gathering information and exploiting it are, to a large degree, two mutually exclusive activities (March, 1991). Exploratory behavior is, however, typically viewed under one of two contrasting perspectives (Warren et al., 2017). One assuming that exploration tendencies have evolved as an adaptive trait in itself, treating information as independently sought-after currency (Dall et al., 2005; McNamara and Dall, 2010; Marvin and Shohamy, 2016). The contrasting, and arguably more mechanistically parsimonious perspective, views exploration as an emerging pattern rather than an adaptive process. Under this view, exploratory behavior emerges from the interactions between simple foraging heuristics, the informational state of the animal, and the environment (Berger-Tal and Avgar, 2012; Avgar et al., 2013; Riotte-Lambert et al., 2017; Davidson and El Hady, 2019). For example, a consumer's decision to exploit a known resource or explore a new one would depend on the perceived likelihood that exploration would lead to improved long-term payoff (i.e., over multiple consumptive events), which in turn depends of the consumer's belief about the availability and quality of yet unexplored resources. Thus, an optimistic consumer will tend to "favor" exploration over exploitation (Berger-Tal and Avgar, 2012), although the adaptive value of this strategy will depend on the dynamics of the environment across space and time.

Optimal Foraging Theory, perhaps more than any other branch of ecology, emphasizes the importance of prior knowledge in determining animal decision-making in the context of the exploration-exploitation tradeoff. Optimal foragers are expected to maximize their long-term intake rate by exploring new patches when their current exploitation rate falls to a rate that is equal to the average intake rate in the surrounding environment (Charnov, 1976; Brown, 1988). However, real-world environments are constantly changing, and foragers do not possess perfect information about them. Bayesian Foraging Theory addresses this reality by assuming that the forager's decisions are based on a prior belief about the expected value of the environment, and about the variability around this expectation, a belief that is constantly being updated as the forager acquires new knowledge (Green, 2006; McNamara et al., 2006; Biernaskie et al., 2009; Berger-Tal and Avgar, 2012). A positively biased prior belief about the quality of other patches thus corresponds to "optimism" as it is typically used by ecologists (prior-based), whereas a positively biased updating of this belief (learning more from positive compared to negative reinforcements) corresponds to "optimism" as it is typically used by psychologists (valence-dependent). If the environment does not change across space and time, and in the absence of valence dependence, prior-based optimists would converge to the optimal exploration rate after learning the true expected value of the environment.

We have previously shown that, in the absence of valence dependence, prior-based optimists are expected to outperform prior-based pessimists (foragers with a negatively biased initial belief about the expected quality of the environment), and, when capable of revisiting patches following a resource renewal process, prior-based optimists should outperform unbiased foragers (Berger-Tal and Avgar, 2012). As far as we are aware, the temporal dynamics and foraging performance of valence-dependent optimists (or pessimists) has not yet been explored in an ecological context, nor have the emerging space-use patterns and consequences of such biased learners when faced with a rapidly changing environment. Our goal here is thus twofold; first, we aim to map the (theoretical) fitness response to various degrees of valence-dependencies under different ecological scenarios, and second, we aim to derive expectations about the relationship between the two types of optimism bias, environmental characteristics, and animal space-use patterns.

MATERIALS AND METHODS

Model Description

The model used here is an individual-based, fitness-maximizing simulation, in continuous time and discrete (albeit implicit) space. This model builds and expends on a model we developed a decade ago to explore the role of prior-based optimism in optimal foraging under uncertainty (Berger-Tal and Avgar, 2012). Simulations start with the forager arriving in a new patch equipped with some initial energy reserves, $E(t = 0)$, and prior beliefs about the average quality of patches on the landscape, $Q(t = 0)$, and the average travel time between patches, $T(t = 0)$. Energy is gained by consuming discrete "food units" (a mouthful, a bite, or a single resource item), and the duration of each such consumption event, Δt, is calculated based on current food availability in the occupied patch, k, following a Type II functional response with search rate a and handling time h (Holling, 1959):

$$\Delta t = \left(a \cdot k\right)^{-1} + h$$

Energy is lost via a constant field metabolic rate, *FMR*, or via reproduction, with a per-offspring reproductive cost, E_r. The forager reproduces whenever energy reserves exceeded the sum of its initial energy reserves and its reproductive cost ($E(t) > E(t = 0) + E_r$), at which point its energy reserves are adjusted accordingly ($E(t) \leftarrow E(t) - E_r$). If at any time, the forager's net energy reserve is insufficient ($E(t) \leq 0$), the forager dies of "starvation". The forager may also die due to "predation" with per-unit-time probabilities p_{travel} (when traveling between food patches) and p_{forage} (when foraging within a patch). Simulations end with the forager either dying, or reaching a predefined longevity threshold, t_{max}. The forager's fitness is its lifetime reproductive success – the total number of offspring it produced. Fitness is thus a product of two aspects of the forager's resource-consumption rate: its long-term mean (which directly translates into reproductive rate), and its temporal variability (which enhances the risk of starvation and predation). The longer a forager lives, and the more it was able to consume during its lifetime, the greater would be its fitness.

After each consumption event, the forager "decides" (sensu Leavell and Bernal, 2019) whether to stay in the current patch, travel to a previously visited (memorized) patch, or travel in search of a new patch. The decision to leave the current patch is based on the forager's expectation regarding the optimal Giving-Up Density (*GUD*; the amount of resources left in a departed patch; Brown, 1988) and associated time and predation costs:

(1) First, assume it is best to leave the current patch; the current food availability in this patch is the optimal *GUD* and so assume that the next patch will be utilized until it reaches this *GUD*.
(2) Based on this assumption, calculate expected consumption rates in each of the alternative patches: n memorized patches + one yet-unvisited patch. Note that n does not remain constant through the simulation but rather increases as the forager visits more and more patches. The expected consumption rate is calculated by dividing the expected cumulative food intake in each of these patches (the patch's expected quality minus the *GUD*) by the expected time it will take to reduce each to the *GUD*, $\tau_{i,GUD}$ $(i = 1 : n+1)$ (Olsson and Brown, 2006). $\tau_{i,GUD} = \tau_{i,travel} + \tau_{i,forage}$, where $\tau_{i,travel}$ is the expect time it will take to travel from the current patch to patch i, whereas $\tau_{i,forage}$ is the expected time it will take to deplete patch i to the *GUD* (the sum of all Δt's starting from $k =$ expected patch quality, and ending at $k = GUD + 1$).
(3) For each of these alternative patches, also calculate the expected survival based on the expected time in each of two movement states (*travel* and *forage*), $\tau_{i,travel}$ and $\tau_{i,forage}$ $(\tau_{i,GUD} = \tau_{i,travel} + \tau_{i,forage})$. The average per-unit-time probability of surviving predation (until *GUD* is reached) is then given by:

$$s_i = \sqrt[\tau_{i,GUD}]{\left[1 - p_{travel}\right]^{\tau_{i,travel}} \cdot \left[1 - p_{forage}\right]^{\tau_{i,forage}}}$$

(4) Next, assume instead that it is best to stay in the current patch for (at least) the duration of the next consumption event, and hence the optimal *GUD* is the current food availability in this patch, minus one. Under this assumption, it is best to forage in the current patch $(i = 0)$ for the duration of the next consumption event ($\tau_{i=0,GUD} = \tau_{i=0,forage} = \Delta t$), with an associated consumption rate of $\tau_{i=0,GUD}^{-1}$, and average per-unit-time probability of surviving predation, $s_{i=0} = p_{forage}$.
(5) "Decide" whether to stay in the current patch or leave to either of the $n + 1$ alternative patches, by choosing the option that maximizes the product of the expected consumption rate and the average per-unit-time probability of surviving predation (s_i).

Once a decision is made, a "starvation mortality" terminates the simulation if the forager's energetic reserve ($E(t)$) is lower than the product of its *FMR* and the time elapsed since its previous bite. The simulation may also end due to a "predation mortality", with probability $1-\left(\left[1-p_{\text{travel}}\right]^{\tau_{\text{travel}}(t)}\cdot\left[1-p_{\text{forage}}\right]^{\tau_{forage}(t)}\right)$, where $\tau_{\text{travel}}(t)$ is the realized duration of traveling ($\tau_{\text{travel}}(t)=0$ if the forager did not leave the patch), and $\tau_{\text{forage}}(t)$ is the time to consume the next bite. If the forager survived, the focal patch's quality is updated by subtracting one bite, and $E(t)$ is updated by adding one bite and subtracting *FMR* expenditure (and, if $E(t) > E(t=0)+E_{\text{r}}$, reproductive cost). If the forager moved to a previously unvisited patch, then n is updated accordingly ($n \leftarrow n+1$). The qualities of the n previously visited patches are updated after each consumption event based on a stochastic logistic regrowth model.

The forager is assumed to "know" the concurrent qualities of all patches it has visited before, as well as the times it takes to travel between any particular pair of patches, as long as that particular journey was undertaken at least once before. What the forager does not know with certainty is the quality (food abundance) of yet unexplored patches, and the travel time between pairs of patches it did not visit sequentially before. Instead, the forager relies on its current (at time t) beliefs about average patch quality, $Q(t)$ and travel time, $T(t)$. Once a new inter-patch journey is decided on or a new patch is visited, the true duration of that journey, $\tau_{\text{travel}}(t)$, or the true quality of that patch, $k(t)$, are sampled from two respective Gamma distributions, each with its own characteristic mean and variance. The foraging environmental is characterized by the values of these means and coefficients of variation $\left(CV=\sqrt{variance}/mean\right)$. The forager's beliefs about the expected values of these quantities is then updated using a simple yet powerful linear approximation to Bayesian learning (McNamara and Houston, 1987; Lange and Dukas, 2009; Berger-Tal and Avgar, 2012):

$$\begin{cases} T(t+\tau) \;=\; \theta_T(t)\cdot\tau_{travel}(t)+\left[1-\theta_T(t)\right]\cdot T(t) \\ Q(t+\tau)=\theta_Q(t)\cdot k(t)+\left[1-\theta_Q(t)\right]\cdot Q(t) \end{cases}$$

where $\theta_T(t)$ and $\theta_Q(t)$ are (temporally dynamic) normalized weights [0, 1].

The novelty of our approach lies in introducing valence-dependent learning by allowing the $\theta_T(t)$ and $\theta_Q(t)$ to vary with the difference between the current beliefs, $T(t)$ and $Q(t)$, and newly acquired information, $\tau_{\text{travel}}(t)$ and $k(t)$:

$$\begin{cases} \theta_T(t)=\dfrac{\eta_T}{\eta_T+(1-\eta_T)\cdot\exp(\alpha_T\cdot[\tau_{travel}(t)-T(t)])} \\ \theta_Q(t)\;=\;\dfrac{\eta_Q}{\eta_Q+\left(1-\eta_Q\right)\cdot\exp\left(\alpha_Q\cdot[Q(t)-k(t)]\right)} \end{cases}$$

Here, η_T and η_Q [0, 1] are the basal normalized weights (learning rates in the absence of a valence effect; unitless), whereas α_{T} and α_Q are valence-dependent learning parameters (with units of time^{-1} and quality^{-1}, respectively). Positive values of α_T and α_Q correspond to an increase in the respective normalized weights whenever $\tau_{\text{travel}}(t) < T(t)$ or $Q(t) < k(t)$, emphasizing new information when this information exceeds expectations. Negative values of α_T and α_Q correspond to an increase in their respective normalized weights whenever $\tau_{\text{travel}}(t) > T(t)$ or $Q(t) > k(t)$, emphasizing new information when this information is disappointing compared to expectations. Consequently, for each of the two environmental variables (patch quality and inter-patch travel time), our model has two "cognitive traits". The basal normalized weight, η, is inversely related to the effect of prior-based judgment bias; in the absence of valence-dependent learning ($\alpha=0$), new information has little effect on the forager's initial beliefs [i.e., $Q(t=0)$ and $T(t=0)$] if it is low (close to 0), whereas new information is heavily weighted and hence prior beliefs are quickly eroded if it is high (close to 1). The valence-dependent learning parameter, α, is our mathematical depiction of valence-dependent judgment bias; if it is positive, the forager's beliefs are affected more by new information if that information is positive ("optimism"), and vice versa.

Through their effects on the forager's space-use decisions (when and where to go), α_T and α_Q affect the forager's resource acquisition rate, risk of starvation, and exposure to predation. Everything else being equal, those values of α_T and α_Q that result in the greatest lifetime reproductive success (a product of longevity and consumption rate), are expected to be evolutionary adaptive.

Numerical Experiments

Our numerical experiments consisted of running 1,000 stochastic realizations of the simulation across a full factorial design of parameter and variable values, as detailed in **Table 1**. While there are many axes along which our model could be investigated, our focus here is on optimal valence-dependent learning bias and its dependence on environmental variability and prior-based bias. Environmental variability is manifested in our "experiments" along two orthogonal axes. First, we varied the coefficients of variation of patch qualities and inter-patch travel times [$CV(Q)$ and $CV(T)$] while keeping the mean values constant (variability across space). High $CV(Q)$ means patches are more heterogeneous in their quality across space, and an exploring forager is more likely to encounter either an exceptionally rich patch, or an exceptionally poor one. High $CV(T)$ means patches are more aggregated in space, and an exploring forager is more likely to travel either for an exceptionally short time, or for exceptionally long time, before encountering a new patch. Second, we varied the prior belief the forager held with regards to each of these two landscape attributes at the beginning of the simulation [$Q(t=0)$ and $T(t=0)$], reflecting a mismatch between the forager's expectations and the true environmental characteristics (e.g., due to abrupt change in mean environmental qualities; variability across time). By varying $Q(t=0)$ and $T(t=0)$, rather than $\hat{Q}$ and $\hat{T}$, we are able to compare foraging performance, and the resulting fitness, across different scenarios while keeping the mean characteristics of the environment constant. We envision a shift into a relatively enriched [$\hat{Q} > Q(t=0)$ or $\hat{T} < T(t=0)$] or degraded [$\hat{Q} < Q(t=0)$ or $\hat{T} > T(t=0)$] environment as one possible cause of prior-based pessimism or optimism, respectively.

TABLE 1 | the various parameters and state variables used in our numerical experiments.

Name	Description	Numerical values
$\hat{Q}$ and $\hat{T}$	mean patch quality (in the absence of depletion), and mean travel time from one patch to another	100 and 10 (respectively)
$CV(Q)$ and $CV(T)$	coefficients of variation of patch quality and travel time	0.1, 0.5, or 1
$Q(t=0)$ and $T(t=0)$	initial (prior) belief about mean patch quality and travel time	50%, 100%, or 150% of $\hat{Q}$ and $\hat{T}$ respectivaly
FMR	field metabolic rate	0.5*
E_r	energetic cost or producing a single offspring	$FMR \cdot \hat{Q}$
$E(t=0)$	initial energy reserves	E_r
t_{max}	maximum longevity	10,000
p_{travel}	predation risk (per-unit-time) while travelling between patches	${t_{max}}^{-1}$, $2 \cdot {t_{max}}^{-1}$, or $3 \cdot {t_{\max}}^{-1}$
p_{forage}	predation risk (per-unit-time) while foraging in a patch	$0.1 \cdot p_{\text{travel}}$
h	the Type II functional response's handling time	1
a	the Type II functional response's search rate	0.02**
r	logistic rate of forage regrowth	0.003***
η_Q and η_T	basal normalized weights for updating $Q(t)$ and $T(t)$	0.01
α_Q and α_T	valence-dependent learning parameters for updating $Q(t)$ and $T(t)$	$-e^2$, $-e^1$, $-e^0$, $-e^{-1}$, $-e^{-2}$, $-e^{-3}$, $-e^{-4}$, $-e^{-5}$, 0, e^{-5}, e^{-4}, e^{-3}, e^{-2}, e^{-1}, e^0, e^1, or e^2

****FMR** was set so as to equal the energetic consumption rate at half $\widehat{\mathbf{Q}}$. **Search rate was set so that consumption rate at half $\widehat{\mathbf{Q}}$ is half the maximum consumption rate ($\mathbf{h^{-1}}$). ***Forage growth rate was set so that, at its maximum (i.e., at half $\widehat{\mathbf{Q}}$), exactly one bite will regrow in the expected time it takes the forager to consume one bite at half $\widehat{\mathbf{Q}}$ and travel to a new patch.*

To reduce dimensionality (and hence make our results as general as possible), we expressed several non-focal parameters and variables as functions of others (**Table 1**). That said, we acknowledge that the robustness of our results depends on a comprehensive factorial sensitivity analysis, an analysis that we view as the next step along this line of investigation. To summarize our results, the outputs of each scenario (1,000 vectors of the various state variables) were bootstrapped 1,000 times, each time recording the average starvation rate, longevity, consumption rate, and lifetime reproductive output, as well as other attributes of the simulated realizations, such as the average *GUD* or home range size (number of unique patches utilized over the forager's lifetime).

RESULTS

First, we examine the relationship between our valence-dependent learning parameters and the resulting beliefs held by the foragers at the end of the simulation (**Figure 1** and **Supplementary Figure 1**). The terminal belief (held at the end of the simulation) about the mean patch quality, $Q(end)$, is always biased low (pessimism) at large negative values of the valence-dependent Q-learning parameter ($\alpha_Q \ll 0$; valence-dependent pessimism), and high (optimism) at large positive values of α_Q (valence-dependent optimism). The α_Q value at which an unbiased terminal belief is obtained $\left(Q(end) = \hat{Q}\right)$ decreases with the initial prior belief ($Q(t=0)$), and the strength of the effect increases with spatial variability in patch quality ($CV(Q)$). These results are mirrored in the relationship between α_T and $T(end)$ (**Supplementary Figure 1**). Note that, high spatial variability in either patch quality or inter-patch travel time translates into skewed distributions of these attributes (for the Gamma distribution, $skewness = 2 \cdot CV$). As a result, the magnitude of terminal optimism at $\alpha_Q \gg 0$ is much larger than the magnitude of terminal pessimism at $\alpha_Q \ll 0$ (**Figure 1**, lower panels), and the magnitude of terminal optimism at $\alpha_T \gg 0$ is much smaller than the magnitude of terminal pessimism at $\alpha_T \gg 0$ (**Supplementary Figure 1**, lower panels).

The fitness-maximizing value of the valence-dependent Q-learning parameter (α_Q), varies with environmental variability across space and time (**Figure 2**). Moderate valence-dependent optimism $\left(\alpha_Q > 0\right)$ is adaptive (i.e., it results in greater lifetime reproductive output) in six out of the nine scenarios depicted in **Figure 2**. Valence-dependent optimism is associated with greatest (relative) fitness gain when the forager is also a "prior-based pessimist" (which may be interpreted as a shift into an enriched environment), and when spatial variability in patch quality is high. Valence-dependent pessimism $\left(\alpha_Q < 0\right)$ is adaptive in only two out of the nine scenarios, when the forager is "prior-based optimist" (which may be interpreted as a shift into a degraded environment), and the spatial variability of patch quality is medium or low. It should be noted that the shape and magnitude of these response curves vary with values of $T(t=0)$, $CV(T)$, and all other variables and parameters (e.g., p_{travel}; **Supplementary Figure 2**). Overall, however, across all scenarios, moderate valence-dependent optimism with regards to patch quality is the most common fitness-maximizing strategy (146 out of 243 scenarios).

The fitness effect of the valence-dependent T-learning parameter (α_T) follows similar trends but is less pronounced than the effect of α_Q (**Supplementary Figure 3**), which is to be expected considering the range of T is an order of magnitude smaller than that of Q. For the same reason, in those

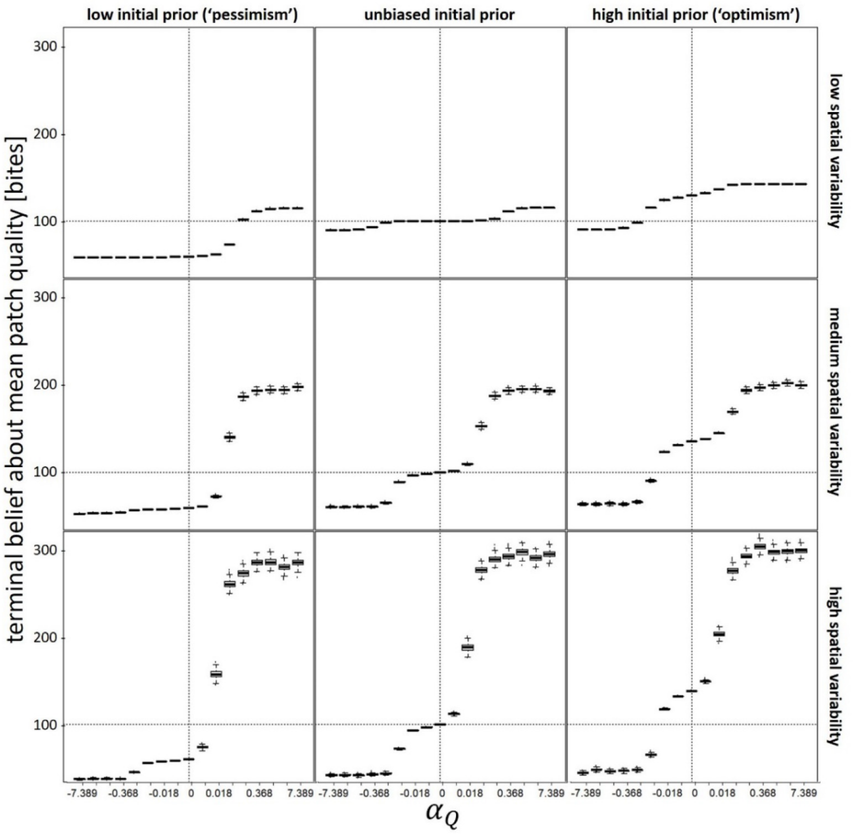

FIGURE 1 | Terminal belief (at the end of the simulation) about the mean patch quality as function of valence-dependence for patch quality (positive values of α_Q correspond to valence-dependent optimism whereas negative values correspond to valence-dependent pessimism). Vertical dashed lines denote unbiased learning ($\alpha_Q = 0$), whereas horizontal dashed lines denote an unbiased terminal belief $\left(Q\,(end) = \widehat{Q}\right)$. Different panels refer to different scenarios: low ($Q(t = 0) = 50$), unbiased ($Q(t = 0) = 100$), and high ($Q(t = 0) = 150$) initial prior belief (columns), and low ($CV(Q) = 0.1$), medium ($CV(Q) = 0.5$), and high ($CV(Q) = 1$) spatial variability (rows). In each scenario, α_T was kept constant at its optimal (fitness maximizing) value. $T(t = 0) = \widehat{T} = 10$; $CV(T) = 0.5$; $P_{travel} = t_{max}{}^{-1}$ other parameters and variables were as detailed in **Table 1**.

scenarios where valence-dependent optimism is adaptive, it is typically extreme ($\alpha_T \gg 0$; **Supplementary Figure 3**). Valence-dependent optimism is adaptive in unchanged or newly enriched environments (i.e., for unbiased or pessimistic priors), but only when $CV(T)$ is moderate or high (patches are aggregated in space). When $CV(T)$ is low, α_T has no significant effect on lifetime reproductive success. When the environment is newly degraded (i.e., for prior-based optimists) and $CV(T)$ is high, lifetime reproductive success is maximized when $\alpha_T = 0$ (i.e., unbiased learning; **Supplementary Figure 3**). Overall, across all scenarios, valence-dependent optimism with regards to travel time is the most common fitness-maximizing strategy (121 out of 243 scenarios).

As for the adaptive value of prior-based biases, optimism is, most often, the fitness maximizing strategy. For both medium and high spatial variability in patch quality, absolute fitness is highest for prior-based optimists, and lowest for prior-based pessimists, across all levels of valance-dependent learning (lower panels of **Figure 2** and **Supplementary Figure 2**). This is also true, albeit to a lesser degree, for prior-based optimism with regards to travel time; for a given value of α_T, the absolute fitness value is highest when the forager is a prior-based optimist, and lowest when the forager is a prior-based pessimist (**Supplementary Figure 3**).

To gain better understanding of these results, we examine the effects of our valence-dependent learning parameters on the components of fitness, namely consumption rate and longevity (lifetime reproductive success is the product of these two variables; **Figures 3**, **4**). The effects of the valence-dependent Q-learning parameter $\left(\alpha_Q\right)$ on consumption rates follow similar trends to those described above for lifetime reproductive output (**Figure 3**). Mild valance-dependent optimism is advantageous in newly enriched environments (i.e., for prior-based pessimists), whereas valance-dependent pessimism is only advantageous in relatively homogenous [low $CV(Q)$] and newly degraded environments (i.e., for prior-based optimists). Prior-based optimism about patch quality is associated with a marked increase in absolute consumption rates across all α_Q values, under both moderate and high values (**Figure 3**). As for the effect of our valence-dependent T-learning parameter (α_T) on consumption rates (**Supplementary Figure 4**), valence-dependent optimism is advantageous in unchanged or newly

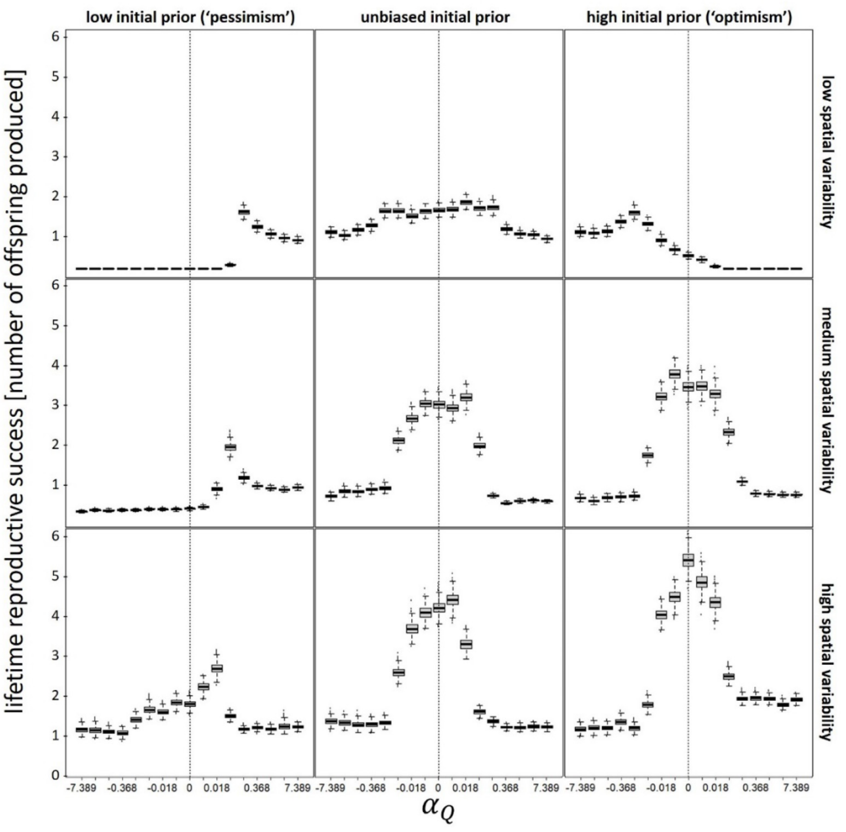

FIGURE 2 | Lifetime reproductive output as function of valence-dependence for patch quality (positive values of α_Q correspond to valence-dependent optimism whereas negative values correspond to valence-dependent pessimism). Vertical dashed lines denote unbiased learning ($\alpha_Q = 0$). Different panels refer to different scenarios: low ($Q(t = 0) = 50$), unbiased ($Q(t = 0) = 100$), and high ($Q(t = 0) = 150$) initial prior belief (columns), and low ($CV(Q) = 0.1$), medium ($CV(Q) = 0.5$), and high ($CV(Q) = 1$) spatial variability (rows). In each scenario, α_T was kept constant at its optimal (fitness maximizing) value. $T(t = 0) = \widehat{T} = 10$; $CV(T) = 0.5$; $P_{travel} = t_{max}{}^{-1}$; other parameters and variables were as detailed in **Table 1**.

enriched environments (i.e., for unbiased or pessimistic priors), but only when $CV(T)$ is moderate or high (patches are aggregated in space). When $CV(T)$ is low, α_T has no significant effect on consumption rate. When the environment is newly degraded (i.e., for prior-based optimists) and $CV(T)$ is moderate or high, consumption rates are maximized when $\alpha_T = 0$ (i.e., unbiased learning; **Supplementary Figure 4**). Finally, prior-based optimism about inter-patch travel times is associated with small but significant increase in absolute consumption rates across all α_T values, under both moderate and high $CV(T)$ values (**Supplementary Figure 4**).

Across all scenarios and parameters values, our simulated foragers typically "died" of "natural causes" (either predation or starvation), with less than 0.01% of simulations reaching $t_{\max}$ (our maximum longevity cutoff). Variability in longevity (**Figure 4**) is driven primarily by variability in starvation mortality (**Supplementary Figure 6**); individuals that die young typically die from starvation, whereas those that live long, eventually die of predation (**Figure 4** and **Supplementary Figures 5, 6**). When spatial variability in patch quality is low $(CV(Q) = 0.1)$, valence-dependent optimism is associated with longer life span (higher probability of survival) in newly enriched environments (compared to the forager's initial expectation, i.e., for prior-based pessimists), whereas valence-dependent pessimism is associated with longer life span in newly degraded environments (compared to the forager's initial expectation, i.e., for prior-based optimists; **Figure 4**). In contrast, when spatial variability in patch quality is moderate or high $(CV(Q) \geq 0.5)$, longevity is typically maximized in the absence of valence-dependent learning (although slight deviations from $\alpha_Q = 0$ have little effect), with the exception of prior-based pessimists under intermediate environmental variability, where mild optimism is associated with distinctly longer life span (**Figure 4**). Longevity is otherwise insensitive to the prior-based bias, and is also unaffected by the value of the valence-dependent T-learning parameter (**Supplementary Figure 7**).

Lastly, we examine the relationship between our valence-dependent learning parameters and emerging space-use patterns (**Figure 5**). Movement rate (% time spent travelling; **Figure 5A**) remain mostly unaffected by the valence-dependent Q-learning parameter, until the latter reaches large positive values (extreme valence-dependent optimism), where movement rate doubles and then plateaus. Exploration rate (% patch departures to new

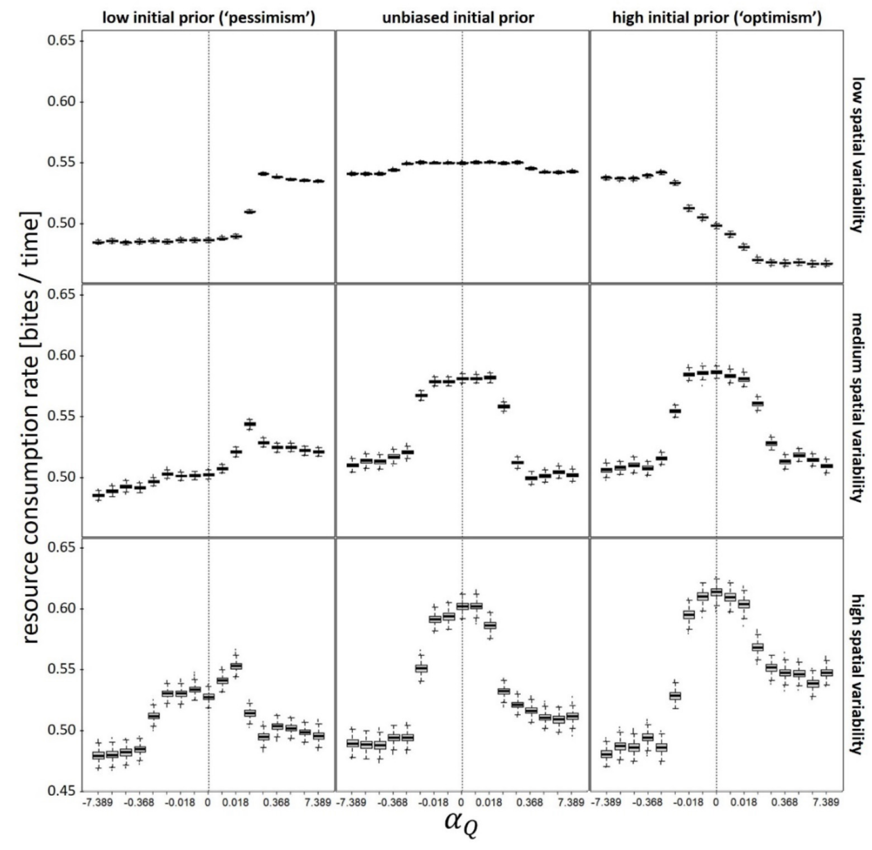

FIGURE 3 | Consumption (feeding) rate as function of valence-dependence for patch quality (positive values of α_Q correspond to valence-dependent optimism whereas negative values correspond to valence-dependent pessimism). Vertical dashed lines denote unbiased learning ($\alpha_Q = 0$). Different panels refer to different scenarios: low ($Q(t = 0) = 50$), unbiased ($Q(t = 0) = 100$), and high ($Q(t = 0) = 150$) initial prior belief (columns), and low ($CV(Q) = 0.1$), medium ($CV(Q) = 0.5$), and high ($CV(Q) = 1$) spatial variability (rows). In each scenario, α_T was kept constant at its optimal (fitness maximizing) value. $T(t = 0) = \widehat{T} = 10$; $CV(T) = 0.5$; $P_{travel} = t_{max}{}^{-1}$; other parameters and variables were as detailed in **Table 1**.

patches; **Figure 5B**) show a double sigmoidal increase pattern with α_Q, with an intermediate plateau at moderate α_Q values (mild pessimism or optimism), followed by full saturation (all patch departures are explorations) at large positive α_Q values. Home-range size (number of unique patches used by a forager over its lifetime; **Figure 5C**), and patch giving-up densities (*GUD*; **Figure 5D**) follow a similar pattern as that or exploration rate. As with other results, these patterns were similar for the effect of α_T, although exploration rate was mostly insensitive to α_T. These patterns also showed slight sensitivities to the values of other variable and parameters, but were otherwise qualitatively similar across all scenarios. Overall, valence-dependent optimists explore more and consequently occupy larger home ranges, and have higher giving-up densities (exploit less), then unbiased or pessimistic learners.

DISCUSSION

Throughout their evolutionary history, animals faced novel environments and situations primarily following dispersal into new territories (Ronce, 2007; Dingle, 2014). However, human-induced rapid environmental changes (HIREC; Sih et al., 2016) makes encountering novel stimuli the rule rather than the exception under many natural situations. Moreover, conservation translocations (in which humans deliberately release animals into novel environments) are increasingly used for the conservation of species or the restoration of ecosystems (Berger-Tal and Saltz, 2014; Berger-Tal et al., 2020). Successful conservation therefore depends on understanding how animals might cope with novel environments and stimuli (Dunlap et al., 2017; Crowley et al., 2019), and how they balance their exploration and exploitation needs in an unknown environment. Optimism is likely to play an important role in decision-making under novel situations, since it is thought to encourage exploration and increase movement rates and home range sizes. This seems to be the case regardless of the suggested mechanism for this cognitive bias – either a positively biased initial belief ("prior-based" optimism; Berger-Tal and Avgar, 2012), or an asymmetric learning process where information about undesirable outcomes is discounted ("valence-dependent" optimism; **Figure 5**).

In this manuscript, we examined the adaptive value of valence-dependent optimism (positivity biased learning). Valence dependence is the main mechanism used by cognitive

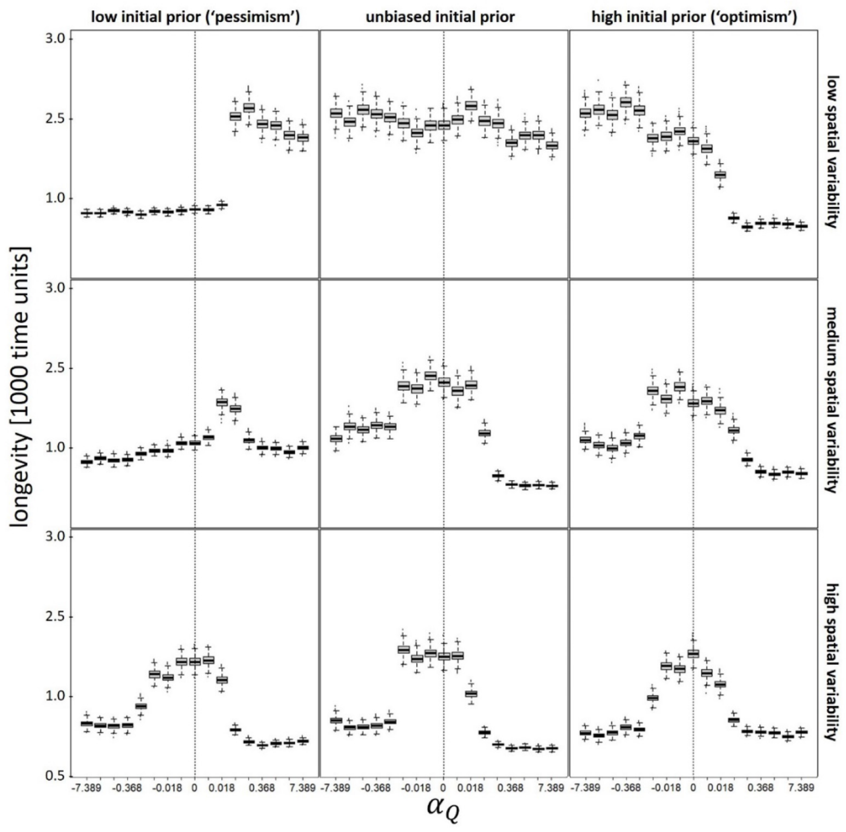

FIGURE 4 | Longevity (life expectancy) as function of valence-dependence for patch quality (positive values of α_Q correspond to valence-dependent optimism whereas negative values correspond to valence-dependent pessimism). Vertical dashed lines denote unbiased learning ($\alpha_Q = 0$). Different panels refer to different scenarios: low ($Q(t = 0) = 50$), unbiased ($Q(t = 0) = 100$), and high ($Q(t = 0) = 150$) initial prior belief (columns), and low ($CV(Q) = 0.1$), medium ($CV(Q) = 0.5$), and high ($CV(Q) = 1$) spatial variability (rows). In each scenario, α_T was kept constant at its optimal (fitness maximizing) value. $T(t = 0) = \widehat{T} = 10$; $CV(T) = 0.5$; $P_{travel} = t_{max}{}^{-1}$; other parameters and variables were as detailed in **Table 1**.

psychologists to explain the emergence of optimism bias (Weinstein, 1980; Sharot, 2011; Kuzmanovic et al., 2015; Garrett and Daw, 2020; Gesiarz et al., 2019), but has rarely been tested in an ecological framework. More specifically, whereas several studies demonstrated the existence of "valence-dependent" optimism in non-human animals, its explicit evolutionary adaptive value has, to our knowledge, never been evaluated. We found that moderate valence-dependent optimism is the most common fitness-maximizing strategy across a wide range of ecological scenarios. Further, valence-dependent optimism results in the maintenance of prior-based optimism (**Figure 1**), and consequently to enhanced fitness in spatially variable environments. Lastly, optimism promotes exploration and consequently always leads to enhanced learning. The resulting rapid acquisition of information may be advantageous even when it results in slightly suboptimal short-term foraging patterns. Taken together, these theoretical explorations suggest we should expect behavioral responses consistent with having positively biased expectations to be the rule in many natural systems.

Optimism, whether valence-dependent or prior-based, promotes exploration. Consistently expecting to find better resources or condition "out there" leads to spending less time in familiar places (exploitation) and more time searching, and consequently learning. We thus expect optimism, which is generally adaptive even in the absence of HIREC, should play an important role in species adjusting their behavioral patterns to new conditions brought about by HIREC. Optimism will not help a species persist in an environment that is degraded to the point it cannot support it, but it should accelerate information-based shifts in behavioral strategies, promoting post-HIREC population viability. It is worth noting that we have found a clear fitness advantage of mild valence-dependent pessimism in scenarios where foragers are (initially) prior-based optimists, and spatial environmental variability is low (e.g., top-right panel of **Figure 2**). This leads to the prediction that species with recent evolutionary history dominated by spatially homogenous yet temporally degrading environments, should be valence-dependent pessimists. Consequently, such species are expected to explore less, be slower to learn, and hence be more vulnerable to HIREC.

In our simulations, mortality was driven primarily by starvation. Extreme valence-dependent optimists or pessimists tend to die of starvation early in life due to low resource consumption rates (except when they are also prior-based

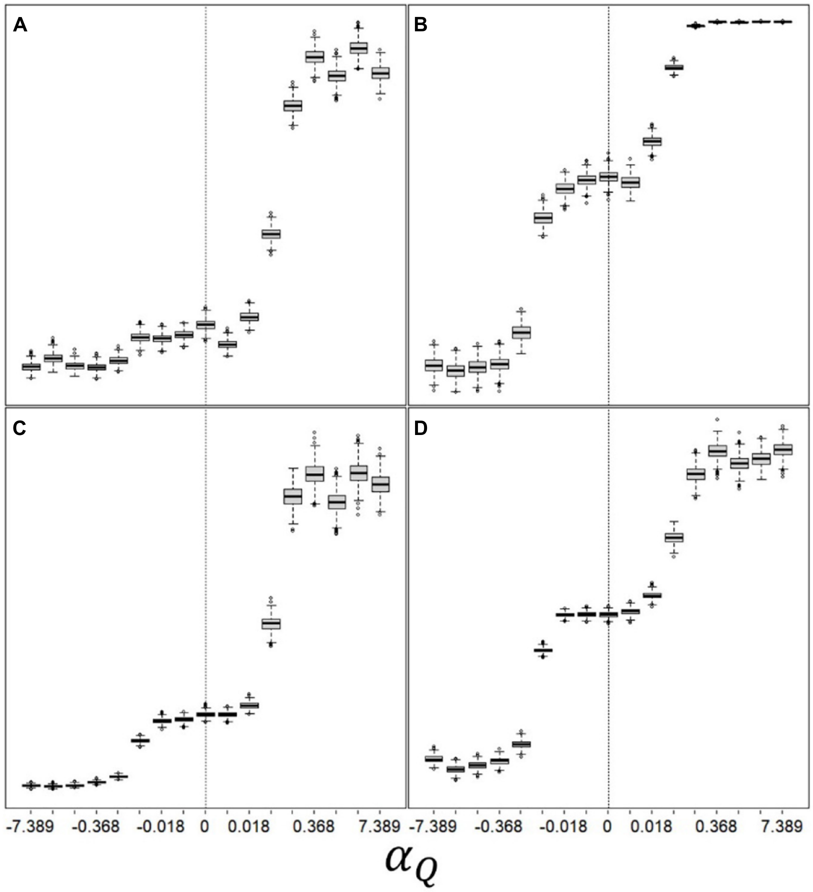

FIGURE 5 | Emerging space-use patterns as function of valence-dependence for patch quality: **(A)** "movement rate" (% time spent travelling; 9–23), **(B)** "exploration rate" (% patch departures to new patches; 55–100), **(C)** home-range size (number of unique patches used during the simulation; 5–24), and **(D)** mean giving-up density (average number of bites remaining in a patch once departed; 36–80) $Q(t = 0) = \widehat{Q} = 100$; $T(t = 0) = \widehat{T} = 10$; $CV(Q) = CV(T) = 0.5$; $p_{travel} = 2\ t_{max}{}^{-1}$; other parameters and variables were as detailed in **Table 1**. α_T was kept constant at its optimal value (which is 0 in this specific scenario).

pessimists or optimists, respectively, and living in homogenous environment). Fitness, however, is a product of life expectancy and reproductive rate, with the latter being tightly linked to resource consumption rate, which is generally highest for mild optimists. Hence, we get scenarios (particularly when environmental spatial heterogeneity is high; e.g., the bottom mid and left panels in **Figures 2–4**) where strategies that lead to longer lives are not necessarily those with the highest fitness. A useful perspective on this tradeoff may be based on the notion of "pace of life" (Careau et al., 2011; Nakayama et al., 2017; Campos-Candela et al., 2018; Mathot and Frankenhuis, 2018; Betini et al., 2019) – a "fast" (optimistic) forager may not live for a longer period of time, but it accomplishes more in the time it has, presumably due to higher exploration rate which allows it to encounter and utilize high quality patches.

Prior-based ("innate") expectations about the environment are an emerging product of the learning process, the prior belief held at its onset, and the characteristics of the environment. Consequently, these beliefs should be viewed as a dynamic state variable (rather than a rigid trait), which continually change through time, even if the characteristics of the environment do not (**Figure 1** here and Figure 1B in Berger-Tal and Avgar, 2012). The rate and direction of this change depend on initial beliefs, environmental heterogeneity, and valence-dependent learning (**Figure 1**). There are at least three processes that may give rise to a prior-based optimism at a certain point in time: an innate disposition that is unaffected by learning (e.g., due to genetic effects or early-life imprinting), a history of learning in a better environment (where expectations would be set high compared to the current environment), and positively biased learning (valence-dependent optimism). We have shown here that the latter is advantageous on its own accord, and is a plausible mechanism for the emergence of temporally dynamics prior-based biases.

The initial value of innate expectations (prior-based bias) has a large effect on both the shape and magnitude of the relationship between valance-dependent learning bias and fitness (**Figure 2**). These interactions deserve an explicitly dynamic investigation, one that will track the trajectories of innate expectations not only within, but also across generations. Such an analysis is beyond the scope of the current work but we would nevertheless like to speculate here about the nature of these dynamics. Assuming first that innate beliefs are passed on from parent to offspring, so that offspring start their life with the same innate beliefs their parents held at the end of theirs, and that the environment does not change across generations. Under these assumptions, the fitness advantage of mild valence-dependent optimism we have observed here should lead to the next generation consisting mostly of prior-based and valence-dependent optimists. These optimists will then suffer reduced fitness compared to either prior-based or valence-dependent pessimists (**Figure 2**). Consequently, we might then expect an emerging pattern of fluctuating selection across generations (despite a constant environment); selection pressure will alternate back and forth between valence-dependent optimism and pessimism. If, on the other hand, the initial beliefs held by offspring are independent of the terminal beliefs of their parents, valence-dependent optimism should maintain (on average) its adaptive advantage. Lastly, let us assume the environment itself fluctuates from one generation to the next (either in terms of its mean quality, or its spatial heterogeneity), and offspring initial beliefs are affected by their parents' environment and/or terminal belief. Under these assumptions, the long-term fitness value of valence-dependent optimism (or pessimism) should depend on the direction (trend) and temporal autocorrelation of this environmental change, with long-term degradation leading to a selection for optimism, and vice versa. Either way, we believe these dynamics should be further studied in the context of evolutionary traps (Robertson et al., 2013; Robertson and Blumstein, 2019), and whether optimism is in fact such a trap, or rather a way out of it.

Other important aspects of foraging dynamics that were not addressed here, for the sake of simplicity, are the effects of competitive interactions, density dependence, and memory decay. Even in the absence of territoriality or other social interactions, an optimal forager operating in a shared space must also consider the effect competitors may have on current patch qualities (via exploitation), and possibly even predation risk (due to a dilution effect; Avgar et al., 2020). It is possible that the effect of resource exploitations by competitors could be boiled down to increased uncertainty in patch quality across space and/or time (Riotte-Lambert and Matthiopoulos, 2020). However, we must consider the possibility that, in the absence of spatiotemporal-specific information about the foraging activity of others, the utility of learning and revisiting a set of patches (known as "traplining") is critically diminished (but see Riotte-Lambert et al., 2015, 2017). In that case, memory decay me be not only more realistic, but also adaptive. Competition may moreover have qualitative effects on the relationship between environmental heterogeneity and fitness (Trevail et al., 2019). At the same time, social information, gained by following or monitoring competitors, plays a major role in the cognitive movement ecology of many species (Kashetsky et al., 2021), and may have non-trivial interactions with the effects of cognitive biases. Lastly, the presence of other individuals with different cognitive strategies (e.g., different levels of optimism) could potentially play an important role in the evolution of an optimal cognitive strategy, and hence the formation of a cognitive niches, via either density- or frequency-dependent selection (Beecham, 2001). The consideration of explicit exploitative interactions among individual foragers, cognitive limitations such as memory decay, and the availability and use of social information are thus important future avenues for research.

Whereas our model focuses on a theoretical exploration of the roles of prior-based and valence-dependent optimism in shaping animal behavior and determining population viability (through their effects on fitness), our model can also serve as the basis for a slew of predictions that can be empirically tested in the field. **Supplementary Figure 8** details some of these predictions regarding the space-use patterns of individuals maintaining an optimal valence-dependent cognitive bias. For example, an increase in predation risk is expected to lead to a decrease in home range size, patch giving-up density, and lifetime reproductive output, but also an increase in both movement and exploration rates. Reproductive output is expected to increase with environmental variability, movement rate is expected to be substantially lower when variability in patch quality is low, but giving-up density is expected to be highest at an intermediate degree of patch quality variability. Lastly, exploration rate is expected to be substantially lower when variability in patch travel time is high (i.e., when patches are more aggregated in space). Whereas some of these predictions are consistent with previous theory (Calcagno et al., 2014; Riotte-Lambert and Matthiopoulos, 2020), some others are counterintuitive and novel, and warrant further theoretical and empirical investigations.

To summarize, we have shown how cognitive biases can serve as an adaptive foraging strategy. The question remains on whether these biases can help individual cope with a rapidly changing environment, or whether changing environments can turn such cognitive biases into dangerous evolutionary traps. As any other model, ours suffers from simplifications, intentional omissions, and operational assumptions that might or might not be important. That said, we believe our carful treatment of "fitness" [considering the effects of predation, starvation, and reproductive investment; (Houston et al., 1993)], and our broad consideration of various ecological scenarios, provide solid foundation for our findings. We are thus optimistic about future extensions of our investigation.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

TA coded and analyzed the model. TA and OB-T designed the study, wrote the manuscript, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Prey Foraging Behavior After Predator Introduction Is Driven by Resource Knowledge and Exploratory Tendency

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Predator reintroductions are often used as a means of restoring the ecosystem services that these species can provide. The ecosystem consequences of predator reintroduction depend on how prey species respond. Yet, to date, we lack a general framework for predicting these responses. To address this knowledge gap, we modeled the impacts of predator reintroduction on foragers as a function of predator characteristics (habitat domain; i.e., area threatened) and prey characteristics (knowledge of alternative habitat and exploratory tendency). Foraging prey had the capacity to both remember and return to good habitat and to remember and avoid predators. In general, we found that forager search time increased and consumption decreased after predator introduction. However, predator habitat domain played a key role in determining how much prey habitat use changed following reintroduction, and the forager's knowledge of alternative habitats and exploratory inclinations affected what types of habitat shifts occurred. Namely, habitat shifts and consumption sacrifices by prey were extreme in some cases, particularly when they were pushed far from their starting locations by broad-domain predators, whereas informed foragers spent less time searching and displayed smaller reductions to consumption than their naïve counterparts following predator exposure. More exploratory foragers exhibited larger habitat shifts, thereby sacrificing consumption but reducing encounters by relocating to refugia, whereas less exploratory foragers managed risk in place and consequently suffered increased encounters while consuming more resources. By implication, reintroductions of predators with broad habitat domains are especially likely to impose foraging and movements costs on prey, but forager spatial memory state can mitigate these effects, as informed foragers can better access alternate habitat and avoid predators with smaller reductions in consumption.

Keywords: habitat domain, behavioral type, predation, memory, individual-based model

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1. INTRODUCTION

Predators are declining globally in both marine (MacNeil et al., 2020) and terrestrial ecosystems (Ripple et al., 2014). Given the myriad ecosystem services that predators can provide (Estes et al., 2011), these declines have elevated discussion of actions aimed at bolstering predator populations (Ritchie et al., 2012), including efforts to reintroduce endangered or threatened species

(Fritts et al., 1997; Hayward et al., 2007a), supplementing small relict populations to aid species recovery (Weinberger et al., 2009), managing problematic species and individuals in human–animal conflict scenarios (Linnell et al., 1997; Athreya et al., 2011), and assisted colonization to attempt to prevent extinctions of species threatened by climate change (Shirey and Lamberti, 2010). Notably, however, predator recovery can have undesirable or unanticipated consequences for ecosystems, as when predators prey on or compete with other threatened species (Marshall et al., 2016), negatively impact prey populations (Hayward et al., 2007b; DeCesare et al., 2010), or fail to elicit expected patterns of anti-predator behavior (e.g., because of human shielding Muhly et al., 2011). Given the variability of predator restoration outcomes for ecosystems, there is need for studies seeking to illuminate the key factors that mediate competitor and prey responses to recovering predator populations (Alston et al., 2019).

When they perceive predation risk, prey individuals commonly sacrifice food in exchange for the safety afforded by differential space use (e.g., refuging), apprehension, or group size (Lima and Dill, 1990; Preisser et al., 2005; Cresswell, 2008; Say-Sallaz et al., 2019). There is growing recognition, however, that such anti-predator investment can vary in nature and intensity as a function of context, or, in other words, properties of the prey experiencing the danger, the predator imposing the threat, and/or the setting of the interaction (Wirsing et al., 2021). For example, prey energetic state (i.e., body condition or hunger), is known to affect risk-taking behavior by mediating individual differences in the incentive to protect vs. seek assets (energy stores) linked to residual reproductive value (McNamara and Houston, 1986; Lima, 1988; Whitham and Mathis, 2000; Olsson et al., 2002; Heithaus et al., 2007). Accordingly, studies exploring these context-dependent drivers of variation in prey defensive behavior should facilitate more reliable prediction of predator recovery in particular systems.

Memory is a state variable that has often been considered in the context of foraging and migratory decision-making (Bracis and Mueller, 2017; Abrahms et al., 2019; Merkle et al., 2019; Tsalyuk et al., 2019), as supported by experimental evidence (Kamil and Roitblat, 1985; Shettleworth, 2001; Stephens et al., 2007). Animals are known to learn from and subsequently avoid predator encounters (Huntingford and Wright, 1989; Wisenden et al., 1994; Griffin et al., 2000; Nomikou et al., 2003). For example, predator-experienced mice (*Mus domesticus*) changed their foraging behavior in response to signals of increased predation risk while predator-naïve mice did not, and those differences in foraging behavior correlated with survival (Dickman, 1992). Thus, memory of predator threats as well as memory of alternative foraging locations may both be components of forager state that influence risk-taking or aid the forager in managing the food–safety tradeoff. In support of this hypothesis, Bracis et al. (2018) showed that spatial memory of food and risk allowed simulated foragers to reduce predator encounters relative to their naïve counterparts without concomitantly reducing consumption, particularly when predators were persistent and weakly correlated with resources across the modeled landscape. No study to date, however, has explored how memory shapes prey habitat use decisions following the restoration of a predator population.

Memory is particularly challenging to study in an ecological context because it can neither be measured directly nor inferred reliably from detailed information on an animal's past experiences (Fagan et al., 2013; Van Moorter et al., 2013). While spatial familiarity has been shown to be an important driver of resource selection and is suggestive of memory (Wolf et al., 2009), it has also been demonstrated that an apparent but non-existent preference for familiarity can arise when habitat models are incomplete (Van Moorter et al., 2013). Accordingly, modeling, whereby memory state can be controlled explicitly, is better suited to generating insight into how this state variable influences predator–prey interactions. Here, in the interest of moving beyond population dynamics to how broader ecosystem properties may be mediated by interactions between recovering predators and prey (Seddon et al., 2007), we used individual-based modeling to examine the impacts of predator recolonization on prey foraging behavior and, in particular, how memory state with respect to the surrounding landscape shapes subsequent habitat shifts by prey. Thus we specifically examine prey who shift their behavior to avoid predators among many other possible antipredator behaviors (Lima and Dill, 1990). Concretely, we introduced predators to a simulated landscape and varied the size of their habitat domain as a measure of the area they threatened. Habitat domain is specifically the spatial extent over which individuals move while foraging, in contrast to home range which can encompass resources to meet other needs, and can also encompass what available microhabitat is used (Preisser et al., 2007; Schmitz et al., 2017). Foraging prey in these simulations differed in their knowledge of the surrounding landscape and how exploratory they were in the face of new habitat. We analyzed movements of the foragers before and after predators were introduced to the landscape to understand how memory influences changes in the behavioral dimension of space use and how those changes are reflected in consumption and time budget. Under the hypothesis that memory facilitates optimization of the trade-off between food and safety, we predicted that (1) informed foragers would exhibit smaller reductions in consumption and spend less time searching for refuge patches than their naïve counterparts following predator exposure. For all memory states, we also predicted that (2) changes to consumption and space use would increase with predator habitat domain, as greater area threatened should reduce the availability of nearby anti-predator refugia and thus necessitate more search time. Finally, we predicted that (3) exploratory behavior would confer greater plasticity to adapt to newly introduced predators, particularly by enabling larger-scale spatial shifts.

2. METHODS

We explored the impact of predator introductions on prey using an existing modeling framework in which foragers move around a dynamic resource landscape, learning patterns of heterogeneity in resources and predator encounters (Bracis

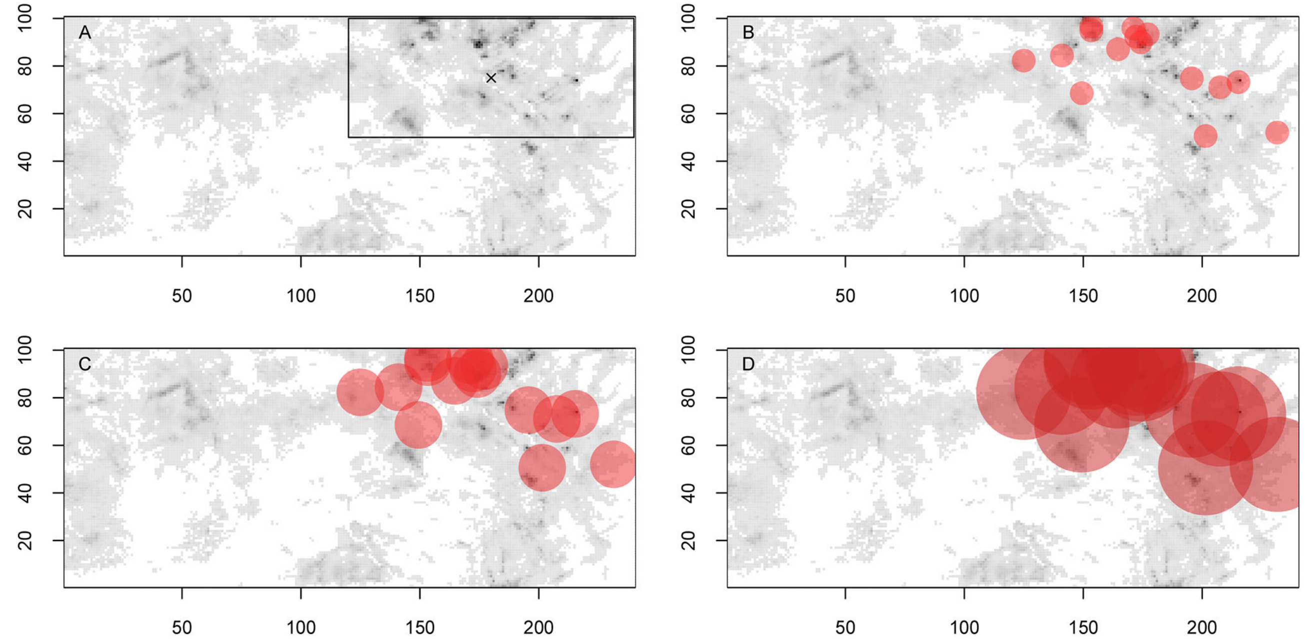

FIGURE 1 | Landscape used in the simulation showing **(A)** habitat quality and box bounding locations of introduced predators with **x** marking the forager's starting location, **(B)** predators with an encounter radius of 5, **(C)** predators with an encounter radius of 10, and **(D)** predators with an encounter radius of 20.

et al., 2015, 2018). Foragers continuously consume resources and switch between a more directed, faster searching behavior and a more tortuous, slower feeding behavior as a function of the consumption rate. Note that these predator introductions could represent reintroductions, recolonizations, or colonization, whether naturally occurring or assisted. These foraging resources deplete and regenerate, making it advantageous for the forager to leave recently depleted locations and return to intrinsically high-quality locations. Resource memory takes the form of two different resource streams of information that drive attractive and repulsive tendencies, respectively (Van Moorter et al., 2009; Bracis et al., 2015). One stream drives the forager away from recently visited and depleted areas; the other returns the individual to high-quality areas that have regenerated. We varied how the resource memory is initialized at the beginning of the simulation to compare foragers with complete knowledge of the landscape to those that must learn their surroundings, and we also varied exploratory potential (see below).

Predators appear at particular locations, remain for one quarter of the total simulation time, then disappear according to a Poisson process for timing and location, thus representing sit-and-wait predators, sit-and-pursue predators, or actively-hunting predators with a small home range. Predator locations are correlated with the forager's resource quality (Williams and Flaxman, 2012; Courbin et al., 2014). The forager detects predators within a given encounter radius, then the forager moves directly away from the predator. Predator encounter radius varies to represent predators with different-sized habitat domains. Encounters are tracked, but there is no death, so that all simulations have the same length. The predation memory is a single stream and is a spatially explicit map of predator encounter locations that decays with time (Bracis et al., 2018). Foragers are attracted to good quality habitat while at the same time seeking to minimize predator encounters. The forager selects its direction probabilistically from a circular distribution which is formed by integrating tracts radiating outward from its position of its spatial memory of resource quality discounted by distance, which is then combined with a circular distribution of predator safety.

2.1. Simulations

We endeavored to use a landscape with realistic variation in vegetation productivity, but where resources were heterogeneously distributed in space and clumped (**Figure 1A**). That is, the forager starts in higher productivity habitat before predator introduction and then has the option of remaining in the higher productivity habitat or switching to previously unused lower productivity habitat. Predators are introduced into the highest quality quadrant, matching a common practice of releasing relocated animals in areas of presumed high quality habitat (e.g., Smith and Clark, 1994; Halsey et al., 2015). The distribution of resources is 42% in the northeast quadrant, 20% in the southeast quadrant, 14% in the southwest quadrant, and 24% in the northwest quadrant. The details of the single landscape used in the simulation can be found in **Appendix A**.

Simulations begin with no predation, then predators appear in the northeast quadrant of the landscape halfway through the simulation. Within this quadrant, containing the best quality habitat, predator locations are correlated with landscape quality. That is, the probability of a predator being at a location is proportional to that location's quality relative to the quality in the quadrant. Different predator encounter radii (i.e., habitat domains) control how much of the northeast quadrant is threatened by predators (**Figures 1B–D**). This variation in encounter radii affects whether there are refugia within the northeast quadrant once it is occupied by predators. Predators relocate, but rarely (predator duration is half the predator period, see Table B1), to represent relatively stable territories for the introduced predators, while still allowing for some shifts.

Foragers vary in their memory initialization, or *memory state*. Some foragers start out *informed*, knowing the spatial pattern of resource quality for the whole landscape. Other foragers start out *naïve* and have a chance to explore the landscape before predators are introduced. It should be emphasized that "naïve" refers to the forager being unfamiliar with the surrounding habitat, not the predator (Sih et al., 2010). That is, it is assumed that the foragers display effective antipredator behaviors: escape and memory of encounters. Memory state is set at the beginning of the simulation by initializing the two-dimensional spatially explicit slower-decaying attractive resource memory stream, and the faster-decaying repulsive resource memory stream (Bracis et al., 2015). In all cases, the repulsive memory stream that drives foragers away from recently used locations is initialized to zero. For informed foragers, the attractive resource memory stream is initialized to the intrinsic resource quality. For naïve foragers, the attractive resource memory stream is initialized to unvisited expectation parameter $M*$; i.e., how unexplored habitat is valued. We used three different values for how foragers could value unexplored habitat: *unexploratory* ($M* = 0$), *less exploratory* ($M* <$ mean quality), and *highly exploratory* ($M* >$ mean quality), with the average habitat quality roughly halfway between the less and highly exploratory unvisited expectation parameter. In all cases, it is assumed that the foragers know the true average consumption rate of the landscape used to switch between searching and feeding behaviors. Thus, foragers differ in their knowledge of the landscape outside their starting region when predators are introduced and how exploratory they are with new habitat.

Simulations start with the forager located in the center of the northeast quadrant, the area of highest quality, where predators are eventually released (**Figure 1A**). All parameters used in the simulation are shown in Table B1. Parameters controlling the resource and predation memories that were not varied are set based on the results from Bracis et al. (2018) assuming high survival. We performed 50 replicate simulations for each set of parameters.

2.2. Metrics

Foragers' habitat use, consumption, and time budget (i.e., division of time between searching and feeding) were tracked to allow for before–after comparisons of forager behavior with predator introduction. Foragers' consumption is a key metric that provides a measure of the non-consumptive effects of predation (i.e., food given up for safety). The number of predator encounters is also important to contextualize resulting consumption changes after predator introduction and as a measure of risk. Finally, in order to compare the space use before and after predators are introduced, trajectories were visually examined and the utilization distribution was calculated with `kernelUD` in the `adehabitatHR` R package (Calenge, 2006).

3. RESULTS

3.1. Space Use Changes

Space use varied dramatically with memory state, and the kernel density of space use clearly changed after predators were introduced across encounter radii for informed foragers and naïve foragers (**Figure 2**). How much of the landscape the naïve foragers explored before predators were introduced depended on memory state. Namely, unexploratory foragers remained at the high-quality patches closest to the release site, while less exploratory foragers exploited the high-quality areas of the eastern half of the landscape, and highly exploratory foragers began the simulations using the entire landscape. The informed forager's space use most closely resembled that of the less exploratory forager but was more tightly focused on the best patches. After predators were introduced, space use changed across all scenarios as foragers were pushed out of the highest-quality areas in the northeast section of the landscape.

Unexploratory foragers (**Figure 2**, row 2) relocated the least after predator introduction. With the smallest predator encounter radius, these foragers moved out of the immediate vicinity of the predators; the utilization distribution for these foragers closely resembled that for the pre-predator phase as they exploited gaps between predators, with just the upper portion of the distribution shifted eastward. As the encounter radius increased, forager distribution shifted southward but remained in the northeast quadrant. Finally, with the largest encounter radius, forager distribution was completely altered, moving into the southeastern quadrant. Thus, by remaining in the highest-quality quadrant despite predation risk, unexploratory foragers tended to maintain high consumption but at the cost of higher encounters.

Less exploratory foragers showed a stronger shift in habitat use after predator introduction. These foragers (**Figure 2**, row 3) continued to utilize the better-quality habitat in the gaps between predators when the encounter radius was small, but also expanded into patches to the south and west. This pattern intensified as the predator encounter radius increased, and the forager shifted to predominately using the patches south and west of the predators. The highly exploratory forager (**Figure 2**, row 4), on the other hand, utilized patches across the landscape before predators were introduced, and predators served to move a greater proportion of use to that more distant habitat. With increasing encounter radius, however, all foragers shifted from using the margins around the predators to being nearly completely excluded from most of the northeast quadrant in the vicinity of the predators.

The space use of **informed foragers** (**Figure 2**, row 1) was most similar to that of less exploratory foragers in how they relocated in the face of predation. The main difference between informed and naïve foragers was that the informed forager was quicker to exploit more distant patches, even when the encounter radius was small. And while the informed forager also continued to exploit habitat close to predators, it did so to a lesser extent that the naïve foragers, especially as the predator encounter radius became large.

The same patterns can be seen with the full trajectories (Figures B1, B2). Namely, the unexploratory forager was the

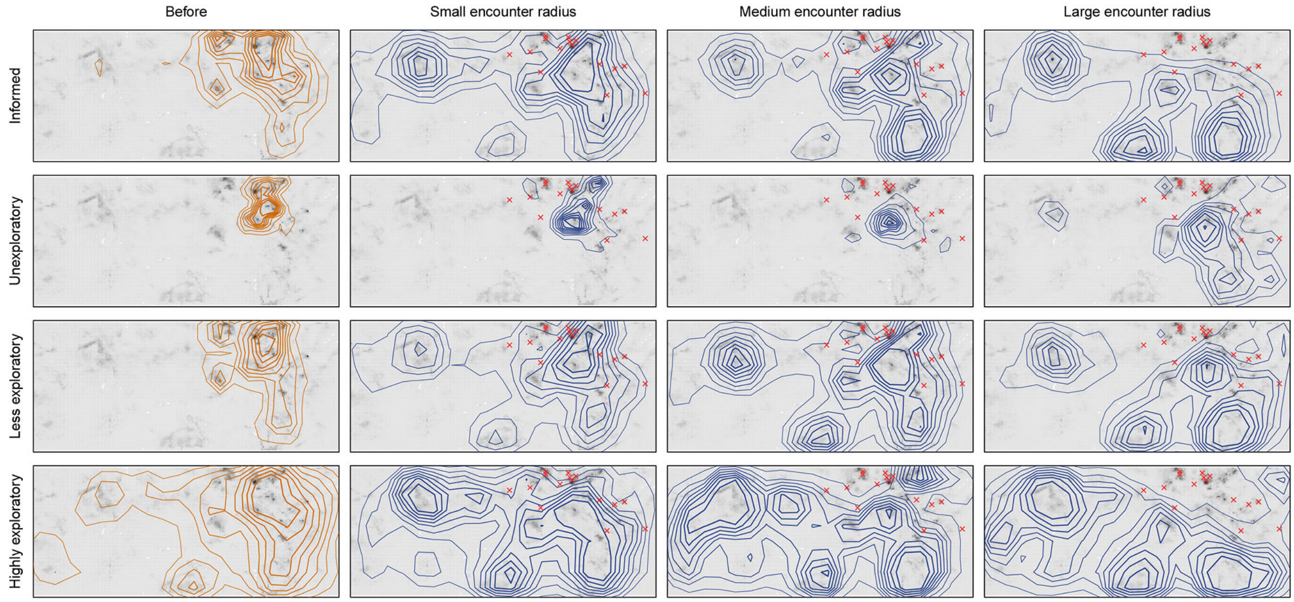

FIGURE 2 | Space use by foragers quantified by kernel utilization distributions comparing before predators (orange, column 1) to after predators (blue, columns 2–4). Rows indicate memory state and columns indicate predator encounter radius. Contour lines show 20–90% utilization. Predator center point locations shown with red **x**'s (see **Figure 1** for radii). Intrinsic habitat quality shown in grayscale.

most constrained with large areas of habitat completely unvisited. Whereas the space use patterns of the informed and less exploratory foragers were broadly similar (**Figure 2**), differences can be seen between the trajectories with the informed forager minimally traveling through unproductive habitat but the less exploratory forager spending more time in unproductive habitat. Finally, the highly exploratory forager had the most dispersed space use across the entire landscape. The partitioning of space by time, with foragers getting pushed out by predators, was clearest with the large predator encounter radius.

3.2. Consumption Changes

The integration of space use changes can be seen with the changes in consumption, where predator introductions depressed the amount consumed relative to the period when predators were absent in all scenarios (**Figure 3**). The forager's memory state partitioned both the pre-predator and post-predator consumption amounts, with higher pre-predator consumption nearly always associated with higher post-predator consumption. Surprisingly, the naïve unexploratory forager consumed the most, followed by the informed forager, the naïve less exploratory forager, and then the naïve highly exploratory forager. Post-predator consumption was mediated by the predator encounter radius, with larger radii associated with larger declines in consumption (Table B3).

In general, higher encounter rates were associated with lower consumption (per memory state), unlike the food–safety trade-off frequently observed in Bracis et al. (2018). Within a given memory state, larger encounter radii led to higher encounters as more habitat within the most productive quadrant was threatened (Table B3). Naïve unexploratory foragers experienced the highest number of encounters with predators, then informed foragers and naïve less exploratory foragers, followed by naïve highly exploratory foragers.

3.3. Time Budget and Consumption Rate Changes

Time spent searching by foragers increased after predators were introduced, driven by foragers leaving their initial habitat to avoid predators and searching for new resources (**Figure 4A**). This pattern manifested even for informed foragers, which had knowledge of other resource locations but still had to relocate, but was more dramatic for naïve foragers that had to initially locate resources. Overall, increases in search time exhibited the same rank order as those for decreased consumption. The increase in time spent searching was also larger with increasing encounter radius as foragers were more completely displaced from their previous habitat.

In addition to changes in time budget, foragers' consumption rates while feeding declined after predators were introduced (**Figure 4B**), implying that foragers shifted to lower quality or already depleted habitat. Note that while foragers did consume resources while searching in our simulations, the bulk of consumption (∼80–90%) occurred while feeding. Declines in consumption rate were more similar across memory states, with slightly larger declines with larger encounter radii, though this was less true for highly exploratory foragers. Thus, the declines in consumption seen with the introduction of predators were a function of both foragers needing to spend more time searching for food as well as selecting lower quality patches.

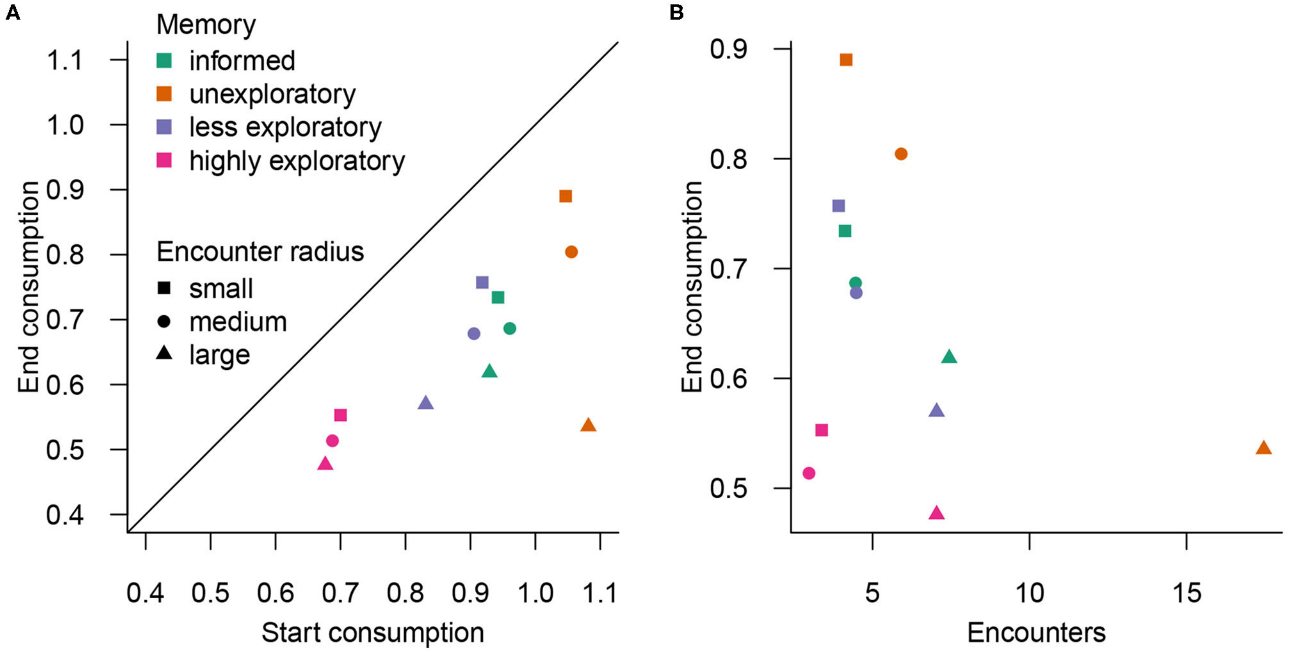

FIGURE 3 | (A) Consumption in the post-predator environment declined in all scenarios compared to the pre-predator environment (i.e., prior to introduction), but was influenced by memory state and encounter radius. **(B)** Higher encounters generally also led to decreased consumption in the post-predator environment. Memory state is indicated by color and encounter radius by symbol.

4. DISCUSSION

Habitat shifts due to changing predation threat have been observed in a wide variety of both terrestrial and aquatic systems (Sih, 1980; Heithaus and Dill, 2002; Wirsing et al., 2007; Belovsky et al., 2011; Dellinger et al., 2019). Yet, previous attempts to predict ecosystem effects of predator reintroductions have neglected prey behavior changes (Baker et al., 2017). Here, to address this information gap, we used individual-based modeling to understand how both predator and prey traits shape behavioral outcomes for foraging prey with the addition of predators to the landscape. Consistent with the non-consumptive effects predators can exert on prey (Preisser et al., 2005), forager behavior, as measured by consumption rates, searching time, and space use, changed after the introduction of predators. The nature of these changes, however, depended on the interplay among the memory state of the forager, the spatial domain threatened by the predator, and the degree to which foragers were exploratory. Namely, in support of our first prediction, informed foragers displayed smaller reductions to consumption and spent less time searching than their naïve counterparts following predator exposure. Furthermore, consistent with prediction two, predator habitat domain correlated positively with reductions to consumption and changes to space use, irrespective of memory state. Supporting our third prediction, the degree to which foragers were exploratory shaped their anti-predator responses, with less exploratory prey managing risk in place and consequently suffering increased encounters while consuming more resources, and more exploratory individuals sacrificing consumption but reducing encounters by relocating to refugia. Together, these findings highlight how understanding prey spatial memory and the movement tendencies of both predators and prey is key to predicting the consequences of predator recovery for subsequent prey distribution and fitness.

4.1. Memory State Influences Prey Response to Predator Recovery

Spatial memory has been shown to shape habitat selection and movements of translocated animals by facilitating location of high-quality sites (Wolf et al., 2009), and inducing long dispersals from release sites in search of areas that are similar to the translocated individual's natal habitat (Stamps and Swaisgood, 2007). Here, we varied prey memory state in terms of their knowledge of alternative foraging locations in order to explore how it might shape anti-predator responses. Overall, we found prey with all memory states to spend more time searching compared to feeding after predator introduction. Notably, however, changes to consumption differed markedly as a function of memory state. Namely, reflecting the advantage of knowing alternate resource locations, informed foragers exhibited modest increases in search time, and correspondingly minimal reductions in consumption rates, after predator introduction relative to most of their naïve counterparts (but not for naïve unexploratory individuals, see below). This finding suggests that foragers with knowledge of habitat beyond the immediate area threatened by introduced predators might be better adapted to cope with the new threat. By extension, in group-living species that depend on

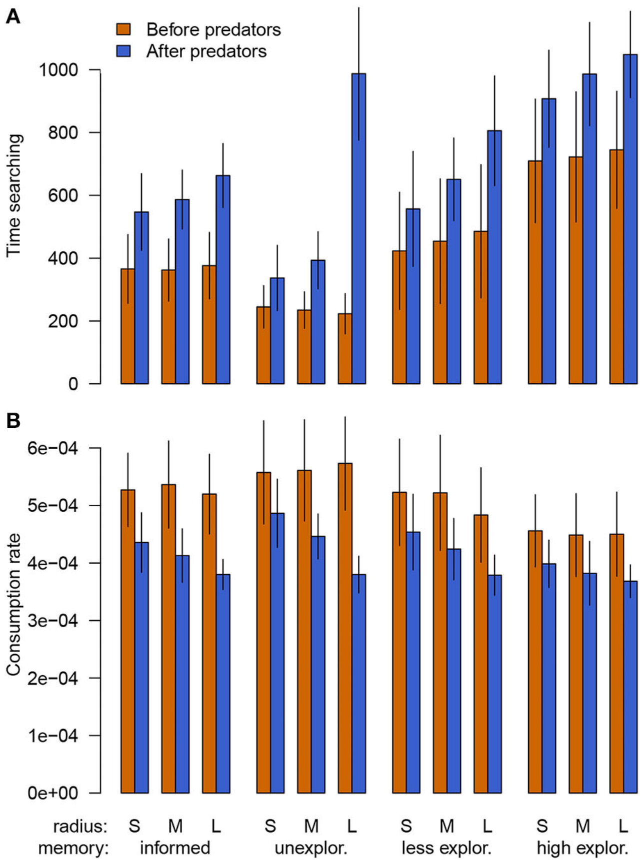

FIGURE 4 | Time budget and consumption rate before and after the introduction of predators across different values for the encounter radius (top line *x*-axis) and for memory state (bottom line *x*-axis) with lines showing the standard deviation. **(A)** Time spent searching as opposed to feeding (a minimal amount of time was spent in the escape behavior, mean 3–17). **(B)** Consumption rate while in the feeding behavior.

decision-making by experienced group members to navigate the landscape (e.g., elephants, McComb et al., 2011), the loss of such individuals could affect the vulnerability of the population to predation danger, human and otherwise, disproportionately. Conversely, it may also indicate that introduced predators in this scenario might struggle to find prey. Thus, in accord with the recommendations of Trainor et al. (2014), predicting the success of predator translocation programs may be aided by a functional knowledge of predator–prey interactions that includes the capacity of the potentially affected prey species to relocate to alternate and predator-free foraging areas. Although differentiating between searching and feeding behavior is more challenging in field situations, this is an active area of research (e.g., using movement patterns extracted from GPS locations or accelerometer data; reviewed in Gurarie et al., 2016), thus permitting measurement of changes in time allocation pre- and post-predator introduction. Accordingly, we may soon be in position to test these hypotheses empirically under field conditions.

4.2. Predator Domain Determines Degree of Impact on Prey

Our results suggest that the spatial extent of predator threat, or, in other words, predator habitat domain, influences the impact of predator risk on forager behavior post-introduction. An animal's habitat domain is the part of the available habitat it uses, with broad-domain species that range throughout much of the available space (and time) differing from those with narrow domains that use only some subset of the available space (and/or time) (Preisser et al., 2007). Applying this paradigm to our modeling approach, increasing encounter radius removed potential refugia in the high-quality habitat for prey analogously to predators switching from a narrow-domain to a broad-domain (or to the difference between a narrow- and broad-domain predator in the same system). Not surprisingly, therefore, predators with large domains induced prey to spend more time searching for refugia away from the introduction quadrant and, as a result, to suffer increased penalties to consumption. Interestingly, when also considering forager memory, our findings align broadly with the "hunting mode–habitat domain" concept (Schmitz et al., 2017; Wirsing et al., 2021). Under this framework, prey with domains that extend beyond those of their predators should rely on avoidance to minimize encounters, whereas those whose domains fall within that of a predator are expected to experience more encounters and utilize defenses that reduce the likelihood of death given an encounter. In our modeling scenarios, informed foragers effectively had more immediate access to a habitat domain that extended beyond that of the reintroduced predator, and consequently experienced relatively few predator encounters. By contrast, naïve foragers were less able to escape the domain of the reintroduced predator, being ignorant of more distant refugia, and thus encountered the repatriated predator more frequently. In particular because of their alignment with theory, our modeling results merit evaluation under laboratory and field conditions. Further, the habitat domain concept may also be extended to consider humans as a potential predator, and thus could fit within the framework of how humans and wildlife coexistence, that is the land sparing–land sharing debate (Fischer et al., 2014). For example, an unexploratory forager combined with a small habitat domain predator could lead to land sharing, while either more exploratoriness or a broad habitat domains results in the forager displacing rather than sharing the land, which would require land sparing.

We can also consider habitat domain in the context of the spatial scale of the predator effect. That is, predators with large domains would be expected to exert a stronger selection on where the forager locates it home range, which we saw with larger forager displacements in response to larger domain predators. Habitat selection and how it gives rise to home range has been considered in terms of a hierarchical process of scales, both in space and time. Thus the factor most limiting fitness would be selected at the largest scale, such as large scale avoidance of predation risk and fine scale selection of seasonally available forage (Rettie and Messier, 2000). However, the processes of habitat selection and home range both emerge from individual movements, in particular how foragers exploit resources through the amount of time spent and the frequency of visits (Van Moorter et al., 2016). As a consequence of this, habitat selection at a given scale is driven not only by the most limiting factor at that scale, but also by which is the most variable (Van Moorter et al., 2016). Indeed, our results show that the scale of predator avoidance (i.e., scale of habitat selection: 2nd vs. 3rd order according to Johnson, 1980) is driven by the scale of variation in predation risk (i.e., predator habitat domain): a large habitat domain leads to home range displacement, whereas a small habitat domain results in smaller shifts in foraging patches.

4.3. Exploratory Tendency Controls Size of Habitat Shift

Individuals can differ consistently along several behavioral axes including activity, aggressiveness, exploration–avoidance, shyness–boldness, and sociability (Réale et al., 2007). These persistent behavioral differences, or behavioral types, within populations can have important ecological implications (Sih et al., 2012), For example, in free-ranging elk (*Cervus canadensis*) introduced to a novel environment, dispersal distance and time varied by individual, with social individuals being more sedentary than solitary conspecifics (Fryxell et al., 2008). Our modeling results reveal that individual differences in exploratory tendency can shape prey movements following predator reintroduction or colonization in ways that influence encounter rates and, by extension, the probability of predator-inflicted mortality (Lima and Dill, 1990). Namely, highly exploratory foragers were minimally affected by degree of predator threat, as they tended to have the most wide-ranging movements and were less likely to remain in the initial release location when the predators were introduced. By contrast, unexploratory foragers tended to remain in the same area despite the introduction of predation risk, leading to higher consumption but also high encounters, a food-safety trade-off also observed in other contexts (Bracis et al., 2018). When predators were confined to a small portion of the landscape, this tendency allowed naïve unexploratory foragers to achieve higher consumption than even informed foragers. However, when predator search radii expanded such that informed and exploratory foragers were pushed out of the high quality and forced to seek new areas, naïve unexploratory foragers performed poorly from a fitness perspective, exhibiting both depressed consumption rates (necessitated by locally searching for refugia) and extremely high encounters. This pattern may help explain why spatial responses are not universally observed after predator reintroductions (Davies et al., 2016). It also highlights the role exploratory tendency appears to play in mediating how naïve prey individuals respond to, and are affected by, restored predator populations as a focus for empirical investigation. Notably, being exploratory may also help prey to regularly refresh their spatial understanding of recent resource changes and thus to optimize space use decisions in the face of predation risk. Here we held resource quality constant, leaving future work to explore the interplay among predator introduction, prey memory and exploratory tendency, and resource dynamics.

4.4. Future Perspectives

Most work on animal movement continues to focus on external factors rather than underlying processes (Joo et al., 2020). By contrast, as memory is likely key to understanding patterns observed in animal foraging (Fagan et al., 2013) and thus an emerging area of research (e.g., Avgar et al., 2013; Bracis et al., 2015; Merkle et al., 2017), we utilize a cognitive paradigm to provide an mechanistic understanding of how animals make movement decisions. Our current work utilizes a flexible modeling framework for exploring how memory can modulate a forager's response to predator introductions, including individual differences in exploratory tendency and habitat knowledge. However, our model utilizes a simple food web comprising the resource, the prey, and the predator. Extending the model to include conspecific interactions or additional predators could provide additional insight, particularly for predator introductions in ecosystems with more complex community structure. For example, multiple predators sharing a habitat domain can reduce the predation risk experienced by the prey, an important consideration for multi-predator systems (Woodcock and Heard, 2011). Other conspecifics may limit where a forager could relocate, particularly for territorial animals (Stamps, 1991; Potts et al., 2012). Here, we examine habitat changes in response to predation, but other antipredator behaviors are possible (e.g., increased vigilance, counter-attack, herd behavior, etc.). Another possible model extension would be to consider different predator hunting modes, such as active hunting vs. ambush/stalking, to examine how this variability affects forager responses. This could include allowing predators to relocate dynamically in response to prey behavior rather than being located solely in response to the prey's resource quality as in the current model. Notably, we differentiated between naïve and informed foragers, but individuals in both of these categories could also differ with respect to the scales at which they mentally map both resources and predation risk. Accordingly, a fruitful avenue for future simulation work in this area would be to explore how foragers' behavior for a given memory state is shaped by the scale of their mental map, before and after predator introduction. Finally, considering dynamic resources (where their intrinsic quality changes) would make it possible to situate this work within the context of environmental change, whether due to habitat loss or climate change.

5. CONCLUSION

In conclusion, our modeling exercise reveals that predator introductions can change habitat usage and consumption rates of foragers to varying degrees that depend on the area threatened by the predator and thus how critical it is to avoid encounters. When foragers do shift habitat use in response to predator introductions, memory state (habitat knowledge) and exploratory inclination (behavioral type) mediate how foragers use alternative habitats and experience changes to consumption rates and predator encounters. Search time increased and consumption decreased after predator introduction across all memory states. For foragers with full knowledge of the landscape, the increase in search time was relatively modest, reflecting the advantage of knowing alternate resource locations. Thus, spatial memory of the surrounding area can mitigate the effect of introduced predators, as foragers can better access alternate habitat refugia. Notably, forager naïveté was costly in terms of the time needed to find refugia, and prey individuals that were both naïve and unexploratory suffered reduced consumption rates and high predator encounter rates. Potential changes in foraging behavior are an important, though often neglected, component of predator reintroductions, given the far-reaching ecological consequences of top-predator losses (Estes et al., 2011). While memory and individual behavioral variation are challenging to consider in experimental studies of reintroduction (Fagan et al., 2013), evidence from modeling here suggests that dynamic interplay among these two factors and key predator traits (habitat domain) is a critical driver of how forager behavior changes.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

CB designed and executed the study. CB and AW interpreted the results and wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.698370/full#supplementary-material

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METHODS
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A Quantitative Framework for Identifying Patterns of Route-Use in Animal Movement Data

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Animal movement along repeatedly used, "habitual" routes could emerge from a variety of cognitive mechanisms, as well as in response to a diverse set of environmental features. Because of the high conservation value of identifying wildlife movement corridors, there has been extensive work focusing on environmental factors that contribute to the emergence of habitual routes between protected habitats. In parallel, significant work has focused on disentangling the cognitive mechanisms underlying animal route use, as such movement patterns are of fundamental interest to the study of decision making and navigation. We reviewed the types of processes that can generate routine patterns of animal movement, suggested a new methodological workflow for classifying one of these patterns—high fidelity path reuse—in animal tracking data, and compared the prevalence of this pattern across four sympatric species of frugivorous mammals in Panama. We found the highest prevalence of route-use in kinkajous, the only nocturnal species in our study, and propose that further development of this method could help to distinguish the processes underlying the presence of specific routes in animal movement data.

Keywords: travel routes, spatial cognition, animal movement, navigation, corridors, unsupervised clustering, routine movement, animal cognition

INTRODUCTION

Technological and analytical innovations in animal tracking and remote sensing have led to increased opportunities in animal movement research (Nathan et al., 2008; Kays et al., 2015). Tracking data are now available at high sampling rates and researchers are using them to understand animal movement decisions (Nathan et al., 2008; Fagan et al., 2013; Kays et al., 2015; Gurarie et al., 2016). One striking feature that emerges in many of these high-resolution datasets is highly consistent, route-like patterns of movement. While the frequency and fidelity of such movement patterns varies, route-use, nonetheless, appears to be taxonomically widespread. Routine movement is of substantial interest due to its relevance to conservation action and because of the insight it provides into animals' cognition (Riotte-Lambert et al., 2016). However, few quantitative methods exist for identifying such patterns of movement.

Routineness, namely, the habitual reuse of the same series of locations over time, can occur as the result of commuting (see Glossary) between a set of target destinations. The more deterministic the ordering of visits to said locations, the more route-like patterns of movement will be (e.g., trap-lining honeybees; Lihoreau et al., 2012; Reynolds et al., 2013). The paths an individual takes during a commute can range from highly variable to highly congruent (see Glossary). In practice, researchers working with animal movement tracks are faced with identifying patterns of spatial behavior, from fully diffusive and exploratory to highly routine, and attempting to infer the processes creating this pattern. Areas where animals exhibit highly routine movement, particularly high path reuse fidelity, are of particular interest, as the habitual use of these areas likely indicate their elevated importance to the animals.

Patterns of high-fidelity path reuse can emerge from a number of environmental and behavioral processes. Routine movements with low directional variability can be observed at specific locations in the landscape simply because an individual was constrained by the geometry of that area. This could be due to completely unsuitable habitat (e.g., a narrow strip of forest through a city) or due to more nuanced relationships between a species and the surrounding habitat. For example, individuals might move through areas based on how their motion capacity (i.e., locomotory biomechanics; Nathan et al., 2008) interfaces with constraints imposed by substrate characteristics following, for example, paths that minimize energy expenditure or predation risk (Adriaensen et al., 2003; McRae et al., 2008; Pullinger and Johnson, 2010; LaPoint et al., 2013; Bastille-Rousseau et al., 2020). Areas where routine movements are generated by external factors are typically referred to as corridors within the conservation literature (Forman, 1995; Rosenberg et al., 1997; LaPoint et al., 2013; Bastille-Rousseau and Wittemyer, 2021).

Routine movement can emerge from the cognitive processes underlying animal search and navigation strategies (Mueller and Fagan, 2008; Bracis, 2014; Bracis et al., 2015; Polansky et al., 2015; Riotte-Lambert and Matthiopoulos, 2019). Highly routine modes of movement behavior can result from an individual's decision to navigate toward a known or perceived target location, and are not necessarily predicted by the physical properties of the environment, but instead by the individual's understanding of the spatial relationships between itself and its targets. When movement processes rely strictly on perceptual information (i.e., oriented mechanisms; Mueller and Fagan, 2008), animals detect some sensory stimulus within their perceptual range and use various forms of taxis (Fraenkel and Gunn, 1961; Braitenberg, 1965) to bias their movement toward that target location (Mueller and Fagan, 2008). Ants and rodents, for example, have been shown to navigate by following chemical trails left by conspecifics as well as by reacting to other olfactory stimuli in their environment (chemotaxis; Kozakiewicz and Kozakiewicz, 2004; Collett, 2010; Svensson et al., 2014; Buehlmann et al., 2015). In dynamic landscapes, where the distribution of resources is variable in time and space, animals that rely purely on taxis will exhibit directed movements with low path reuse fidelity as a consequence of navigating directly toward the stimulus. In static landscapes, however, animals that rely purely on taxis will always respond the same way to a particular point in space and thus will move predictably between resources. The resulting movement will exhibit a high degree of path reuse fidelity and commute determinism, and produce a similar pattern of routine behavior as seen in corridors.

Even if animals cannot sense their target, if they remember where it is, repeated patterns of high-fidelity movement are expected to arise. These "memory mechanisms" are defined as movements where an individual has prior information about the location of its resources (Mueller and Fagan, 2008). Individuals can then use their prior experience to navigate to resources beyond their perceptual range. Unfortunately, this conceptualization does not explain the differences between patterns generated by oriented mechanisms and memory mechanisms, or the variation in patterns generated by different memory systems such as response learning and place learning. In response learning (see Glossary; reviewed in Goodman, 2021), behavioral responses to specific cues (landmarks) are reinforced if they lead to rewards such as food. Under this mechanism, animals may develop habitual sequences of spatial behavior, such as traplines, without needing to model or "map" their environment. Alternatively, with place learning (see Glossary; reviewed in Goodman, 2021), animals may learn the distances and directions between important locations and plan routes between them. Often referred to as a "cognitive map," consistent decision-making with the use of place learning may lead to route-formation, but the use of the memory mechanism by animals remains debated. Clarifying the differences between memory systems greatly facilitates an understanding of how routine movement behavior relates to spatial cognition, but the first step in this process is accurately and reproducibly identifying patterns of routine movement.

Within behavioral ecology, and primatology in particular, areas featuring routine movement behavior are typically referred to as "routes." Influenced largely by early work by Tolman (1948) and O'Keefe and Nadel (1978), these studies point to the repeated use of routes as evidence for egocentric memory systems. Their treatment of "routes," however, presupposes spatial cognition as the underlying process, and the classification of a path segment as a route is typically done by eye or by grouping similar looking path segments together *via* some arbitrary distance threshold (Di Fiore and Suarez, 2007; Valero and Byrne, 2007; Presotto and Izar, 2010; Garber and Porter, 2014; Bebko, 2018; de Guinea et al., 2019). We define routes as areas exhibiting sequential behavior with low directional variability and high-fidelity path reuse. Spatial learning can lead to route-use, but routes can also emerge from non-cognitive processes (**Figure 1**). Furthermore, reliance on expert opinion can lead to challenges fostering generalizable understandings about the process itself, can lead to difficulty comparing across systems, and can hinder reproducibility.

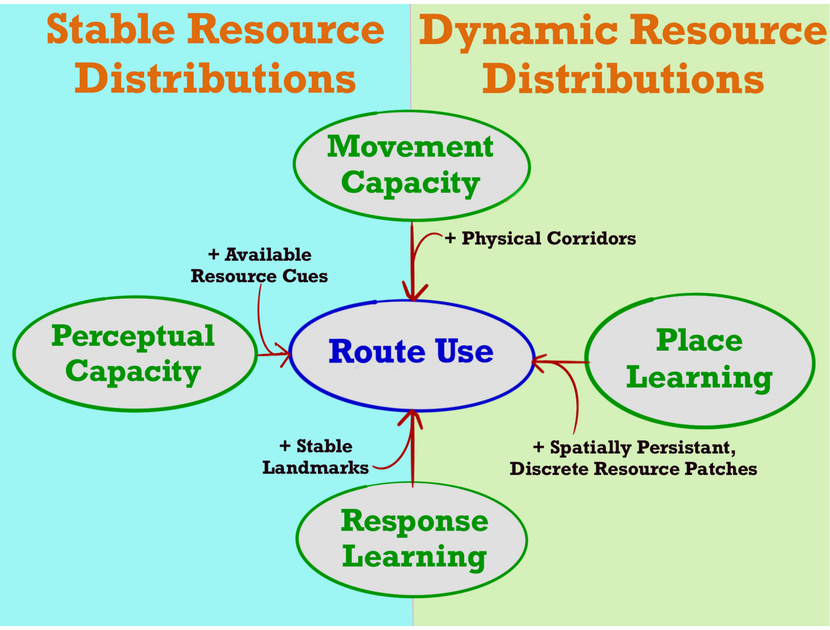

FIGURE 1 | Multiple processes can lead to route use, dependent on the stability of the environment. When a resource gradient is persistent through time, animals that perceive that gradient can form routes by consistently following it (Perceptual Capacity). Similarly, when other permanent perceptual cues indicate the direction of a persistent resource, animals that have learned navigational responses to that cue will generate routes in the cue's presence (Response Learning). In dynamic environments, animals may also develop routes through response learning, albeit more slowly, so long as average resource acquisition is spatially heterogenous. Whether or not resource distributions are stable in an environment, some animals may form routes due to heterogeneity in their ability to use specific substrates, following paths of least resistance (Movement Capacity). Animals capable of place learning, though less likely to follow routes overall, may consistently infer direct paths between known locations, generating route-like patterns even in dynamic environments or the absence of local landmarks.

Clearly, routine patterns of movement can arise from a mix of external and cognitive processes. Determining what explains the emergence of routine behavior in a given part of an animal's range will require developing carefully thought-out analyses. The ability to design any analysis of routes, however, presupposes that the routes established by an animal have been previously identified. Before we can properly design studies that differentiate between route generating processes, we must first develop approaches to accurately and reliably identify patterns of routine movement. Hereby, we introduce a method for quantifying the degree to which movement is routine from animal tracking data, and discuss how the results of this approach can be elaborated on to infer cognition.

QUANTITATIVE APPROACHES

The majority of the quantitative tools for identifying areas with highly routine movement have been developed to examine revisits to target destinations (e.g., Riotte-Lambert et al., 2016; Ayers et al., 2018; Bracis et al., 2018). Examining recursions to target destinations provides valuable insights into the temporal dynamics of resource use and can provide insights into processes such as traplining, however, these methods aren't explicitly designed to examine the trajectories animals used between recursive visits. Methods to detect the actual routes an animal used have largely come from research on conservation corridors. These methods may be suitable for recognizing routine movement when it is generated by external factors, however, they may not be ideal when the pattern is generated by spatial cognition. Dynamic Brownian bridges have been used to reveal shared bird migration corridors (e.g., Buechley et al., 2018). Dynamic Brownian bridges, however, are kernel approaches designed for interpolating missing location information in animal tracks (Bullard, 1999; Calenge, 2006). In some cases, the resulting density may reveal areas that visually resemble routes, however, this approach may miss navigation decisions at very local spatial scales, as well as fail to detect route-like spatial patterns in non-migratory species with limited home ranges. Objective comparison across individuals with non-overlapping ranges, however, is not straight forward, and the actual deterministic use of those areas are not accounted for.

Promising approaches are available that involve (a) sweeping through a track with a circular buffer to identify areas of low directional variability and high speed (LaPoint et al., 2013), or (b) binning movement data into grid cells and performing unsupervised clustering on network centrality metrics calculated for each cell (Bastille-Rousseau et al., 2018; Bastille-Rousseau et al., 2020). There are potential drawbacks to both approaches. First, both approaches implicitly assume independence in the data at the scale at which they segment the movement data. The circular buffer approach allows for variable step lengths and sets the buffer radius size to the step length, while the network approach sets the grid size to the median step length.

Ideally, an alternative approach would ensure that the scale at which movement is autocorrelated would be estimated and the cell/step sizes would be large enough to capture independent displacements (Fleming et al., 2014; Gurarie et al., 2017, Noonan et al., 2019). Second, these approaches both define corridor behavior as fast, repeated movements with very constrained directional variability (LaPoint et al., 2013; Bastille-Rousseau et al., 2018; Bastille-Rousseau et al., 2020). The speed assumptions about corridor behavior are based on the assumption that animals don't forage in corridors (Forman, 1995; Rosenberg et al., 1997), while studies of spatial navigation posit that (a) certain forms of taxis can result in movement that is necessarily slow (e.g., Svensson et al., 2014) and (b) animals will establish routes that increase their likelihood of encountering food and will forage along routes (Di Fiore and Suarez, 2007; de Guinea et al., 2019). We do not dispute this conceptualization of corridor behavior; rather we acknowledge that corridor use may be a particular class of route. We define a corridor as a route that emerges due to external constraints and independent of spatial learning (see Glossary). Studies of spatial cognition may require methods designed to detect routes more generally, in order to facilitate the detection of routine behavior emerging as a function of spatial cognition. In this case, a method that does not assume a relationship between route-use and velocity may be more generally useful. Finally, the approach presented by Bastille-Rousseau et al. (2018) characterizes locations utilized by an animal in terms of their graph theoretic properties, some of which may well capture the persistent and deterministic features of routine route use. They do not, however, attempt to explicitly identify or characterize any locations as routes or areas of highly routine behavior.

Here, we present a workflow using unsupervised-learning to estimate the degree to which locations exhibit routine behavior and differentiate habitual routes from other used locations.

MATERIALS AND METHODS

Frugivore Movement Data

Study Site

Data were collected for a larger study on resource selection and cognition, and were not collected with this paper in mind. Data were collected at the Smithsonian Tropical Research Institute field station on Barro Colorado Island (BCI), a 1,560-ha island of semi-deciduous tropical lowland forest in Lake Gatun, Panama (9° 09′N/79° 51′W). For a full description see Leigh (1999). The island exhibits a distinct dry season from mid-December to mid-April. Fruit availability during the dry season is largely restricted to *Dipteryx oleifera,* resulting in nearly identical resource distribution for the entire community of frugivorous mammals on the island.

GPS Collaring and Study Species

We fit GPS/3-D accelerometer collars (e-Obs Digital Telemetry, Gruenwald, Germany)[1] to individuals from four species, two primates, capuchins (*Cebus capucinus*), spider monkeys (*Ateles geoffroyi*), and two procyonid carnivores, kinkajou (*Potos flavus*) and coati (*Nasua narica*).

Collars were programmed to collect a burst of six consecutive (1 hz) GPS locations every 4 min during the animal's active periods: 06:00–18:00 for capuchins and spider monkeys, 06:00–18:30 for coatis, and 23:00–6:30 for the nocturnal kinkajous. 3D acceleration was recorded at 1-min intervals to determine activity profiles. Collaring occurred in 2015 and in 2017, with 20 individuals tagged the first field season and 26 individuals tagged the second field season. 8 spider monkeys, 7 capuchin monkeys, 16 coatis, and 14 kinkajous were tagged in total. From December 2015 to March 2016, the GPS sampling regime of collars on kinkajous and coatis was ACC-informed, with collars collecting data as described above when accelerometer readings were above a specified threshold (1,000 mV). ACC-informed sampling was not used in the second field season, from December 2017 to March 2018. All collars were programmed to timeout if they did not acquire a fix after 90 s.

One additional kinkajou was collared during a separate field season in 2019, with GPS programmed to sample every 6 min from 18:00 to 23:00 and every second from 23:00 to 5:00.

GPS Data Processing

The last fix of each burst consistently had the best horizontal accuracy measurement, therefore only the last fix of each burst was used for all analyses. All data were uploaded to Movebank, an online repository for animal movement data[2]. Duplicate and outlier fixes were removed using Movebank's data filters, filtering fixes by the height above ellipsoid. All fixes with height above ellipsoid values less than or equal to 21 or greater than 244 were marked as outliers. This corresponds to the first quartile minus twice the interquartile range and the third quartile plus twice the inter quartile range, respectively. Subsequent outlier detection was done using the ctmm package in R (Calabrese et al., 2016), using error information, straight line speeds, and distances from the median latitude and longitude to manually identify outliers *via* the outlie() function. Further, obviously impossible locations, such as location estimates in the water and clearly outside the boundaries of the island, were marked as outliers.

For ACC informed collars, GPS locations were interpolated for times when the animals were below their ACC thresholds. The error on the interpolated positions was modeled to replicate the observed GPS error of a stationary collar in a tree, and was drawn from a negative binomial distribution with a mean of 5. 46 m and a dispersion parameter of 2.4 m.

Simulations

We simulated animal movement tracks to illustrate our predictions regarding the spatial patterns we expect to emerge from each learning mechanism outlined in **Figure 1**. The simulated tracks associated with each prediction are presented in **Figure 2**. The movement of individuals in this model vary along three axes related to our movement pattern predictions: the consistency of the patch selection (choice determinism),

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[1] http://www.e-obs.de

[2] www.movebank.org

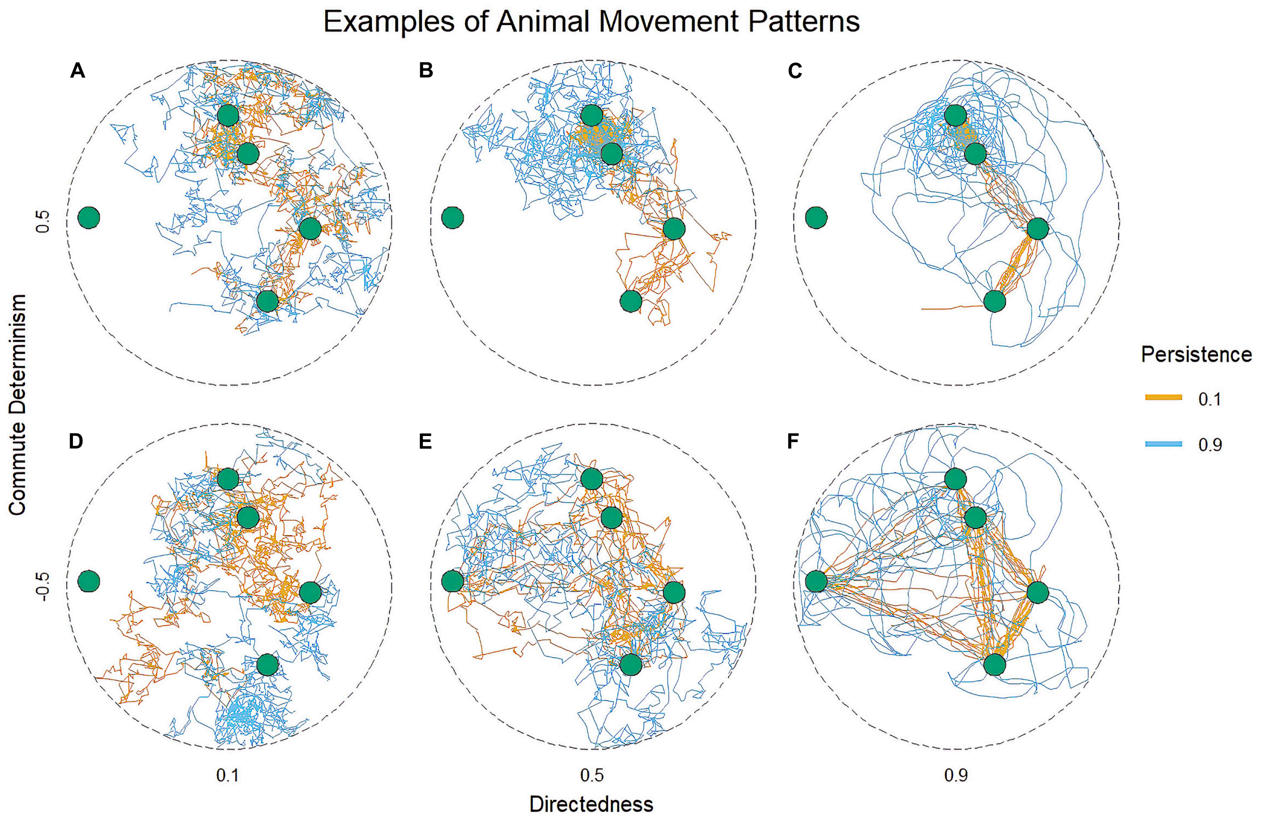

FIGURE 2 | Examples of animal movement patterns. Variation in three movement parameters can produce movement patterns in simulated foraging agents that resemble different degrees and types of route use. All agents foraged by (1) selecting from a set of spatially persistent, renewing resource patches about which the agent had complete information, (2) moving in accordance with the indicated parameter levels until the selected patch was reached, (3) moving at random within the patch while depleting it, and (4) selecting a new patch. Where directedness is low, movement is random regardless of the other parameter levels **(A,D)**. Where commute determinism and persistence are both high, agents produce variable commutes **(C)**, blue path. Where commute determinism is high, but persistence is low, agents produce route-based commutes **(C)**, orange path. Given response learning, animals' movement patterns ought to resemble paths simulated with high determinism and decreasing persistence over time [top panels **(A–C)**, orange paths, left to right]. The paths of place learning animals may develop in a number of ways over time depending on the structure of the environment, including the formation of route-based commutes in highly stable environments (top panels, orange paths), the formation of routes with low commute determinism in environments where patch values are temporally asynchronous [bottom panels **(D–F)**, orange paths], or the formation of variable commutes where secondary resources are dynamically distributed (blue paths, left to right, top, and bottom).

the persistence of their movement direction through time (persistence, a proxy for variable commutes), and the directness of their movement toward a goal (directedness). Details regarding the simulation framework, the parameterization of each agent and the associated environmental constants (including resource density, patch regeneration functions, extraction rate, giving up density, etc.) are provided in **Supplementary Material 1**, along with R code from which our simulations can be reproduced.

Route Detection Framework

Here, we propose a procedure for differentiating route-based movement patterns from other patterns of movement within an animal's range. Our approach is to identify segments of movement tracks that exhibit route-like behavior by calculating a grid cell resolution based on the autocorrelation structure in the data, binning the sampled locations into the grid cells, calculating a series of metrics describing the orientation and determinism of GPS fixes within each cell, and clustering cells with similar modes of movement using unsupervised clustering.

Code for this analyses are available on github: https://git.io/JP1vF.

Path Reconstruction

The first step in the workflow is to reconstruct the original continuous movement path from the sampled four-min GPS track. This serves two functions: to more easily reveal segments with similar modes of behavior, and to maximize the effective sample size of orientations in each cell. To accomplish this, we fit the sampled tracks to continuous time stationary movement models, using the continuous time movement modeling framework (Fleming et al., 2014; Calabrese et al., 2016). The semivariance of the movement tracks are used to estimate the best fit stationary movement process, and model parameters are estimated *via* maximum likelihood. The best fit model is selected using information criterion (AICc and BIC).

TABLE 1 | Variables calculated for each cell.

Statistics calculated for each grid cell			
Intensity of use	**Directionality**	**Neighboring cell similarity**	**Determinism**
Density of points in cell	Hellinger distance	MSD Point density	Recursions
	Number of modes in distribution of orientations	MSD Hellinger distance	
	Distance between modes	MSD Number of modes	
	Range of orientations	MSD distance between modes	Repeats
	Standard deviation of orientations	MSD Range of orientations	
		MSD STDV orientations	
		Number of empty neighbor cells	

All variables intended for use in an unsupervised clustering algorithm. The Hellinger distance is used to determine how different the distribution of cell orientations is from a uniform distribution. Cell similarity is calculated as the mean squared difference (MSD) between a focal cell and its surrounding neighbors. Recursions are calculated as $n(n-1)/2$, where is the number of visits to the cell. Repeats are visits to a given cell that were part of an identical sequence of three or more cell visits.

We then used the best fit model to interpolate between real sampled locations by simulating realistic movement from the movement model, conditional on the data. Possible trajectories between each set of locations are simulated several times, and the average across the simulated trajectories are used as the interpolated segment of tracks. We simulated 10, 20, 30, 40, and 50 tracks between observed locations in order to determine how sensitive the accuracy of the reconstructed tracks are to the number of iterations used to generate them. All model fitting and simulations were implemented using the ctmm package in r (Calabrese et al., 2016).

The limitations of this path reconstruction approach were assessed by subsampling a 1 hz GPS track to increasingly coarse sampling rates, reconstructing the resampled tracks to continuous time using the ctmm package as described above, and calculating the distance between the location estimates from reconstructed track and observed locations from the original 1 hz GPS track.

Binning

The second step in the workflow is to estimate a reasonable grid cell resolution for each individual. Because animal movement data is typically autocorrelated, we attempt to determine a grid size that takes the autocorrelation in the behavior into account. For individuals where the best fit movement model exhibits autocorrelated positions and autocorrelated velocities, the timescale of autocorrelation in the velocity (τ_v) give us information about the timescale at which the fine scale behavior of the animal is independent. In other words, τ_v is the timescale at which the movement remains linear, beyond which the behavior changes (Fleming et al., 2014; Gurarie et al., 2017, Noonan et al., 2019). Animals exhibiting small τ_v tend to have highly tortuous movement, while animals exhibiting large τ_v exhibit highly directed movement (Fleming et al., 2014; Gurarie et al., 2017, Noonan et al., 2019). Given that τ_v is a timescale, we can derive a pseudo-step-length by multiplying τ_v by the average speed and getting a distance. This distance represents the spatial scale at which the movement behavior remains the same on average, thus any changes in orientations happening in locations at least this distance apart are assumed to be independent from each other. Therefore, if the best fit movement model is a model with correlated velocities, then the cell resolution is calculated by multiplying τ_v by the root mean squared speed (a convenient summary statistic obtainable from the movement model). If the best fit movement model is a model with independent changes in velocity, then the grid cell resolution is simply set to the mean step-length. The raster package (Hijmans, 2021) and rgdal package (Bivand et al., 2021) were used to generate the grid after the cell resolution was determined.

Cell Level Metrics

We previously defined routes as locations exhibiting movement with a high degree of path fidelity, specifically high intensity of sequential use and low directional variability. In the context of a spatial grid, this translates to a series of connected cells whereby the overall number of visits to a cell are relatively high, the distribution of orientations within the cell reflect limited and consistent entry and exit points, and the sequence of cells used preceding entry and following exit of a focal cell are also consistent. After data are binned, the following metrics (summarized in **Table 1**) are calculated for each grid-cell: Density of points; Hellinger distance; the number of modes in the distribution of orientations; the standard deviation of headings; the value range of the orientations; the distance between the modes of the orientations; the mean squared difference of all the above metrics to all neighboring cells; the number of empty neighboring cells; the total number of independent visits to each cell, and the number of cell sequence repetitions (reoccurrences within a single path of consecutive visits to three or more cells) that include the given cell. These metrics were chosen because of their simplicity, their concordance with our definition of routes, and because we think they reflect what researchers are perceiving when classification *via* expert opinion is attempted. Relative intensity of use is captured by the density of points in the cell. The consistency and constraints on entry and exit points are captured by how significantly different the distribution of orientations is from uniform (Hellinger distance), number of modes in the distribution (e.g., bimodal distribution indicating a bidirectional route and unimodal inticating a unidirectional route), the distance between the modes (closer to 0 indicating highly unidirectional, closer to π indicating highly bidirectional), and the standard deviation and value range of the orientations in the cell. The similarity to neighbor cells (mean squared difference of a focal cell to its neighbors for each metric) and the number of empty neighbors reflect the contrast in relative intensity of use of a route compared to other locations. Finally, calculating how deterministic the sequential visits to a cell are was achieved

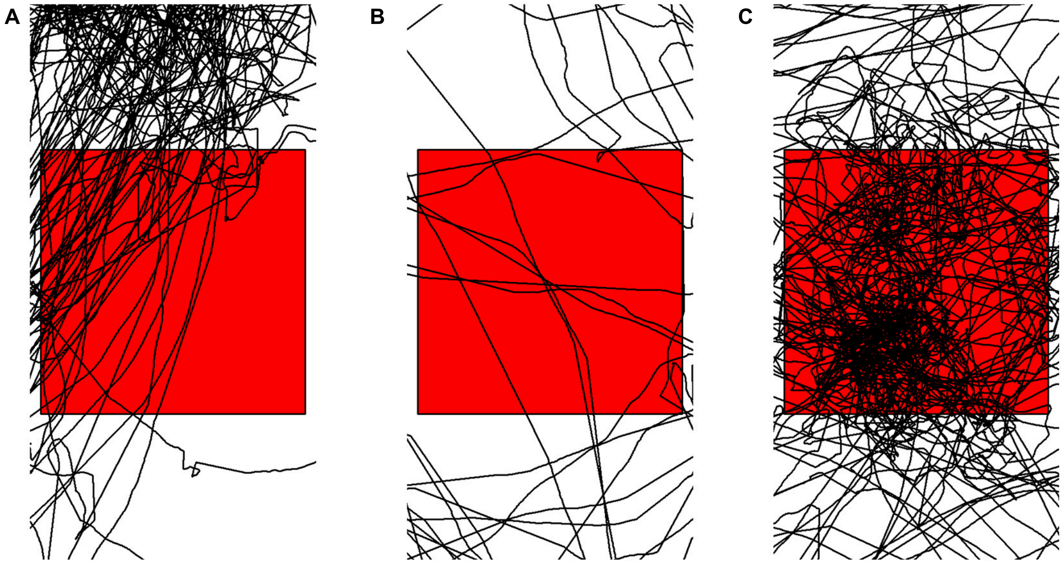

FIGURE 3 | Examples of cell level data showing **(A)** high use, highly deterministic and bi-directional behavior; **(B)** low use, not deterministic and directionally variable behavior; and **(C)** high use, not deterministic and directionally variable behavior.

by adapting methods from Ayers et al. (2018) for identifying traplining behavior, with the assumption that animals utilize routes the same way every time. We quantified the degree to which an animal passed through a given cell while traveling along particular routes by calculating (1) the number of possible comparisons between any two times an individual visited the given cell (recursions, $n(n-1)/2$, where n is the number of visits to the cell) and (2) the number of recursions in which the compared visits to the given cell were part of an identical sequence of three or more cell visits (repeats). Examples of cells with track segments exhibiting different value ranges from the metrics in **Table 1** are visualized in **Figure 3**.

Unsupervised Clustering

We use a Gaussian mixture model to cluster cells with similar movement behavior as estimated from the cell level variables above in order to identify cells with similar degrees of path fidelity and sequential behavior. Model based clustering was preferred over hierarchical and k-means clustering because instead of using a heuristic approach, the clusters are modeled as mixtures of distributions and cluster assignment is handled probabilistically. This enables us to use model selection *via* information criterion to determine how many clusters best fit the data, as well as accounting for variance rather than assume spherical clusters. Gaussian mixture models were fit using the GMM() function in the ClusterR package (Mouselimis, 2021). In an attempt to compare across individuals, all individuals across all species were included in the same model, and BIC was used to determine the optimal number of clusters [Optimal_Clusters_GMM() function in the ClusterR package], resulting in 10 clusters for each animal. The distribution of values of each covariate were compared across clusters to determine which covariates were most distinguishable across cluster categories. The covariates with the clearest separation (density of points per cell, recursions, and repeats) were used to construct a "routineness score" for each cluster. Quartiles for point density, recursions, and repeats were calculated based on the mean values for each cluster category, and cluster categories were associated with their corresponding

TABLE 2 | Error estimates of the path reconstructions.

Path reconstruction error estimates					
Iterations					
10	20	30	40	50	
Mean (STDV) (m)					
4.40 (3.92)	4.30 (3.90)	4.27 (3.91)	4.26 (3.90)	4.25 (3.90)	
Sampling rate (min)					
4	8	16	32	60	120
Mean (STDV) (m)					
4.40 (3.92)	6.72 (5.87)	11.31 (11.16)	19.13 (17.36)	35.25 (35.27)	62.52 (57.24)

Comparison in the mean and standard deviation in the difference from the original track. Iterations refer to the number of simulations included in the averaged track. Sampling rate refers to the sampling rate after down sampling the original track.

TABLE 3 | Mean and standard deviation of grid cell size across species.

Summary of grid cell resolutions		
Species	**Mean (m)**	**STDV (m)**
Ateles geoffroyi	31.03	9.2
Cebus capucinus	25.01	7.73
Nasua narica	32.29	8.82
Potos flavus	30.18	8.25

quartile for each covariate (0.25, 0.5, 0.75, and 1). The routineness score was calculated as

$$\frac{Q_{d_i} \times Q_{rec_i} \times Q_{rep_i}}{\sum_i Q_{d_i} \times Q_{rec_i} \times Q_{rep_i}}$$

Where Q represents the quartile assignment of each cluster based on point density, recursions, and repeats, respectively. This provides a continuous score for each cluster category representing how intensely used a cell is, weighted by how deterministic visits to that cell are and how predictably sequential movements in and out of that cell are. Larger values represent more routine behavior.

We compare the prevalence of routine behavior across our four study species using hierarchical Bayesian regression. Priors were improper flat following $Student - T(3,\ 0,\ 2.5)$, and the model was implemented using the brms package (Bürkner, 2017; Carpenter et al., 2017; Bürkner, 2018).

RESULTS

Continuous time movement models were able to facilitate high fidelity and high-resolution path reconstructions. Increasing the number of simulations did not change the observed error between the reconstructed tracks and the original 1 hz track. Coarsening the sampling rate resulted in substantial increases in error between the reconstructed tracks and original track (**Table 2**). Movement models fit to lower resolution data were not able to recover fine scale movement behavior, and sampling rates of 30 min or more resulted in error estimates well beyond that of standard GPS error from animal tracking collars and handheld GPS units. Sampling intervals under 30 min had error estimates within or below typical stationary error exhibited in the real animal movement data, and at sampling rates under 10 min reconstructed tracks were nearly indistinguishable from the original 1 hz track. **Supplementary Figure 1** shows the increasing distortion in the path reconstructions when models are fit to data resampled to coarse sampling rates, while **Supplementary Figure 2** shows a high-fidelity reconstruction overlaid on the original track.

The unsupervised clustering was able to reveal varying degrees of routine behavior across the four focal species. A summary of grid cell resolutions for each species is provided in **Table 3**. The density of points in a cell, total recursions and total repeats were the variables with the clearest and most consistent separation between clusters (**Figure 4**). **Figure 5** provides example trajectories from a spider monkey, capuchin, coati, and kinkajou plotted against the boundaries of the study area. **Figure 6** shows the outcome of the route detection procedure on those same individuals, with the tracks colored by the estimated "routineness score."

All species show a mix of locations with routine and non-routine behavior as indicated by their routineness scores. The

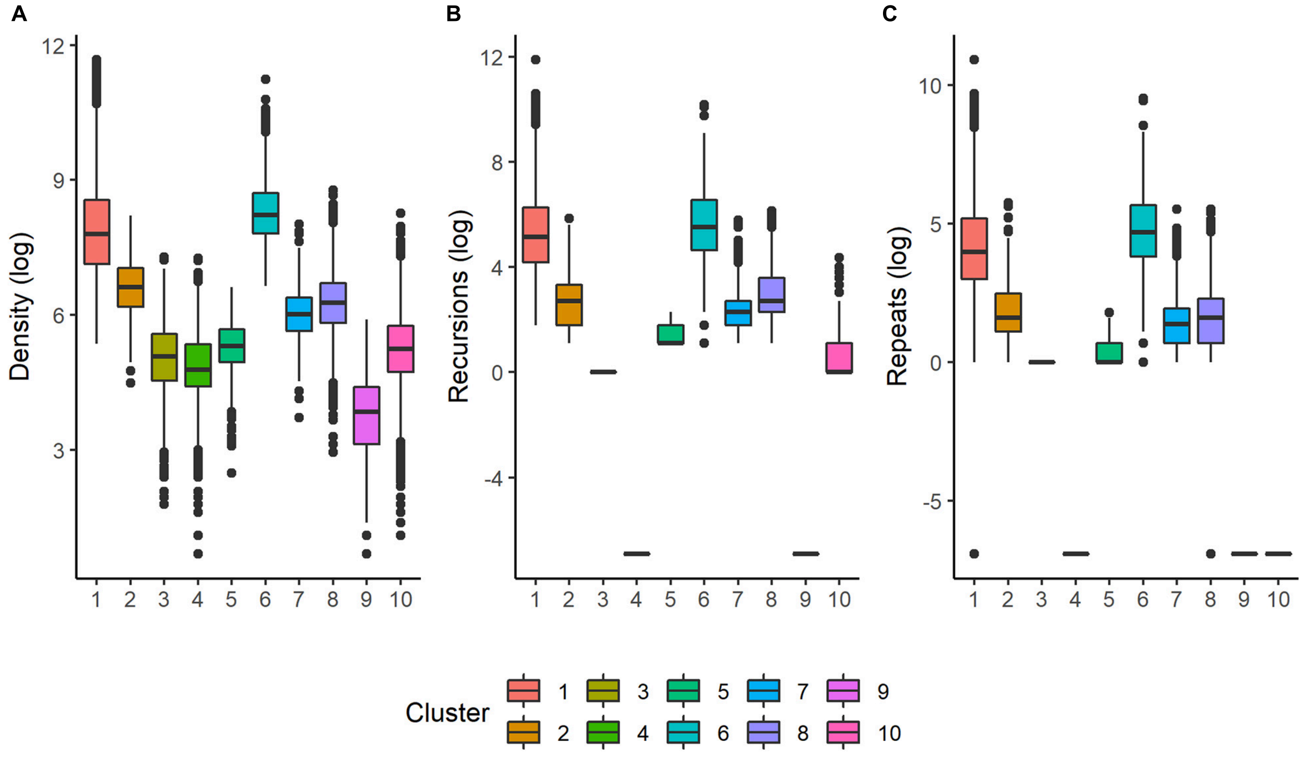

FIGURE 4 | Boxplots of the variables with the clearest separation across clusters. **(A)** The number of fixes in a focal cell; **(B)** The total number of recursions to that cell (see "Methods and Materials" section); **(C)** the total number of repeats (sequential recursions, see "Methods and Materials" section) to that cell.

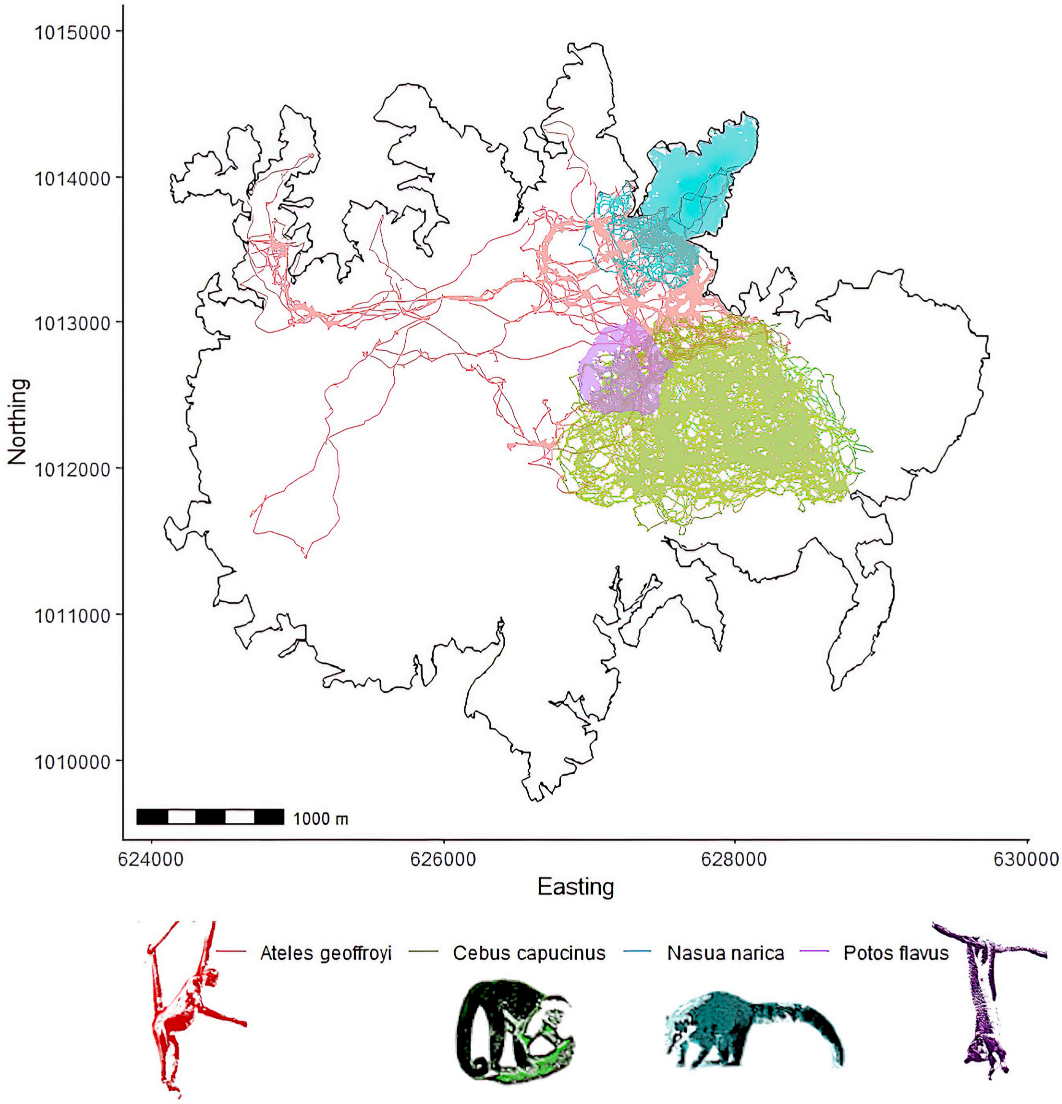

FIGURE 5 | Example trajectories from a spider monkey, a capuchin monkey, a coati, and a kinkajou. All tracks plotted relative to the outline of the island to illustrate any routine behavior due to potential geographical barriers such as the shoreline.

spider monkey and coati both exhibit the highest routineness scores along the shoreline. In the case of the coati, most of the locations with high routineness values might be explained by the fact that the majority of its range falls within a peninsula, strongly suggesting environmental constraints on movement. The spider monkey in comparison does demonstrate some route-like behavior along the shoreline, but also exhibits high routineness scores at locations unconstrained by the geometry of the island. The capuchin and the kinkajou both exhibit evidence of route-use independent of the geometry of the island, with the capuchin range being far from the shoreline, and the kinkajou seeming to predominantly rely on routine behavior to navigate its range. Kinkajous exhibited the highest overall routineness relative to the any other species (hierarchical Bayesian regression, **Figure 7**).

DISCUSSION

The utility of our approach lies in explicitly quantifying the degree to which behavior in a given location is routine, providing researchers a means of differentiating potential habitual travel routes from other locations within an animals' range. Our routineness score provides a simple and interpretable means of characterizing a location as route-like, with higher values indicating habitually high-use, sequential, and directional behavior. Further analyses can be designed to diagnose whether the presence of routine behavior at a given location is explainable by environmental constraints or if there is evidence for a learned navigation route. This could be achieved by testing the relationship between the presence of the physical features in **Figure 1** and the routineness score of a region. For example, the

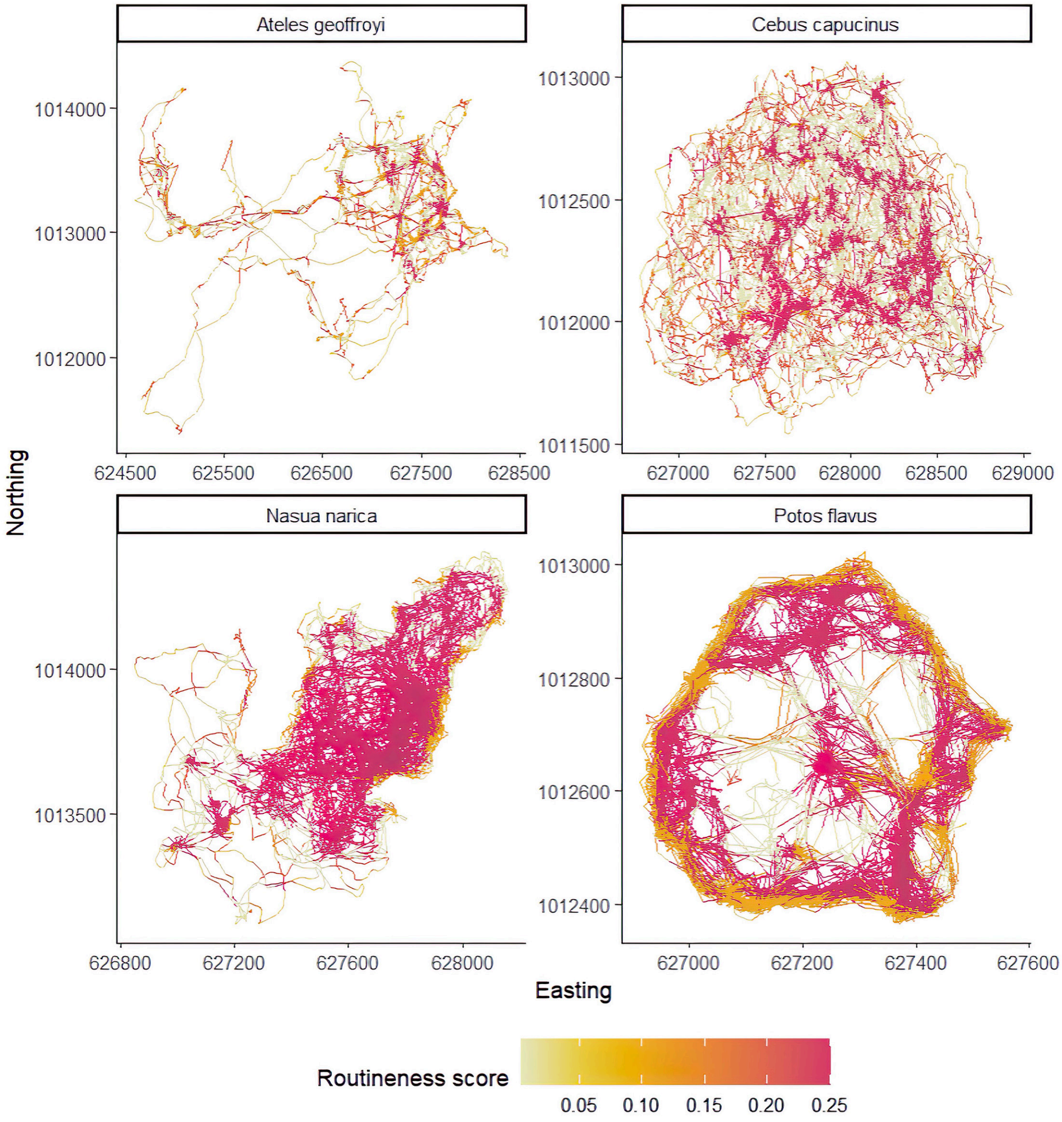

FIGURE 6 | Example results of the route detection procedure. All individuals are the same individuals presented in **Figure 5**, however, the axis scales are unique for each individual to facilitate easier visual comparison. All track segments have been annotated with the "routineness score" of the cells they occupy.

coast of the island in which our data were collected creates a type of physical corridor; areas closer to the coast tend to have higher routineness scores for the coati in **Figure 5**. Researchers interested an animal's perceptual capacity might estimate the distance from important resources at which routineness scores increase, while those interested in response learning might estimate the effect of notable landmarks on nearby routineness scores. Simulations such as those presented in **Figure 2** can be used to create useful references for the routineness scores that might be expected under different conditions.

Interestingly, our results indicate that among our four study-species, kinkajous, which are both nocturnal and arboreal, exhibited the most consistent and pervasive routine behavior throughout their ranges. One factor that may lead to a greater degree of routine behavior in kinkajous is the perceptual limitations of nocturnal activity. Greater reliance on local landmarks, such as the pattern of foliage against the night sky (Chaib et al., 2021), may require kinkajous to remain within narrower regions of space in order to stay oriented. At the same time, kinkajous may have a greater number of locations that they visit frequently and consistently than other species in this study. First, kinkajous typically limit their sleep to a repertoire of 1–3 secure sleep sites (Kays and Gittleman, 2001), while other species in this study are more flexible, perhaps due to the added security of group-living. Second, recent research in another asocial carnivore, the cheetah, has highlighted the importance of communication nodes for the transfer of information between neighboring conspecifics (Melzheimer et al., 2020). Dependence on a limited number of sleep sites and the routine visitation of communication hubs could limit the ability for kinkajous

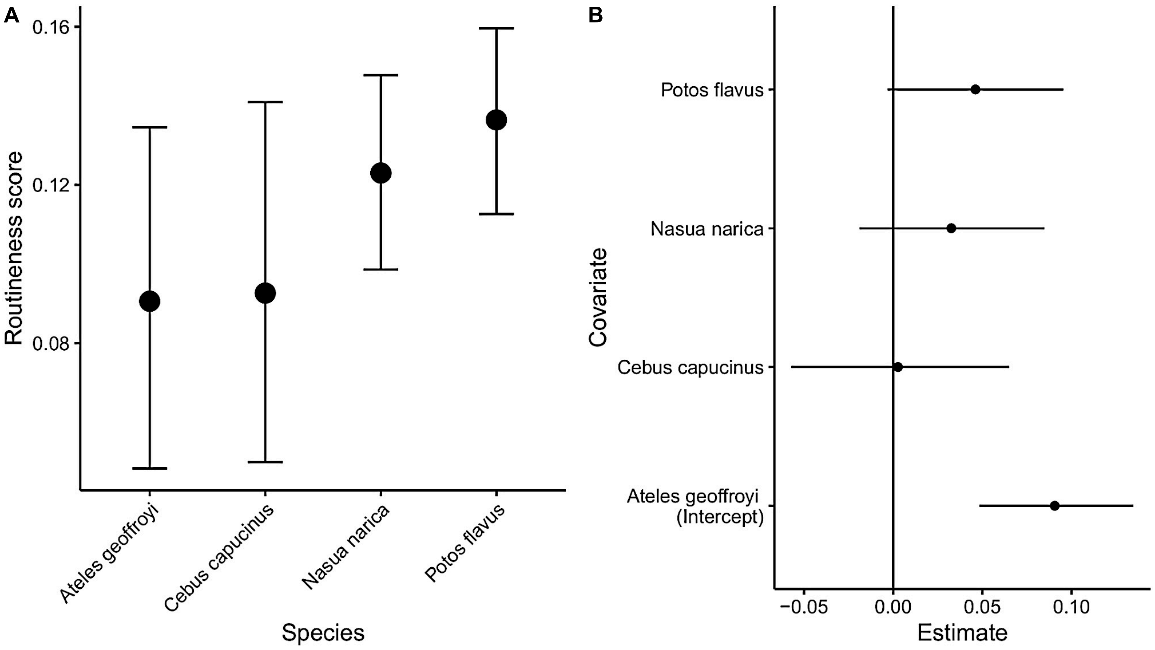

FIGURE 7 | Results of the hierarchical Bayesian regression model. **(A)** The conditional effects of species on routineness scores. **(B)** Posterior intervals of Bayesian beta regression. The dots are posterior means and intervals are 95% uncertainty intervals.

to flexibly adjust their movement strategies with changing distributions of food resources. Understanding downstream effects of nocturnality and asociality on navigation and space-use strategies will be an important goal for future research.

Elaborations on our method for quantifying routine behavior may be useful in further distinguishing the cognitive mechanism that mediate the relationship between an animal's ecology and its space-use. Neuropsychologists describe an animal's mental representation of space as stemming from two parallel memory systems, a relative system where space is experienced in relation to the observer (egocentric), and a geometrically explicit system where the vectorial relationships between locations are independent of the observer (allocentric) (O'Keefe and Nadel, 1978; Nadel, 1992; Nadel and Hardt, 2004). Egocentric systems emerge from the integration of perceptual processing and response learning, such that individuals learn and remember the sequence of responses to some reference cues that lead to successfully acquiring some sought after target (reviewed in Goodman, 2021). Through response learning, for example, animals can use unique cues (landmarks) to behaviorally and neurologically (Knierim and Hamilton, 2011) connect valuable resources separated by spaces greater than the animal's perceptual range. Such learning on its own typically produces highly routine movements in which both the order of resources visited and the paths taken between them remain consistent over time, as in bumblebees (Lihoreau et al., 2012; Reynolds et al., 2013) and hummingbirds (Garrison and Gass, 1999) foraging on spatially persistent, renewing sources of nectar. The high degree of routine behavior in kinkajous may suggest that they rely more heavily on response learning strategies, relying on stimulus response behavior to encounter important resources. This is in contrast to place learning, whereby the animal learns and remembers the position of some object relative to an absolute frame of reference, independent from the animal's own position (reviewed in Goodman, 2021). In this case, and with relevant information about its own position relative to this frame of reference, an animal can navigate toward the resource on future occasions regardless of the individual's starting location, and is not restricted to repeating the exact sequence of movement behaviors it exhibited previously. In **Figure 8**, we identify additional metrics of routine movement paths that could be used to interrogate the cognitive mechanisms underlying specific routes. Supplementing applications of this route-detection workflow with data on perceptual ranges and resource distributions will aid in determining whether areas of high routineness are best explained by taxis, response learning, or place learning (**Figure 8**).

While the method presented here is a promising step toward diagnosing these particular patterns of behavior, it is important to note its limitations. Our approach does not attempt to explain the paths an animal took as a function of the environment, as methods like step and path selection facilitate (e.g., Fortin et al., 2005; Cushman and Lewis, 2010; Zeller et al., 2015). Similarly, this method is not a tool for estimating unobserved locations that an animal may have used (e.g., *via* the Brownian bridge movement model). Rather, our approach incorporates an already available continuous time modeling framework as an integral step in our data processing procedure. Because our approach is built around reconstructing the data to continuous time, the accuracy of the reconstructed movement paths are sensitive to the

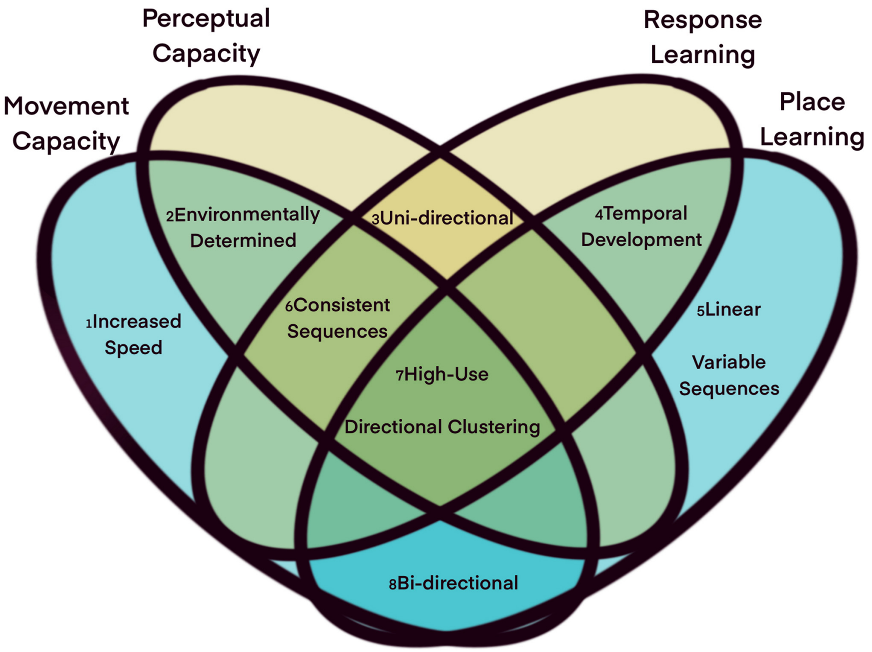

FIGURE 8 | Process dependent route characteristics. Not all routes are the same, and they may have different properties depending on the process from which they arose. (1) When an animal selects a path based on its ability to move, it is less likely to forage in that space and may be able to move faster in that terrain, resulting in in a route characterized by high speed relative to other locations in which the animal moves. (2) When routes emerge from an animal's capacity to perceive or move along local features, those same features should be identifiable *via* human observation or remote sensing. (3) Animals following a perceptual gradient or developing learned responses to landmarks should be consistent in the direction of their responses to those cues. (4) Routes emerging from memory processes should show higher path fidelity over time, as an animal's movement responses are reinforced or their mental map becomes more accurate. (5) Routes that emerge from place learning should be linear and direct, as they represent the animal's ability to consistently select the shortest path between two locations. Additionally, place learning animals may mix and match route segments as they track temporal changes in resource availability. (6) Routes generated by non-place learning processes should exhibit minimal branching, with animals moving from location to location in the same order along each path through the region. (7) All routes, as defined by our framework, should exhibit frequent use with high spatial fidelity and directionality. (8) Routes emerging for their efficiency, either in movement capacity or distance traveled, may contain paths in either direction through the region.

resolution of the data. Our results show that the reconstructions stay reasonably accurate at sampling intervals less than 30 min. At coarser resolutions, the error increases substantially. With high resolution data, this approach does a remarkable job recovering the fine scale tactical decisions made by the animals and has the ability to detect fine scale route use. As sampling rates get more and more coarse, the autocorrelation in the velocity becomes difficult or impossible to estimate, and diffusive models that assume independent velocities must be used (Fleming et al., 2014, Gurarie et al., 2017). Under these circumstances, the grid cell size will equal the mean step length, making this approach analogous to other available approaches. For low resolution datasets, there may not be an advantage to using this approach over the approaches presented by LaPoint et al. (2013) and Bastille-Rousseau et al. (2018).

Areas where animals exhibit routine behavior, particularly route use, indicate the importance of that area to the animals either because they have learned that moving through those locations will lead them to high valued target destinations, or because external factors have constrained their set of usable locations to those areas. We have reviewed the cognitive and non-cognitive mechanisms that can lead to the emergence of routine behavior, particularly route-use, and have suggested one potential way of identifying this pattern of behavior in animal movement data. This conceptual framework and method of classifying routine behavior should provide a helpful step toward the study of these cognitive and non-cognitive mechanisms.

DATA AVAILABILITY STATEMENT

Animal tracking data used in all analyses for this project are hosted on Movebank (Processed data: Movebank ID 1120749252; Unprocessed data: Movebank ID 468460067). Code for all analyses are hosted on github: https://git.io/JP1vF.

ETHICS STATEMENT

The animal study was reviewed and approved by the Smithsonian Tropical Research Institute IACUC protocol numbers 2014-1001-2017, 2017-0912-2020, and 2017-0605-2020, and UC Davis IACUC protocol number 18239.

AUTHOR CONTRIBUTIONS

SA and AV conceptualized the study, developed the glossary, definitions, and developed the figures. SA developed the computational framework and R script for the route-detection procedure and led the writing of the manuscript. AV developed the simulations. RH, LH, MC, BH, DC, and RK collected the data. All authors contributed equally to the text.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.743014/full#supplementary-material

Supplementary Figure 1 | The results of path reconstruction across different sampling rates. Plot **A**. is the original 1 hz GPS data and the basis for comparison against all reconstructions. The 1 hz track was down sampled to emulate data collected at coarser sampling rates. Each down sampled track was fit to its own model and that model was used to reconstruct each down sampled track back to 1 hz. Plots **B-G** are the resulting reconstructions for each sampling rate. The transparency of the track decreases with time to facilitate readability.

Supplementary Figure 2 | Reconstructed 1 hz path against the original 1 hz track. The original unaltered track is plotted in black, and the reconstructed track is plotted in red. The 1 hz track was down sampled to a four min resolution in order to reflect the sampling rate of our GPS data. The mean error is reported in **Table 2**. Majority of the track was within two meters of the original data.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

GLOSSARY

BOX 1 | Glossary of terms used in the paper.

Exploration: A process of movement determined solely by the internal state of an animal. Results in "random" movement, analogous to the use of "local" information or internal states.
Taxis: The combined cognitive processes that allow an animal to perceive and categorize perceptual cues and direct its movement relative to specific cue types. Analogous to the "taxon" system.
Response Learning: The process of mentally associating perceptual cues to physiological outcomes through specific behaviors.
Place Learning: The process of mentally associating one location (or other mental representation) to another by a distance and a direction.
Path: The actual locations an animal occupied over some contiguous period of time.
Track: An animal path that has been subsampled to a time-series of discrete points in space (e.g., by a GPS collar).
Route: A region of space with high path reuse fidelity: relatively high use by one or more animals in which the animals' movement bearings exhibit low variability across paths.
Corridor: An environmental feature that causes route-use in the absence of response learning.
Targeted Destination: A region of space with relatively frequent re-use by one or more animals in which movement vectors have low average velocity and relatively low correlation in bearings.
Commute: A habitual transition between two targeted areas.
Variable Commutes: A set of commutes between two targeted destinations that do not occur along a route.
Route-Based Commutes: A set of commutes between two targeted destinations that occur along one or a few routes.
Commute Determinism: The predictability of an animals next commute given its presence at a specific targeted location.
Trapline: A sequence of targeted locations that frequently occur in the same order due to a series of highly route-based commutes.

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ORIGINAL RESEARCH
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Individual Network Topology of Patch Selection Under Influence of Drifting Site Fidelity

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Network theory has led to important insight into statistical-mechanical aspects of systems showing scaling complexity. I apply this approach to simulate the behavior of animal space use under the influence of memory and site fidelity. Based on the parsimonious Multi-scaled random walk model (MRW) an emergent property of self-reinforcing returns to a subset of historic locations shows how a network of nodes grows into an increased hierarchical depth of site fidelity. While most locations along a movement path may have a low revisit probability, habitat selection is maturing with respect to utilization of the most visited patches, in particular for patches that emerge during the early phase of node development. Using simulations with default MRW properties, which have been shown to produce space use in close statistical compliance with utilization distributions of many species of mammals, I illustrate how a shifting spatio-temporal mosaic of habitat utilization may be described statistically and given behavioral-ecological interpretation. The proposed method is illustrated with a pilot study using black bear *Ursus americanus* telemetry fixes. One specific parameter, the Characteristic Scale of Space Use, is here shown to express strong resilience against shifting site fidelity. This robust result may seem counter-intuitive, but is logical under the premise of the MRW model and its relationship to site fidelity, whether stable or shifting spatially over time. Thus, spatial analysis of the dynamics of a gradually drifting site fidelity using simulated scenarios may indirectly cast light on the dynamics of movement behavior as preferred patches are shifting over time. Both aspects of complex space use, network topology and dynamically drifting dispersion of site fidelity, provide in tandem important descriptors of behavioral ecology with relevance to habitat selection.

Keywords: complex network topology, site fidelity network, multi-scaled random walk, characteristic scale of space use, home range resilience

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INTRODUCTION

Animals' cognitive capacity to utilize a memory map in their quest for optimizing habitat selection continues to be verified empirically from data on vertebrate movement, including amphibians (Pasukonis et al., 2014), ungulates (Gautestad et al., 2013), primates (Boyer et al., 2012) and many other taxonomic groups (for a review, see Piper, 2011). Individual movement may be considered to be a mixture of exploratory moves and some occasional events of return, where the latter generate site fidelity but depend on spatial memory. Some locations will over time become more frequently revisited than others; a property that may be called non-random self-crossing of the individual's movement path. In overall terms the animal's home range becomes an emergent property of the tendency to revisit historic locations. Thus, memory map utilization is a key aspect of cognitive movement ecology.

Memory map utilization invites to study animal space use from two complementary perspectives, topologically and spatio-temporally. This report has thus two main objectives; first, I use simulations involving memory-dependent site fidelity to explore in phenomenological terms the network-topological aspect of the emerging network of nodes (targets for return events). Secondly, I toggle from the topological aspect of networks to the spatio-temporal aspect of space use under this premise. Based on the dispersion of large sets of sampled locations (fixes) of simulated paths using a specific model, the Multi-scaled Random Walk (MRW) algorithm (Gautestad and Mysterud, 2005; Gautestad, 2021), I specifically propose a new method to analyze the effect of instability of local and temporal site fidelity in real space use data and how statistical-behavioral model parameters for the strength of habitat utilization is influenced under these terms. Interestingly, the proposed method does not require explicit knowledge of the physical location and dispersion of active network nodes, which are verified indirectly and in a statistical-physical manner.

Exploring the dual nature of MRW both from the network-topological and the spatio-temporal (Eulerian) angle represents a novel analysis of this model. A will be shown, it opens for alternative methods to study behavioral-ecological aspects of site fidelity and habitat selection within the context of statistical physics of complex phenomena. Since this report provides the first introduction to this approach, the theoretical framework is kept relatively general, and the theory is likewise illustrated by a simple empirical analysis—a pilot test—of real space use data.

Network Topology

In general terms we are surrounded by networks, both real and virtual (Watts and Strogatz, 1998; Barabási and Albert, 1999; Barabási et al., 2003). On the World Wide Web two Websites are connected if there is a URL pointing from one site to another. Statistically, most websites are referred to by a few other sites, while a few sites have a tremendous number or referring sites (Albert et al., 1999). Mathematically the distribution tends to self-organize into power law compliance: k times larger Website popularity is reduced by a factor $1/k^{\gamma}$. The distribution $P(k) \approx k^{-\gamma}$ is scale-free over the range of the part of $P(k)$ where γ is stable, and is said to be complex over this range. Popular sites apparently grow in popularity in a self-reinforcing, positive feedback manner ("rich get richer"). Complex network topology is also found in the distribution of how often scientific papers are referred by others (Redner, 1998). Human mobility is also explored by applying network topological analysis (Song et al., 2010). Other examples regard power grid structure (Watts and Strogatz, 1998; Strogatz, 2001), inter-colleague collaboration among actors (Barabási et al., 1999), metabolic processes (Jeong et al., 2000) and spread of epidemic outbreaks (Barthélemy et al., 2004). In short, networks are at the center of studying and ultimately understanding complex systems in very broad terms. On the other hand, a non-complex ("regular") distribution would be expected to comply with an exponential rather than a power law decline of popularity. In this case γ is not stable over a large range of k, and the frequency of ultralarge-k events becomes negligible in comparison to the power law range, which tends to enlarge the "fat tail" of the distribution. In the context of animal space use, while most locations have a low revisit probability, emergence of extreme patch "popularity," albeit rare, are also expected.

Distinguishing between true scale-free distributions and look-alike power law distributions are challenging (Broido and Clauset, 2019). However, in the present context the main topological property under scrutiny regards the evolution of "hierarchical depth" in the emergence of node weights over time, and how some nodes appear as "super-nodes" due to a positive feedback process, not if a true power law is satisfied in a strict statistical sense.

From a network theoretical perspective locations along a movement path may be said to represent potential nodes. Actual nodes will emerge from memory-dependent returns to a small subset of these historic locations. This kind of individual-centric network topology deviates conceptually and qualitatively from the geometrically explicit dispersion of patches the animal is attracted to and the paths the animal follows to commute between them. For example, the set of the closest patches in the network may be independent of the Euclidean distance between the network node and its neighbor nodes (**Figure 1**). Independence between physical distance and closeness based on historic re-visitation events has been supported empirically in American bison *Bison bison* (Merkle et al., 2014, 2017) and Fowler's toads *Anaxyrus fowleri* (Marchand et al., 2017).[1]

For the present context of cognitive movement ecology I label the scenarios "Site Fidelity Network" (SFN). Analyses of both the SFN topology and the space use pattern in Euclidean terms are performed under two premises; a statistical-physical level of system abstraction, and application of MRW, which embeds both occasional returns to previous locations and a scale-free distribution of exploratory step lengths.[2]

The emerging system of site fidelity from an individual entering an area, the animal's home range, is growing in spatial extent over time due to the mixture of exploratory moves and occasional return events, but much slower in comparison to movement in the absence of site fidelity. From the topological perspective, SFN exemplifies growth of an individual-centric virtual network where new network nodes appear in two variants; (a) nodes that immediately connect to the network and contribute to its growth, and (b) potential nodes. Steps leading to immediate node growth imply that the individual is revisiting a location,

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[1] See, for example Marchand et al. (2017, p. 68):
"The assumption that toads returning to a previous refuge choose one at random may seem unrealistic. Yet it fits the data better than two alternative models we tested, where the probability of return and/or the choice of refuge were distance-dependent."

[2] The present simulations and analyses are performed under the MRW Simulator 2.0, developed by the author (www.gautestad.com).

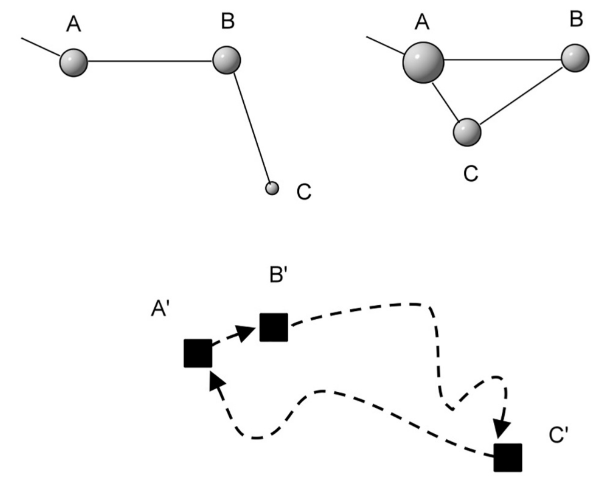

FIGURE 1 | In a virtual network, if the animal revisits a node from another node the topological distance between the two nodes is shortened in an incremental manner for each such revisit between the two. Such return events represent inter-node attachment growth. Short-cuts where for example the individual moves in the node sequence A-B-C-A contributes to increasing the connectivity strength (called the degree, illustrated as bullet size in the illustration) of the revisited nodes. When the animal returns directly to A from C, node A is advancing upwards in the hierarchy of node connectivity strength, which is shown by the new connecting line segment from C to A. This new connection means that A and C also move closer in network topological terms. In contrast, the physical (Euclidean) distance between nodes A, B and C (the "patches" A', B' and C' in the lower part of the illustration) remains the same regardless of node degree and respective topological distances. Along the dotted path only A', B' and C' belong to the network due to previous revisits, while the rest of the path (dotted line) represents potential nodes with still unrealized connectivity to the network of actual nodes.

starting from a location that so far has not been revisited. The latter then becomes part of the evolving network due to the return event. Thus, only return events from locations outside the present network of revisited nodes contribute to network growth, while returns from an existing node to another node contribute to strengthening the relative degree of the target node (**Figure 1**). In this case both the start and the target locations were already part of the network. On the other hand, locations that have been visited only once represent a pool of potential nodes. These locations do not immediately link to the present network of actual nodes, *but are remembered* and may thus connect to the network later on. This aspect of spatio-temporal memory makes it necessary to extend the architecture of classic network topology to the SFN-specific topology, containing both "insiders" and "outsiders."

From the topological perspective, compliance with a scale-free network distribution of node weight (relative popularity of revisited nodes) regards an emergent property from the movement model's definition of return events under a premise of network growth; i.e., system openness. A wider the distribution implies a deeper hierarchical depth of node weights. Further, the topological distance between nodes, as exemplified by the length of the connecting lines A to B, B to C and C to A between nodes in **Figure 1**, is independent of the physical step length distribution *per se* (distances between successive steps between given time increments; exemplified in **Figure 1** by the three distances A' to B', B' to C' and C' to A'). Thus, with respect to the scaling properties of node weights, any movement algorithm involving memory-based return events could be applied, given that the properties are studied from the topological side and not from the Euclidean spatio-temporally side. On the other hand, in Euclidean terms, "scale-free" is a property of the movement process in physical space, as defined by the MRW model's step length algorithm (see below). Similar to the Internet-related example above, a distribution of step lengths obeying $P(k) \approx k^{-\gamma}$ is scale-free over the range of the part of $P(k)$ where γ is stable, and is said to be complex over this range. In step length terms, we study the distribution of binned step lengths. In other words, when log-tranforming the distribution of step lengths one should expect a linear relationship. Thus, two complementary aspects of "scale-free" space use are scrutinized in this report—topological and Euclidean.

How to link an animal's emerging network topology to its spatio-temporal pattern of site fidelity? Distinguishing between true network nodes from memory-based, intentional return events and exploratory moves that just happen to revisit a site by chance (random path crossing) becomes a challenging and probably unsolvable empirical task, in particular, when these nodes are shifting positions in space over time ("drifting site fidelity"). Still, the cognitive process behind targeted returns leads—in overall terms—to a qualitatively different kind of space use process than movement where each return happens by chance; i.e., independent on memory map utilization. In this report I propose and explore an alternative way to resolve this empirical challenge to differentiate between intentional and random returns. I show how simulations involving memory and site fidelity where properties are known from the given model conditions may reveal important statistical aspects of this kind of space use dynamics.

Given the issues just outlined, the aspect of self-reinforcing use of a subset of nodes in network terms needs to be studied indirectly from the spatial distribution of fixes in physical space, including how such pattern of site fidelity may evolve and change over time. This is where the Euclidean properties of the space use model become crucial, complementing the topological aspects of site fidelity as introduced above. In particular, I show how the abovementioned challenge to pinpoint actual return events from non-intentional returns to specific locations selection may be circumvented by analyzing space use in a statistically "coarse-grained" manner; i.e., from the perspective of statistical physics. This approach may thereby reveal topological aspects of site fidelity indirectly, by observing the system's complementary properties of the spatio-temporal movement pattern rather than the network topology directly. However, the applicability of this approach critically depends on the realism of the space use model that is applied.

The Multi-Scaled Random Walk Model

MRW simulates movement to be studied at a coarsened temporal resolution; i.e., at a temporal unit scale which is coarse enough to ensure that successive steps are randomly distributed in directional terms. This satisfies the premise of a statistical-physical observations of the process in a more simplified mathematical context, relative to studying the process at finer ("hybrid") temporal resolutions where deterministic, "tactical" behavior and directional step persistence becomes more influential on the movement path (e.g., correlated random walk). The return steps are memory-dependent and describe site fidelity. What regards the statistical-physical aspect, analysis of individual space use is typically based on fixes that are collected at large time intervals relative to the temporally fine-grained deterministic behavioral response time for successive movement-influencing events within the animal's current field of perception. For example, GPS fixes from vertebrate space use may be collected at intervals of 1–2 h or larger, embedding much intermediate, tactical and unobserved movement behavior. Thus, theoretical simulation and the accompanying analysis of the space use process at this coarsened "strategic" temporal scale is statistical-physical by nature and in compliance with common empirical protocols.

Three main arguments support the choice of MRW as the basic statistical-physical model for memory-implemented space use. First, based on analyses of real data, area demarcation (home range, *A*, using various demarcation methods) has been shown to satisfy the MRW-characteristic power law $A \approx \mathrm{N}^{0.5}$ for all species we have studied so far, for example including free ranging sheep *Ovis aries* (Gautestad and Mysterud, 1993, 2012), black bear *Ursus americanus* (Gautestad et al., 1998) and red deer *Cervus elaphus* (Gautestad et al., 2013). A similar power law compliance was also found in a meta-analysis embedding many vertebrate species (Gautestad and Mysterud, 1995) and recently also in a pilot study on roe deer *Capreolus capreolus*, based on data from Ranc et al. (2020).[3]

Second, by superimposing a virtual grid on the spatial scatter of relocations and counting the number of grid cells containing one or more fixes (incidence, *I*) as a function of grid resolution (a common approach to observe complex space use from a statistical-physical perspective), we have also consistently found a power law relationship, from which we could estimate the fix scatter's fractal dimension, *D*. Typically, we find $D \approx 1$, which indicates that fixes are statistically distributed in a scale-free (self-similar) manner. In other words, fixes tend to show aggregations over a range of spatial resolutions. This range of the fractal dimension describes a strong aggregative tendency due to $D << 1.5$ (Gautestad and Mysterud, 2012; Gautestad et al., 2013), which again is an indicator of positive feedback with respect to local habitat utilization and thus behavioral complexity in statistical-physical terms. Consequently, in our analyses the overall empirical results are MRW-compliant also from this perspective. In other words, some parts of the home range under study were visited more often than others, and this pattern repeated itself statistically in what is called a self-similar ("fractal") manner toward finer resolutions, apparently not mirroring a simple linear proportionality with local habitat attributes like food resources at respective resolutions. In short, since the estimate of *D* covers a set of fixes that is collected from a range of local and temporal conditions, the within-range habitat heterogeneity effect on *D* is effectively "averaged away" from the spatio-temporal pooling of fixes when estimating *D*.

Third, when the successive fix distances from red deer movement were analyzed ("step lengths," *L*, at 2 h time resolution), we found that a power law fitted the distribution F(*L*) better than the negative exponential, where the latter would be expected from a scale-specific and classic random walk-like kind of movement rather than scale-free space use (Gautestad and Mysterud, 2013; Gautestad et al., 2013). Thus, both small and very large displacements were more common than expected from classical movement models, and again in compliance with MRW properties. A pseudo-scale-free variant where the animal is switching between different scale-specific movement modes—making the total distribution look power law-like (composite random walk) was discarded as explanation of these data (Gautestad and Mysterud, 2013). Recently these aspects of complex space use, expansion of space use, A(N), fractal self-similarity of site fidelity, and the frequency of inter-step movement lengths F(*L*), have been verified empirically and explored theoretically also by other researchers (Boyer et al., 2012; Boyer and Romo-Cruz, 2014; Boyer and Solis-Salas, 2014; Evans et al., 2019).

In short, the scale-free property of movement steps follows from the model premise that the animal under MRW conditions is assumed to relate to its environment at many spatio-temporal scales in parallel over a given scale range (Gautestad, 2021). In contrast, the classical use-availability analysis of habitat selection is based on a premise of independent revisits to respective sections of a home range; i.e., a memory-less and area-constrained process in cognitive movement terms (Boyce et al., 2002), and the behavior is consequently assumed to comply with some variant of standard (Brownian motion-like or Lévy walk-like) random walk properties in statistical-physical terms. This paradigm premise is neither compatible with an evolving network of nodes, nor compatible with the MRW model, which is formulated to be compliant with evolving memory map utilization and a scale-free kind of space use at the statistical-physical level.[4] Thus, the present analyses not only explore the feasibility of the MRW model to reveal complex patterns of site fidelity, but also contribute to highlight the fundamentally different system premises on which MRW rests, relative to standard space use models.

To summarize, a theoretical framework to study cognitive movement ecology under condition of spatial memory and scale-free habitat utilization is beginning to emerge, and the MRW seems to be a feasible model platform to study site fidelity in the context of habitat selection (Gautestad, 2015, 2021). The MRW model provides opportunities to indirectly reveal the dynamics of site fidelity under various conditions: both from the network-topological and the Euclidean (spatially explicit) perspective.

In particular, from behavioral-ecological arguments one should expect the return probability to specific sites to decline

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[3] See Author's blog post "Roe Deer Comply With the MRW Model," dated August 11, 2020, at www.animalspaceuse.net.

[4] For details on the MRW model, visit www.animalspaceuse.net.

as a function of increased uncertainty of site profitability or increased risk in connection with return to historic locations; e.g., due to increased environmental variability and unpredictability, or due to a predator's local search map being influenced by learning the prey's habits. On the other hand, site familiarity provides crucial benefits with respect to utilizing a memory map (Piper, 2011). These aspects will be scrutinized by the present simulations by varying the temporal stability of existing memory-based targets for an individual's return events. A sub-set of previously published telemetry data on 15 black bear females (Gautestad et al., 1998) is also explored with respect to the present method to reveal degree of (in) stability of site fidelity.

MATERIALS AND METHODS

Network Topology Under Site Fidelity

Network Terms

Within the area traversed by an animal, some locations may over time be re-utilized in a self-reinforcing manner at the expense of proportional use of other patches of *a priori* similar qualities—owing to the process of occasional but directed returns to known localities (Gautestad and Mysterud, 2010b). This very general property of vertebrate movement may be simplified into parsimonious model algorithms to simulate memory-enhanced space use.

In general terms; i.e., whether MRW or another kind of statistical-physical algorithm is applied to simulate memory-involving animal space use, the model defines a return step protocol. For example, on average every μth time increment ($\mu >> 1$) in the simulated series the given step is followed by a directed return to a randomly and uniformly distributed chosen previous location in the series (called "neutral connectivity"). Alternatively, the protocol could define "preferential connectivity," where visited locations gain increased probability for additional revisits. Anyway, the probability for a revisit to a given site under the chosen connectivity scheme on average declines geometrically over time, due to an incrementally larger pool of potential return targets as the total path expands. A large μ indicates that returns happen at a low frequency relative to exploratory steps, but from a topological perspective μ does not influence the distributional form of the actual node weights, only the relative magnitude of potential nodes in comparison to the smaller but evolving set of actual nodes (network growth). The reason is that the size of the network grows as a function of actual nodes. Thus, the speed of this growth depends on the frequency of returns, $1/\mu$; i.e., smaller μ implies relatively stronger growth, but the distribution of node weights (its power exponent) does not.

The network topology of actual, inter-connected nodes—based on the set of return target locations—were studied by analyzing the so-called degree distribution and the accompanying weight of nodes (popularity): frequency of nodes as a function of connectedness (number of returns to a given location), which also increases some nodes' weight on expense of less visited nodes. Gephi version 0.7 alpha2 and version 0.9.2 (Bastian et al., 2009) were used in these analyses.

In practice, series of simulated return targets and the respective locations from which the individual initiated a given return event were successively separated from the developing path series into a two-column spreadsheet, which was then imported to Gephi for analysis. In order to reveal the degree of power law compliance, the degree distribution of node weight was subject to geometrical binning. Further, the spatial locations of the most "popular" nodes were superimposed on a dispersion of a set of fixes, in order to illustrate—in phenomenological terms—the juxtaposition of these locations with relatively high return frequency relative to the over-all spatial pattern of fixes.

Only the first 10^4 return targets in each series of 10^5 or 10^6 MRW steps using returns at every $\mu = 10$ time steps on average were analyzed for scaling properties, due to their strongest network maturity; in the initial part of the step series had the longest history of return events and consequently providing the highest analytical potential to distinguish a scale-free or approximately scale-free; i.e., an approximately log-log linear degree distribution, from scale-specific network topology (semi-log linear). The latter parts of the series consisted mainly of potential nodes (not yet part of the set of actual nodes due to lack of becoming return targets). By comparing the network graph of the first 10^4 return targets from a 10^5-step series with the graph from the first 10^4 return targets from a 10 times larger series one gets a qualitative impression of how the "hierarchical depth" of the graph is progressing as the SFN evolves over time.

Balancing Exploration and Site Fidelity in Euclidean Space

Above I have already given the three main arguments for choosing MRW as the basic model when flipping from network topology to the Euclidean properties of memory-influenced space use. Under the premise of the MRW framework, space use emerges from a combination of exploratory moves and occasional returns within a defined time resolution and spatial extent. What regards simulation of exploratory steps of space use, MRW series of length 2^*10^7 steps, representing successive path locations at the defined unit time interval *t*, were simulated in a homogeneous environment as a set of successively independent step vectors of length:

$$L_{MRW} = \alpha(RND)^{-1/(\beta-1)} \mid L_{MRW} < L_{max} \qquad (1)$$

with $\alpha = 1$ and $\beta = 2$. RND is a random number between 0 and 1. Hence, median step length is $0.5^{-1} = 2$ length units. The maximum step length, $L_{\max}$, is by default set very large, meaning that this cut-off of step length does not influence the present results. Eq. 1 (without the added property of memory inclusion; see below) is a common formulation of so-called Lévy flight, representing a true Lévy walk that is simulated at a coarsened (statistical-physical) temporal scale, defined by *a*. A constant α at the unit temporal simulation scale implies a given average step length for the simulations; i.e., movement speed is for simplicity assumed constant on average over space and time during the given time resolution and extent.

From a network perspective, steps from Eq. 1 represent potential nodes and extending this basic algorithm with return steps implements the memory process. This MRW models give birth to a new actual node (targeting a previously never revisited location of the historic path) or contributes to increasing the popularity of an already existing node. Since the first part of the present analyses is targeting the properties of the network topology of popular nodes that emerge for memory-influenced space use, other aspects of habitat interactions (for example, relations to specific habitat elements in a heterogeneous environment, including difference in local movement speed as reflected by differences in the parameter a or difference in the return frequency $1/\mu$ during respective time periods) are for simplicity not specified. This simplification is chosen for the sake of remaining focused on the duality between complexity of node connectivity in topological terms and site fidelity in explicit spatial terms. Running the simulations with millions of steps at statistical-physical resolution is an unrealistically large sample size to represent real individuals. However, this magnitude is chosen to allow for a proper study of theoretical aspects of the system's network topology and the complementary spatio-temporal properties of MRW.

Under the implicit premise of a statistical-physical system simulation even at unit time scale $t = 1$, successive inter-step directions of the exploratory steps (Eq. 1) are drawn uniformly from 0 to 2π radians. Before considering the complication from return steps, large series of steps L_{MRW} represents scale-free distribution of moves ("exploratory steps"), sampled at constant intervals of length t, thus complies with sampling a Lévy walk (Shlesinger et al., 1993; Reynolds and Rhodes, 2009); thus, *de facto* becoming a series of steps called a Lévy flight.

The log-formatted bin width of the distribution of step lengths from Eq. 1 is set somewhat larger than the median step length in the sample at time resolution t, to study the functional form of the long-tail part of the step distribution at the chosen temporal sampling scale. For example, if median step length is found to be L_{med}, unit bin width is by default set to be 50% larger.

However, MRW deviates from Lévy walk/flight by adding the effect from spatial memory and site fidelity. This property makes the process potentially scale-free also in the time domain, and not only in the spatial domain. On average every μth time increment in the simulated series the step was followed by a directed return to a randomly and uniformly distributed chosen previous location in the series (neutral connectivity; i.e., the default condition of MRW), or by preferential connectivity, where visited locations gain increased probability for additional revisits. The magnitude of μt (where μ is an integer larger than one) defines the general strength of this "homing" tendency; larger μ implies weaker site fidelity due to longer return intervals on average. Ecologically, a larger μ may for example imply space use under less favorable conditions than where μ is small. In the present simulations with respect to network analysis I used $10 < = \mu < = 100$ under the condition of neutral connectivity (all historic locations relative to a given instant has equal probability for a revisit). For Medium preferential connectivity I used an added condition that returns either takes place with 50% probability to a randomly chosen target among existing network nodes; i.e., a location that has already been visited before, and 50% probability for returning to a randomly picked target regardless of status. This implies a "preference" to return to already revisited locations relative to neutral connectivity. For Strong preferential connectivity I used 90% probability to return to an existing, actual node and 10% to a randomly picked location (using 100% return to actual nodes would terminate network growth). Thus, the choice of 50 and 90% strength of preference represents two levels of skewedness on the continuum from 0% (neutral connectivity) toward—but not including—100%). With respect to spatio-temporally varying site fidelity (next section), I used $\mu = 100$ for all conditions of connectivity strength.

Further Coarse-Graining of the Process: Fix Sampling and Analyses

Each series was sampled as one "observed fix" (t_{obs}) pr. 1000t; i.e., a coarser time resolution than the average return interval at the scale of steps at unit time resolution, t ($t_{\mathrm{ret}} = \mu t = 100t$) in the simulations of varying site fidelity. Hence, intrinsic serial auto-correlation was effectively eliminated at the temporal scale of $t_{\mathrm{obs}} >> t_{\mathrm{ret}}$.

Sets of fixes from each series were in the present context collected at temporal scale $t_{\mathrm{obs}} = 1000t$. Thus, analyses of movement in physical space represents a small subset of the original path; in contrast to the introductory study of network topology (above), which were analyzed at unit scale $t = 1$.

Incidence, I, which represents the number of virtually superimposed grid cells embedding at least one fix, is applied to quantify spatial use in an Eulerian (spatially explicit) manner. While traditional estimates of home range area A(N) where A is given by an area-demarcating method, have many complicating challenges, the I approach allows for a coherent fractal-geometrical analysis of the spatial fix pattern. The sample size dependence of incidence as a function of sample size of fixes, I(N), at a properly chosen resolution of grid cells called the Characteristic Scale of Space Use (CSSU)[5](Gautestad, 2021), can under MRW be expressed by the power law (Gautestad and Mysterud, 2005, 2006, 2010a):

$$I(N) = cN^z \tag{2}$$

where c and z are parameters. The intensity of habitat utilization is expressed through the combination of c and z; c regards CSSU, and is—under a given average step length of exploratory steps—a function of the frequency of returns, $1/\mu t$, to previous locations (space use intensity). CSSU is thus expressing the behavioral balance between space use expansion (exploratory steps; Eq. 1) and contraction (site fidelity from returns at frequency $1/\mu$). The parameter z expresses how intensity of space use is distributed across scales. Stability of z implies a scale-free kind of relationship to the habitat over a range of spatial resolutions of the environment. A value of $z \approx 0.5$ [I(N) increasing proportionally with square root of N] implies by a MRW postulate that the animal is "relating" to its environment over a range of scales with the same space use intensity; i.e., a next-step movement to a neighborhood at a k^2 times coarser scale is $1/k^2$ times less probable (Gautestad and Mysterud, 2005).

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[5] See, for example, http://www.animalspaceuse.net/2017/12/statistical-mechanical-details-on-space.html

Theoretical expectancy is $z \approx 0.5$ for the idealized MRW (Gautestad and Mysterud, 2010a), with some variability expected from so-called space-fill and dilution effects from choosing too coarse or fine grid resolutions, respectively (Gautestad and Mysterud, 2012). In other words, the analysis should be performed after having "zoomed" grid resolution to a magnitude close to CSSU. Zooming to estimate *c* is necessary due to the process' combined expression of exploratory steps (influenced by *a* and β in Eq. 1) and return step effects. Too coarse or too fine grid resolution relative to the intrinsic CSSU scale will both lead to observed instability of *c* and *z* over the range of N (see a practical example in **Supplementary Material**).

The sample size of fixes, N, can be drawn incrementally from the total series in two ways; either by adding new fixes in a time-incremental manner (continuous sampling; a sample size that is proportional with sampling time) or by increasing sampling frequency within the total time period for the simulation (including every nth fix within the total time period, by increasing n until $n = N$). In the present analysis I—crucially—applied both protocols, and additionally calculated the geometric average of *I*(N) for each magnitude of N from these alternative sampling schemes.

In this manner, by averaging *I*(N) over continuous and frequency sampling and studying the difference between the non-averaged *I*(N) series from the two protocols, one may compare the statistical effects from *intrinsic* auto-correlation in the data ($t_{obs} <= t_{ret}$) with the statistics of the non-averaged *I*(N) series. The differences will be of key interest to the present topic of quantifying the effect of *extrinsically* induced autocorrelation even when $t_{obs} >> t_{ret}$, due to an environmentally imposed shifting mosaic of site fidelity.

In addition to the CSSU concept and its relationship with Eq. 2, memory effects under MRW terms impose yet another aspect of space use intensity; the property of self-similar (fractal) dispersion of fixes. In other words, a sample of fixes from the underlying process combination of Eq. 1 in combination of targeted return steps will tend to be spatially distributed as aggregations over a range of resolutions of the superimposed grid (in contrast, Eq. 2 is expressing the N-dependence of incidence at given grid resolution; the balance scale of CSSU). For non-auto-correlated fix samples we have shown theoretically and verified by simulations (Gautestad and Mysterud, 2010a) that,

$$z = 1 - D/2 \qquad | 1 < D < 2, N > N_{min} \tag{3}$$

where D is the fractal dimension of the spatial distribution of fixes. N_{min} approximates a small-sample artifact of N. D can thus be calculated from D = 2(1-*z*), as an alternative approach to zooming over a range of grid resolutions (see section "Introduction").

Combining Eq. 2 and Eq. 3 gives,

$$I(N) = cN^{1-D/2} \,|\, N > N_{min}, I \equiv incidence \tag{4}$$

In particular, $D \approx 2$ implies *I*(N) is constant beyond N_{min}. This satisfies the paradigmic "home range size" concept, where the size is assumed to expand asymptotically toward the range's size as N is passing N_{min} from below. On the other hand, $D \approx 1$ implies *I*(N) is increasing proportionally with $N^{1/2}$ far beyond N_{min}. In practice, N_{min} is very small under $D \approx 1$ relative to $D \approx 2$ dispersions, since the latter is more "dense" in statistical-fractal terms and thus require a larger set of fixes to minimize the small-sample artifact of *I*(N).

In the present context, *c* is the most important ecological aspect of the model. Representing CSSU, it reflects the characteristic scale of space use intensity on average within the respective spatial and temporal scale extents:

$$c = I(N)/N^{1-D/2} = I(N)/N^z \tag{5}$$

Under condition of $z \approx 0.5$, a larger *c* implies a more coarse-grained CSSU on average in the spatio-temporal range that is embedded by the data.

Non-stationary Site Fidelity

In the present simulations the parameter values for *a* and β in Eq. 1 (exploratory steps) and the return frequency to historic locations (relative strength of site fidelity, 1/μ) are kept constant. However, as indicated above, extrinsically imposed serial auto-correlation of fixes may influence the observed statistical properties of space use. Thus, in this report I study to what extent the resilience of key statistics under the given model parameters under default (stationary) conditions are influenced by a shifting mosaic of site fidelity.

To simulate a varying environment with respect to influencing stability of site fidelity and—in particular—whether this environmental heterogeneity is influencing *c* and *z* (or conversely, how resilient these parameters are under increased environmental complexity), three conditions are explored by varying strength of so-called "punctuated site affinity." At regular intervals (the punctuations) the model individual is narrowing its time horizon for memory-influenced movement by disregarding utilization of the older parts of its historic path during return events. At these intervals the movement path is thus simplistically split into "sections." Older parts of potential nodes are not any longer included in the process of return decisions. However, it continues to return to a given percentage of the latest part of the foregoing section in addition to all the new locations in the current section. By varying the length of the sections and the length of the retained part of the foregoing section, a variable strength of spatially shifting site fidelity may be simulated (Gautestad and Mysterud, 2006).

Under the first condition, **A**, the animal is keeping the last 10% of the path locations in foregoing section of the path, each of length 1/10 of the total series length of magnitude 10^7 steps, as potential return targets on equal footing with the successively emerging locations in the current section. The simulations are run under condition of neutral connectivity of return events.

Under the second condition, **B**, 50 rather than 10 time sections for partially punctuated site affinity is invoked, and 2% rather than 10% of the previous section's path of locations is retained (section length $2*10^5$ steps, and last $4*10^3$ steps of foregoing section retained). This condition implicitly reflects a situation where site fidelity is drifting more smoothly but also more strongly in overall terms than in the foregoing scenario, due to a smaller subset of previous locations to select among as return targets and a more frequent resetting of potential return targets. The simulations are run under condition of neutral connectivity of return events.

Under the third condition, **C**, drifting site fidelity is similar to **A**, but with no memory of previous sections. Number of sections is increased from 10 to 20, but no historic parts of the path of 1/20 of total length is retained during this fully expressed "punctuated shift" of site fidelity. The first location in each of the 20 successive sections is chosen randomly within the total arena. This scenario reflects the most dramatic shift of site fidelity. Again, the simulations are run under condition of neutral connectivity of return events.

From each series of locations in the three variants of shifting site fidelity, each variant replicated 10 times, fixes are sampled at frequency 1:1,000 of respective series. Within each sequence of stationary site affinity; i.e., in the respective sections between the successive punctuation events during which the conditions for site fidelity were temporally stable, this situation implies serially non-autocorrelated steps (Swihart and Slade, 1985). However, this condition is expected to change to serial autocorrelation as the data set embeds several re-settings of site fidelity (fixes covering several sections) and thus a spatially drifting space use. Thus, auto-correlation may emerge under the respective conditions of temporally non-stationary space use, because of two random locations within a section may tend to be closer in space than two locations from different sections in the total set of fixes. In short, auto-correlation is expected to occur even under the condition where $t_{ret} = \mu t = 100t$ is set to be smaller than the fix sampling interval $t_{obs} = 1000t$, because of the temporally shifting pattern of site fidelity (extrinsic forcing).

A resolution of the virtual grid that is superimposed for the analysis of $I(N)$ is fixed for all simulations ($k = 1/40$, linearly, of total arena scale of $k = 100{,}000$). This resolution approximates the CSSU scale under the given model conditions prior to adding the complexity from drifting site fidelity. In other words, $\log(c)$ approximates zero after normalization to linear grid resolution of $k = 100{,}000/40 = 2{,}500$ units.

All conditions **A**, **B** and **C** above were simulated under neutral connectivity. In order to explore the effect of preferential connectivity in isolation from drifting site fidelity, $I(N)$ for strong preferential connectivity is also analyzed as **condition D**; i.e., under standard MRW terms for return events (site fidelity not influenced over time by external forcing).

Pilot Testing on Telemetry Series

With respect to illustrating the new method on empirical data, a sub-set of previously published telemetry material on female black bear is presented with respect to $I(N)$, including the stability and distribution of c and z from Eq. 2. According to the MRW framework, z should be independent of both c and N after respective series are zoomed toward best-fit scale for CSSU estimation. The data is reflecting standard radio telemetry procedures and equipment from the 1970s, reflecting both relatively large triangulation errors and subsequent rounding of fix coordinates to nearest 100 meters. Fixes were collected at intervals of one or more days. For details of the telemetry material, see Gautestad et al. (1998).

RESULTS

Network Topology

The MRW simulations with respect to network topology of nodes and neutral connectivity illustrate compliance with a gradually emerging hierarchical depth of these nodes. Some of the initially appearing nodes gain further revisits, in a positive feedback-resembling growth process (**Figure 2A**). Over time, an understory of additional hierarchical layers of nodes with less revisit frequency appears, while most nodes are visited only once (**Figure 2B**). The first 10^3 links were generated from 10^4 to10^5 return events to previous locations along the animal's path (total series length 10^5 and 10^6 respectively, due to $t_{ret} = 10t$). Under neutral connectivity, in the early stage of space use (**Figure 2A**) most nodes have only one link, and the number of hierarchical levels is limited to four. By increasing the series length 10-fold (**Figure 2B**) the structure of links (the degree) to the initial 10^3 nodes has become more complex with six levels, and thus reflecting a more mature network with respect to its hierarchical property. The temporal drifting toward a scale-free topology is indicated by the rarity of nodes with a large degree relative to the large population of low-degree nodes. Whether this is actually scale-free or not depends of compliance with a power law in the distribution of connectivity strength (see below). However, this example illustrates that even neutral connectivity leads to re-use of sites in a self-reinforcing manner due to the site's added statistical weight with respect to the probability of becoming target for new visits.

Before leaving the topological aspects, **Figure 3A** exemplifies a MRW simulation under stationary site fidelity and neutral connectivity, and how the network of nodes is dispersed in space. The actual spatial locations of the five dominating nodes—super-nodes—are marked by colored squares. Hierarchical node dominance is not clearly correlated with local density of fixes (local "core areas" of more intense use, called the utilization distribution in home range theory). This apparent independence between node degree (connectivity strength) and strength of the utilization distribution in Euclidean space is illustrated by the locations of the two peripheral nodes in relatively low-density regions of the scatter of fixes, which reflects not only the actual nodes but also the dispersion of potential nodes. This result may seem counter-intuitive from standard home range premises, but is in fact expected from the simulation's condition of MRW's independency between a start location for a return event and the target's temporal sequence position in the series. While this example shows super-node distribution under neutral connectivity, a similar pattern in qualitative terms appeared under preferential connectivity (not shown).

Figure 3B shows the distribution of node degree for the virtual network of the data in **Figure 3A** (upper pane). The super-nodes represent the right-hand part of the distribution. However, they are few in number. Thus, they become visible only in the log-log distribution (inset), which resembles a power law with

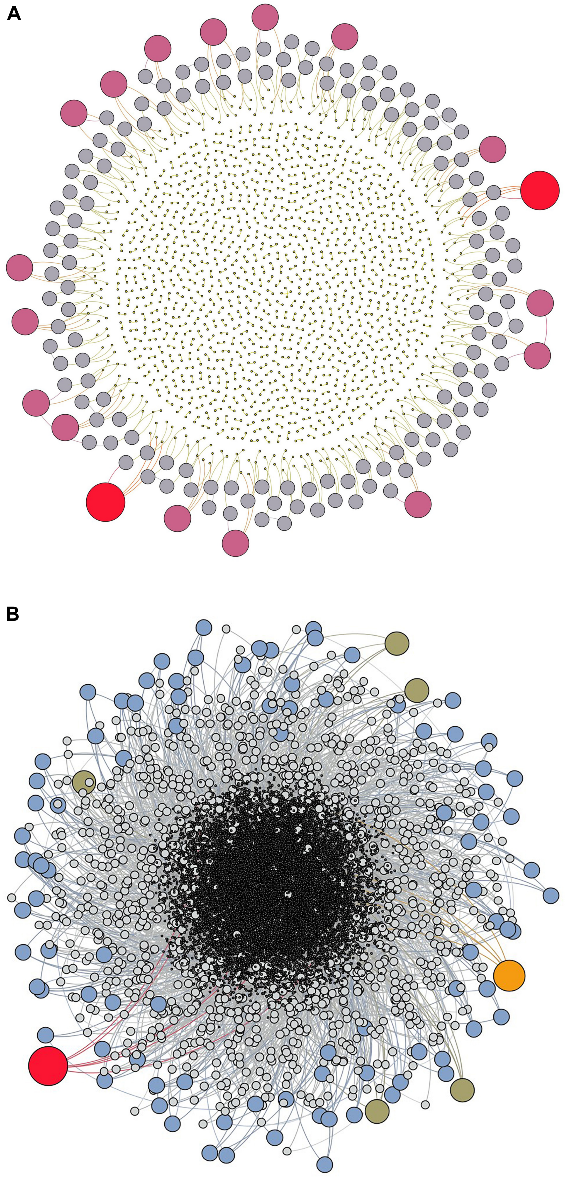

FIGURE 2 | Network graphs (produced in Gephi 0.8.2 and 0.9.2) (Bastian et al., 2009) illustrate how a site fidelity network (SFN) even under neutral connectivity becomes increasingly complex by increasing number of hierarchical levels of connected nodes (re-used locations) over time. Each series consists of 10^4 steps with a new potential or realized node creation every 10 step on average (t_{ret} = 10). Node degree is expressed by the size of the bullets, while colors only serve to distinguish the respective magnitudes of degree. **(A)** The center part of the network visualization represents Level 1, containing nodes with only one connecting link (smallest network fragments). **(B)** The link structure of the initial 10^4 return events of a series of 10^5 steps becomes more complex with more levels when studied as the initial sub-section of a 10 times larger series than in **(A)**. In other words, the network is more "mature" owing to the longer time span of development of the initial part of the network.

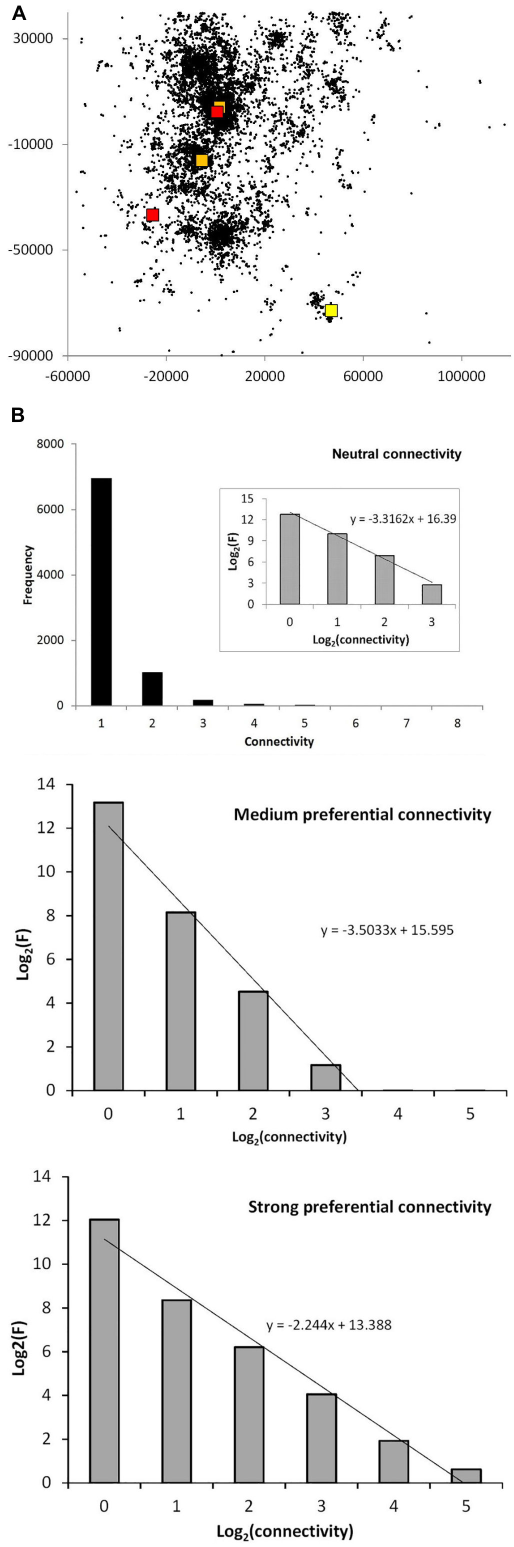

FIGURE 3 | (A) The scatter shows the spatial dispersion of a set of simulated MRW locations under neutral connectivity, including both actual nodes (re-visited locations) and other sampled locations of the actual path (representing potential nodes). The path is sampled at frequency 1:1,000 relative to unit

(Continued)

exponent β = -3.3. Based on additional simulations, the middle and lower pane give the log-log degree distribution for medium and strong preferential connectivity, respectively (average result

FIGURE 3 | time increments. The return interval was set to t_{ret} = 10. The colored icons locate “super-nodes,” the nodes with the highest node weight; i.e., with largest connectivity strength in the virtual network. Yellow: 8 return events to this location; orange, 7 events (2 locations); red, 6 events. In the latter category only 2 of the 5 locations are shown, since the other 3 were nearly overlapping with another super-node. **(B)** The degree distribution of node weights (connectivity) for the data in **(A)** (upper panel), with inset showing log-log transformation. In this inset the super-nodes are included in the right-hand column and part of the second-right-hand column. Ten independent series were produced, and the respective replicates were averaged. The middle and lower panes show the log-log transformed degree distribution for medium and strong preferential connectivity, respectively.

from 10 replicate series pr. condition). The latter shows an increased hierarchical depth*;* i.e., a wider distributional range of node weight, and consequently a reduced slope with exponent β = -2.2.

Spatio-Temporal Space Use Under Drifting Site Fidelity

Under partially punctuated site affinity and neutral connectivity (10 sequences and 10% overlap of targets for returns; condition **A**) a tendency for drifting home range is apparent from the somewhat lower magnitude of spatial overlap between 100 fixes from early, middle and late part of the series (**Figure 4A**). However, the spatial drift of space use is weak. Within each of the 10 sequences the animal’s site fidelity is evolving without extrinsically invoked interruption of side fidelity. When the 10 time sequences are analyzed separately in a regression and averaged (**Figure 4B**), the two sampling conditions under intra-sequence periods give similar-sized average incidence over the range of log[I(N)], with power exponent close to the expected z = 0.5 (z = 0.474, SE = 0.008). The total set of fixes shows a similar average log[I(N)] (z = 0.499, SE = 0.009). These results verifies absence of visible autocorrelation at the intra-sequence temporal scale, but—due to the shown divergence of time-continuous and frequency-based fix sampling for the total set—some magnitude of auto-correlation in the total series embedding a shifting pattern of site fidelity. The similar intercept with the y-axis, log(c) implies stability of the characteristic scale of space use (sequences: z = 0.344, SE = 0.076; total series: z = 0.431, SE = 0.048), CSSU.

Second, a more continuous shift of site fidelity (condition **B**) is shown in **Figure 5**: returns are limited to a trailing time window that contains the last 2% of locations over a shift every 1/50 part of the total series. Under this condition, the divergence of plots between the two sampling schemes is more pronounced (averaged set: z = 0.57, SE = 0.014).

Third, the most dramatic shift both with respect to space use and in the pattern of I(N) under the two fix sampling schemes (condition **C**) appears where site fidelity is set to re-generate from scratch at every instance of re-setting of site fidelity (**Figure 6**).

In **Figure 7**, where strong preferential connectivity (Condition **D**) is simulated under stable (rather than drifting) site fidelity, shows that the scaling slope $z{\approx}0.5$ seems to be uninfluenced by the magnitude of preferential relative to neutral connectivity (z = 0.535, SE = 0.029). This result is thus similar to the condition of stable site fidelity under neutral connectivity, as was shown within the separate sections presented by green and red icons in **Figure 4B**. However, CSSU – estimated as $c^{0}.^{5}$ = 1000k for medium preferential connectivity and $c^{0}.^{5}$ = 667k for strong preferential connectivity—were both smaller than $c^{0}.^{5}$ = 2500k under neutral connectivity [not explicitly shown, since in all I(N) presentations, c is calibrated to unit scale; i.e., log(c)≈0].

Applying the Method on Black Bear Telemetry Data

Figure 8 illustrates by empirical data some of the basic principles that are presented by the simulations. **Figure 8** shows the average I(N) for a set of 15 female black bears, showing close compliance with a power exponent $z{\approx}0.5$ when averaging over time-continuous and frequency sampling of N, and thus in line with the default MRW expectation (z = 0.50, 95% confidence interval 0.46–0.55; SE = 0.02). Divergence between the two sampling schemes indicates some level of serial autocorrelation; i.e., indicating some magnitude of drifting site fidelity. For all plots where $\log_2(\text{N}) > 2$; i.e., $\text{N} > 4$, frequency sampling produced larger I(N) than time-continuous sampling. Further, **Figure 9** shows that the distribution of CSSU estimates for the 15 series is wide. However, analyses to reveal ecological correlations (like strength of habitat selection) to study the pattern behind respective series were not performed. Crucially, in **Figure 9**, middle and lower pane, z shows independence of both c (giving the CSSU estimate) and N, as predicted by the model’s basic premises.

DISCUSSION

Network Topology in an Site Fidelity Network Context

With respect to ecological aspects of memory-influenced animal space use, the difference between a complex and a regular network topology may have substantial influence on the organic growth and stability of site fidelity. In general, a scale-free network topology is expected to show a high resilience against perturbations. For example, the hierarchical distribution of routers and inter-domain connectivity of the World Wide Web is expected to communicate unaffectedly even when experiencing unrealistic high failure rates given that the errors are randomly distributed among the nodes (Albert et al., 2002). On the other hand, if the dominant nodes have a higher degree of failure than expected from random shutdown both the network resilience and its hierarchical structure easily breaks down (Albert et al., 2002). Under such events the most popular nodes are being specifically attacked rather than being subject to random error on equal terms with other nodes. Hence, scale-free networks have an Achilles heel, which may counter-balance the general advantages from hierarchical system topology: robustness from such organization of nodes makes the structure vulnerable if the dominant nodes are specifically targeted and destroyed.

Returning from the general network theory above and back to ecology, if the nodes that are utilized most intensely are destroyed, the consequence should be expected to be more severe

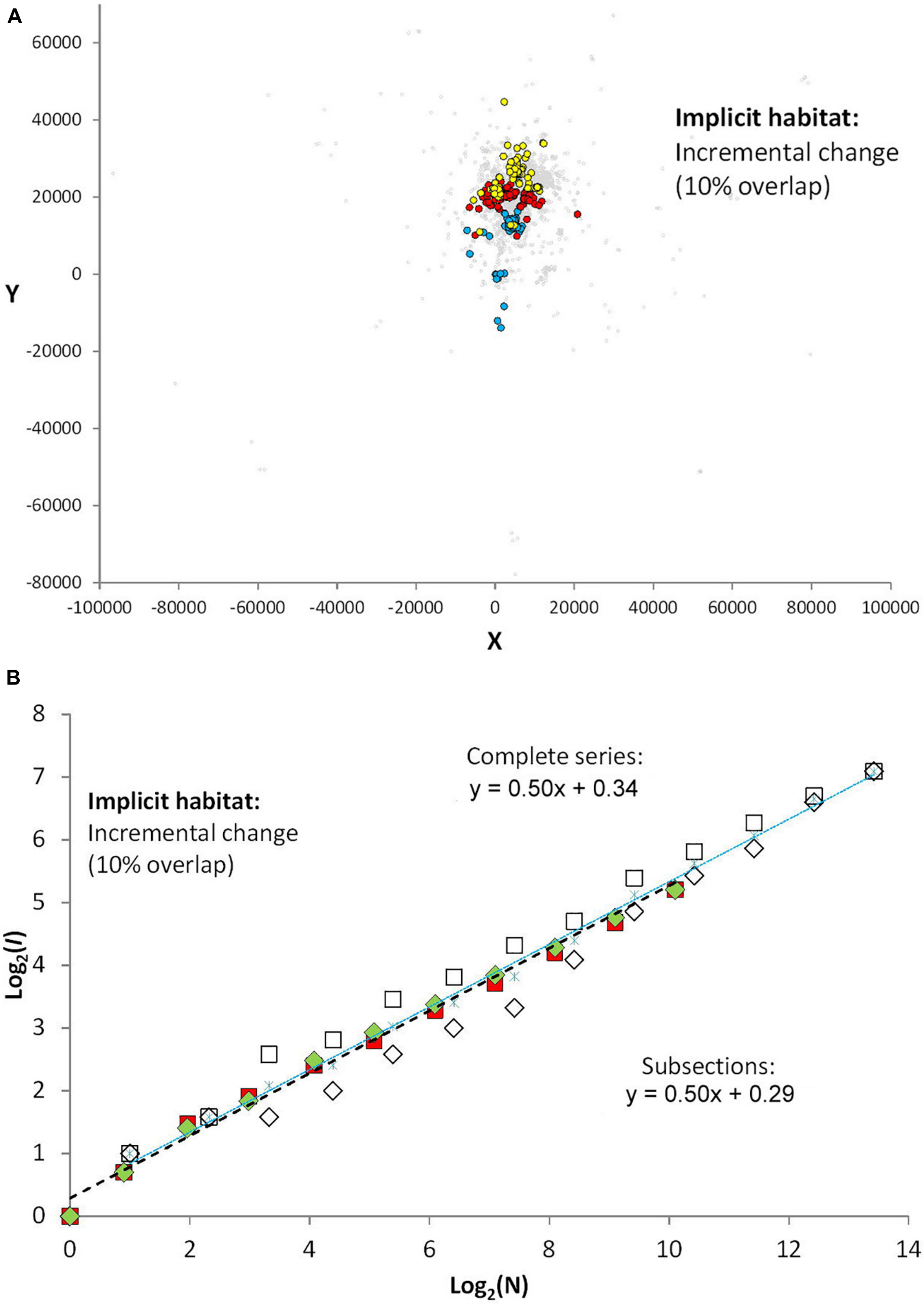

FIGURE 4 | Each scenario in this and the following presentations of simulation results is replicated ten times, and respective plots of I(N) both for time-continuous and frequency-distributed sampling of N are presented. Using the average log[I(N)] over the range of log(N) for the two sampling schemes time-continuous and frequency-based sampling is used to quantify the difference between serially non-autocorrelated and autocorrelated series. The influence on c and z as autocorrelation from extrinsic origin is increased (influencing instability of site fidelity) can also be revealed in each of the three scenarios, by studying log[I(N)] in the respective sections of stable site fidelity between punctuation events where intrinsic autocorrelation is absent due to $t_{obs} >> t_{ret}$. **(A)** Under partially punctuated site affinity (condition **A**; 10 sequences, see main text) a tendency for drifting home range is apparent from the somewhat lower degree of spatial overlap between samples of 100 fixes from early, middle and late part of the total series, presented by, respectively, colored dots. **(B)** The spatial drift under condition **(A)** is weak, which is reflected in the relatively narrow difference between sampling N fixes by a frequency-based sampling (open squares) or a continuous time scheme (open diamonds). The average log[I(N) is shown as blue stars. When the ten time sequences are analyzed separately (green and red-colored icons), the two sampling conditions give similar-sized incidence over the range of N as the average log[I(N)] from the total set of fixes (the average of the section series is the mid-point between the respective sets of colored squares and rectangles, but is not shown for the section series). The y-intercept, Log(c), under the two sets of analysis is of similar magnitude, both within sections and for the overall series containing all sections.

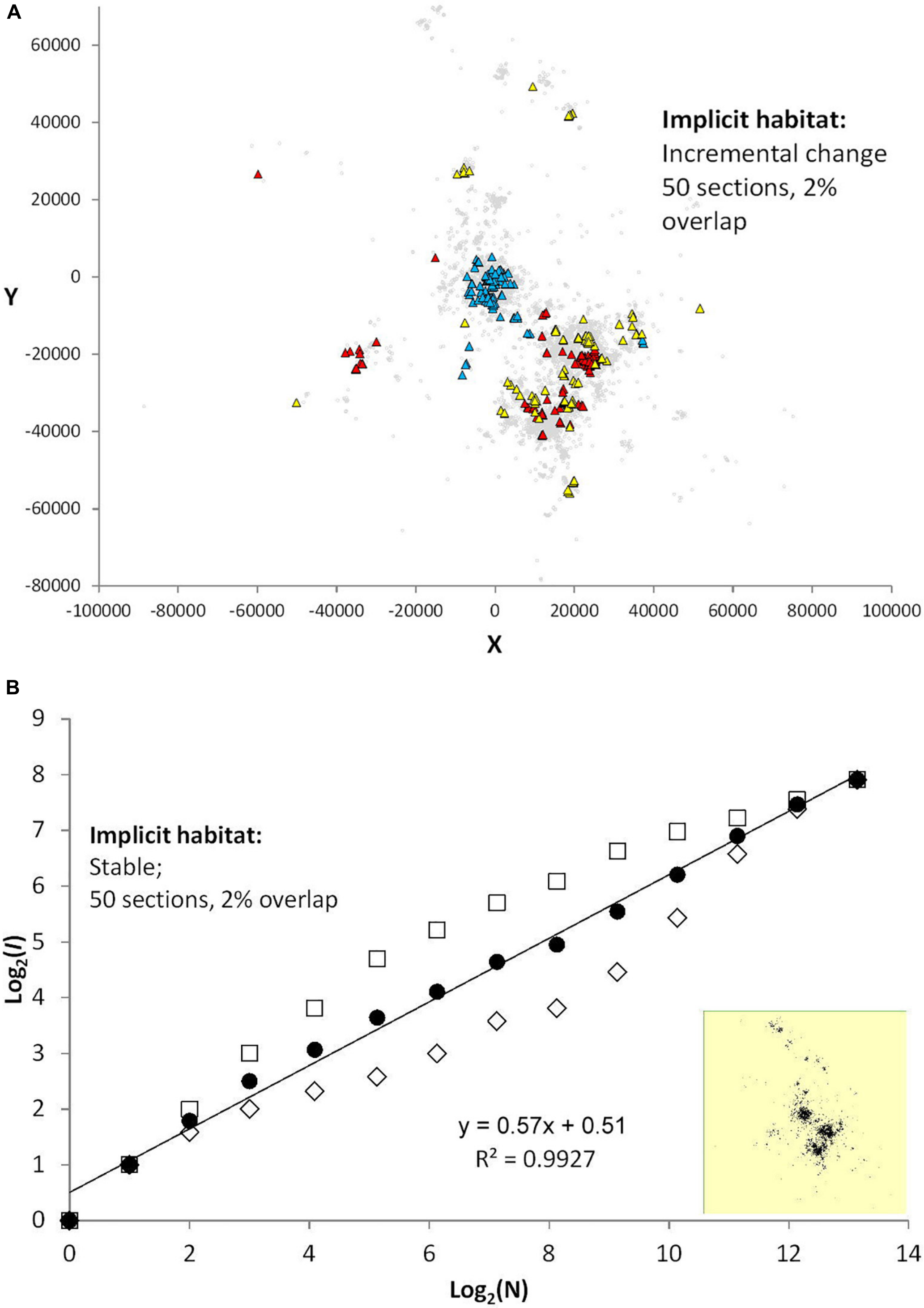

FIGURE 5 | (A) When only 2% of last-section path is retained and the number of sequences for partially punctuated site affinity is increased from 10 to 50 within the same magnitude of total series length (condition **B**), the drift of site fidelity increases in strength. Consequently, overall space use becomes wider (gray dots relative to the three subsamples shown by colored dots) and the respective *N* = 100-samples are less overlapping. **(B)** This effect becomes apparent in the analysis of incidence, *I*(N), which owing to the stronger spatial auto-correlation shows a widened difference between log(y-intercept) for a given log(N) the two fix sampling methods. However, when log(y-intercept) from the two sampling methods continuous and frequency-based are averaged (filled circles) the slope is—as in (**Figure 4**—approximately) log-linear and thus power law compliant. As in the foregoing results, log(*c*) from such averaging seems quite resilient, and thus CSSU seems to be little influenced even by this strongly shifting pattern of site fidelity.

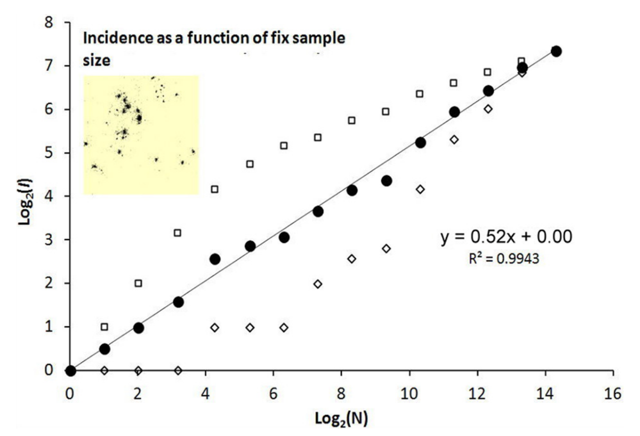

FIGURE 6 | Condition C: site fidelity is set to re-generate from scratch at every instance of re-setting of site fidelity. The inset shows the dispersion of fixes.

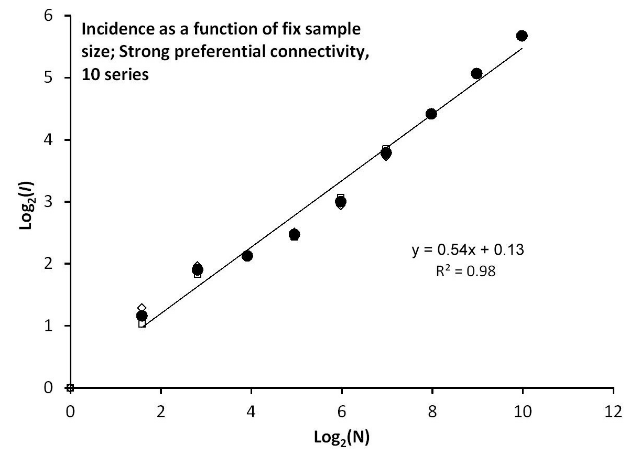

FIGURE 7 | Condition D: *I*(N) under strong preferential connectivity and no drift of site fidelity (average of 10 series).

than expected from their node degree alone; i.e., the percent use of given nodes relative to all nodes' degree, where degree is synonymous with relative popularity. However, under SFN terms, which represent a non-classic variant of complex networks, disruptions may have both external and internal causes. In the latter case, consider an animal that (gradually or more abruptly) for ecological reasons is choosing to abandon its present set of preferred patches in total or in part, for example due to intra-seasonal habitat phenology or other changes of space use. This kind of shifting mosaic of site fidelity takes place (under the premise of the MRW model) at many temporal scales in parallel, and represents an important aspect of cognitive movement ecology to be explored. Thus, SFN introduces a qualitatively different kind of resilience against perturbations than expected from premises of a classic, scale-free network.

First of all it is interesting that a scale-free kind of node hierarchy (the degree distribution) is found under memory utilization and site fidelity, but not necessarily depending on the MRW scale-free properties of the MRW model [the spatially explicit step length distribution and the *I*(N) function]. Space use complexity in terms of network topology might thus be expected over a very broad range of environmental conditions and cognitive processing of spatio-temporal memory, given that the actual animal complies with site fidelity. What about space use vulnerability to perturbations? Animals that use spatial memory to revisit patches in a self-reinforcing manner may as a side-effect also develop resilience against destruction of even a large percentage of its revisited patches. Like the stream of data over the Internet, the traffic simply finds alternative routes and—over time—swiftly absorbs the perturbations by developing alternative nodes and links, including shortcuts.

In ecological terms, nodes may represent localized food items or food-rich localities, which may occasionally be temporally destroyed or made less attractive either by the individual's foraging activity or by competitors. A range of other external factors may also reduce the assumed profit from returning to a given locality, in the shorter or longer term. If resource availability generally becomes less abundant, site fidelity and the emerging scaling property of space use may even break down, as illustrated by simulations (Gautestad and Mysterud, 2010b). Thus, under a combination of general resource depletion and disruption of resource patches (self-inflicted or not), the animal may drift (or swiftly move) toward other localities and develop a modified space use network. The present results indicate how the degree of site fidelity, from resilience to drifting or re-building, may be studied in the *I*(N) function with respect to the difference between the two sampling schemes for varying N. Stronger degree of shifting mosaic of utilized patches is expected to show a wider gap between the two scheme results of *I*(N) relative to the log-log line for their geometric mean.

In terms of fitness, a self-reinforcing feedback type of patch use may lead to fine-scaled habitat auto-facilitation (Gautestad and Mysterud, 2010b). Habitat facilitation is normally a descriptor of how a keystone species may facilitate the habitat for other species (Arsenault and Owen-smith, 2002; Fox et al., 2003; Liess and Helmut, 2004; Korpinen et al., 2008; Pringle, 2008). However, a species like a grazing ungulate may also auto-facilitate—self-facilitate—a given habitat in a self-reinforcing manner, and thereby improve or maintain the local habitat's grazing potential for a given individual, family group, herd or local population. Mild grazing, i.e., below or at an optimum intensity of patch use, may induce a higher re-growth rate and/or maintain a high level of digestibility for some important food plants (Mobæk et al., 2009).

However, as the utilization rate increases a critical threshold is always lurking. The positive feedback may then switch into a negative feedback, at least until the patches may be restored with respect to their attractive attributes (Gautestad and Mysterud, 2010b). The development of a network of nodes as a consequence of site fidelity is a two-edged sword also from other reasons: by becoming increasingly attached to the most utilized super-nodes (**Figure 3**) the animal may simultaneously make itself vulnerable. For example, predators may learn where these nodes are located, and gradually adapt their search behavior accordingly. The present simulations may thus open new and interesting directions

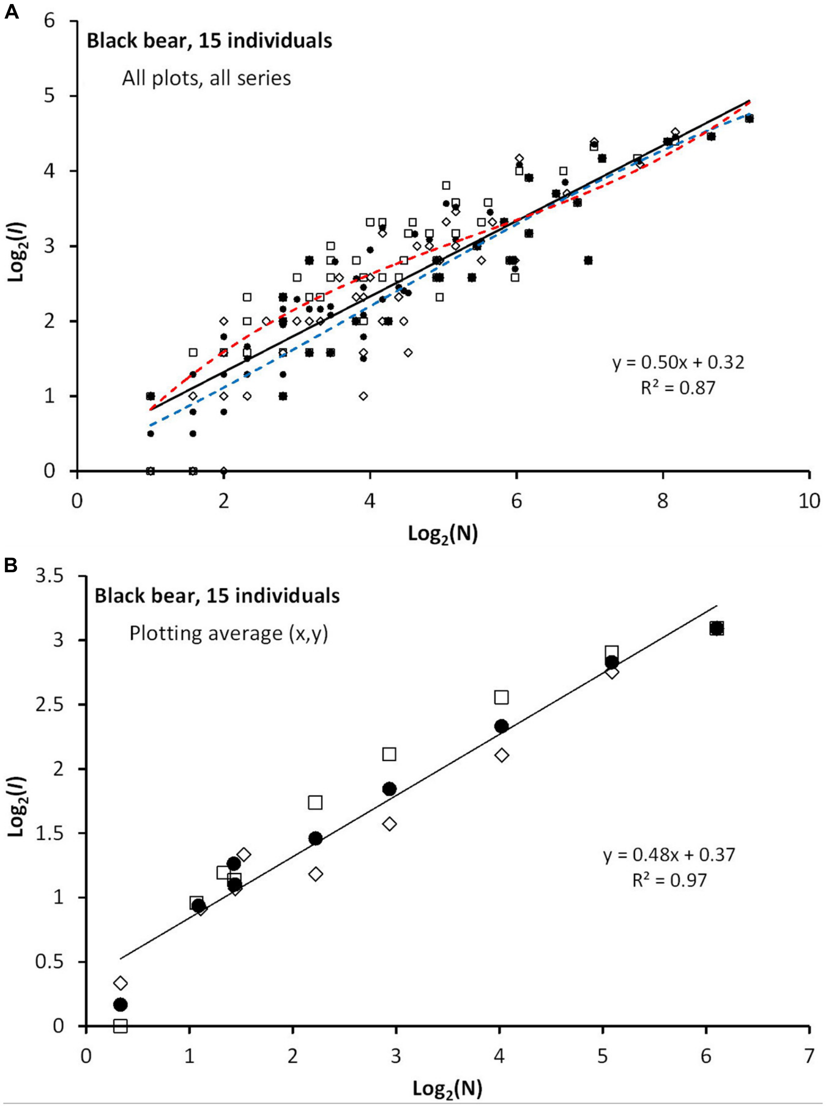

FIGURE 8 | (A) Results of re-analysis fixes from a sample of 15 telemetry series of black bear, where N-dependency for respective series is analyzed by *I*(N) rather than R/S (see main text). Plots of $\log_2[I(N)]$ for time-continuous (diamonds), frequency-distributed sampling (squares) and the log-average of the two schemes (black circles) shows compliance with power exponent z≈0.5 for the latter (continuous line). All sets from all schemes are superimposed, which implies a mixture of series with different N_{max}. The slight non-linearity of time-continuous and frequency-distributed sampling is visualized by curve-fitting by third order polynomials (blue and red dashed lines, respectively). **(B)** The divergence between the two fix sampling schemes over the mid-range of N is better visualized by averaging over respective series' N- and *I*(N)-plots.

of research, based on the various complex aspects that are successively revealed in a Russian doll manner on the interface between virtual network theory and animal ecology.

Network Topology in Relation to Local Density of Fixes

The distribution of node degree (connectedness) in the oldest part of the Site Fidelity Network (SFN) does not comply with expectation from a regular (non-complex) network system, but resembles a complex (hierarchically structured) space use over a wide range of connectivity conditions. Another interesting aspect of the present analyses regards the absence of a clear correlation between spatial locations of the dominating nodes from the virtual network space—"super-nodes"—relative to the areas of most intense use. The latter regards the nodes of the more traditionally considered utilization distribution, which is based on local density of fixes (for example, core areas from multi-modal kernel density estimates). In contrast, under MRW the local density modality emerges as a multi-scale mixture of network node locations and dispersion of exploratory moves.

The unexpected result in **Figure 3** regarding distribution of "super-nodes" opens for interesting speculations with respect to cognitive movement ecology and animal space use in general:

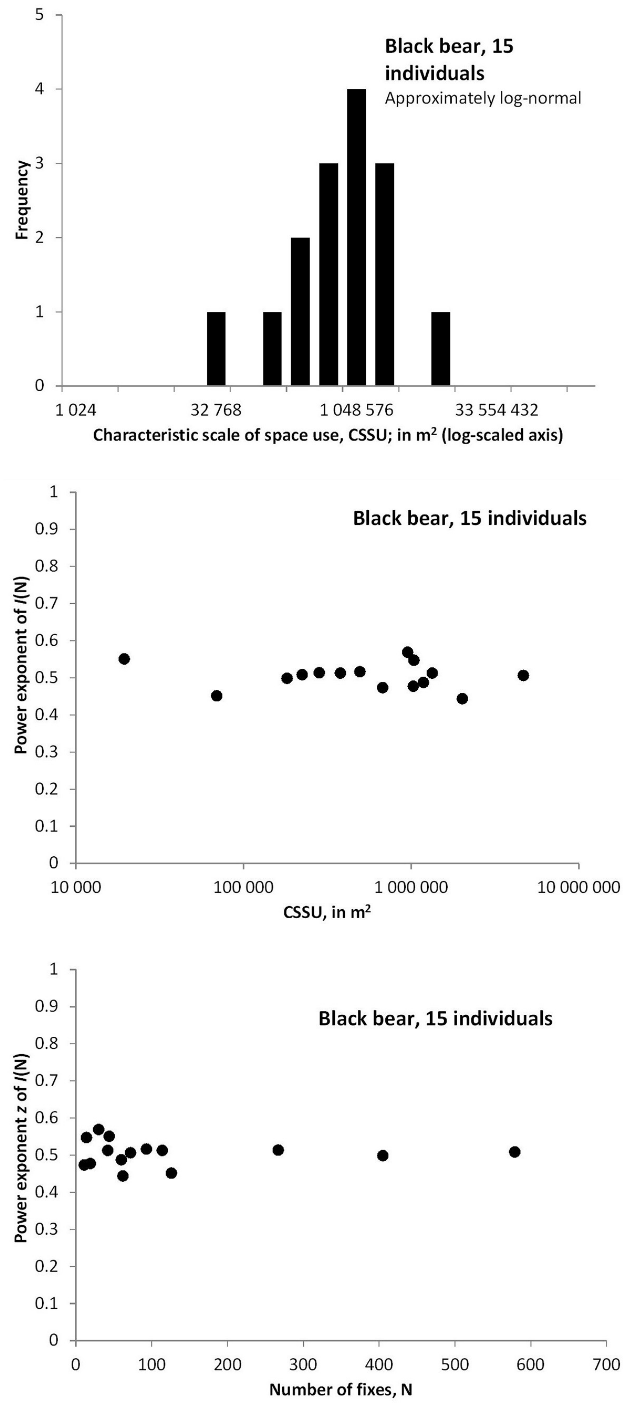

FIGURE 9 | Upper pane: The CSSU estimates for the respective series varies strongly. Middle pane: *z* is independent of the parameter CSSU, and varies little between the series. Lower pane: *z* is independent also of fix sample size N, and varies little between the series.

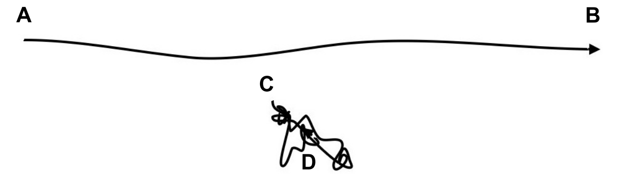

FIGURE 10 | The movement path from fix locations A to B has the same total length as the path from locations C to D, but in the latter case the path includes return events, which curls the path. Since a location along the latter path has a relative short distance from any other location, the energy expenditure from returning to an old location (close to C) is of similar magnitude as revisiting a relatively recent location (close to D). Thus, in the present simulations return events take place without penalty from time since last visit to the target location.

even if a spatial grid cell containing a super-node contains a low local density of relocations relative to many other parts of the animal's home range, the actual super-node may represent a locality with stronger importance than revealed by the traditional utilization distribution alone. However, even if the overview of complex network properties in *Introduction* referred to a network's susceptibility to perturbations of the most visited nodes, one may speculate that an animal's network of site fidelity may show stronger resilience overall, due to spatial memory. If a super-node is destroyed of abandoned, the individual may take advantage of shifting to an alternative location in the understory of potential nodes in the hierarchy of historically utilized and remembered locations. In this respect the presently described SFN, due to its large set of potential nodes, deviates qualitatively from more traditional network theory, whether complex or regular. Thus, ecological inference with respect to analysis of space use under condition of site fidelity should take both the Euclidean and the virtual network topology into consideration.

While the set of network nodes is small relative to the large majority of locations that are revisited only 0–1 times, resilience of nodes determines both the emergence of a "home range" and its degree of spatial stability. The present results show that the super-nodes may be surprisingly uncorrelated with a home range's core areas, which reflect the utilization distributional peaks; i.e., the spatial density of relocations of an individual. Thus, a maturing network of habitat utilization may to a large extent be determined by the non-trivial dispersion of the rich understory of less frequently visited nodes relative to the most visited ones.

In this respect the local "peaks" that are represented by the location of the super-nodes in **Figure 3A** will typically go undetected in a standard Kernel Density Estimate function, which is "smoothing" the utilization distribution under the statistical premise that the underlying space use process complies with diffusion-like, scale-specific dynamics in statistical-physical terms; i.e., the distribution may under this condition be represented by a multi-modal function of a superposition of many normal distributions, which then are implicitly expected to reflect environmental heterogeneity. The node peaks in **Figure 3A** will thus easily become "averaged away" due to applying an erroneous biophysical framework for the analysis. On the other hand, the super-nodes are also undetectable by direct visual inspection, as illustrated by the complex dispersion of fixes in **Figure 3A**. This aspect of the MRW model underscores the importance of studying local space use intensity from variation in CSSU rather than studying the local density of fixes directly.

The SFN model may point toward exploring a novel aspect of animal space use where conditions for site fidelity are satisfied, by showing how the physical (Euclidean) and the virtual network of nodes and links represent complementary aspects of memory-influenced movement. Specific aspects and properties may even be uncorrelated between these representations. The theory of network topology may thus spin off new and unexplored hypotheses, which in a fruitful development in tandem with ecological field experiments may give further insight with respect to the dynamics of animal space use and dispersal. For example, the vulnerability to surgical node destruction in combination with the present insight that these nodes may be uncorrelated with a home range's primary core areas (**Figure 3**) may lead to modified protocols with respect to protection of wildlife. It may also provide guidelines for the opposite: more effective destruction of the conditions for local persistence of pest species.

Drifting Site Fidelity

In sum, the present simulation conditions for drifting fidelity cover a wide range of memory horizons. In parsimonious model terms, they thus cover a wide range of situations where the animal is utilizing a memory map during adaptation to a temporally shifting mosaic of habitat heterogeneity.

The similarity between the average log[I(N)] slopes with z close to 0.5 at the CSSU scale for all punctuation conditions under neutral connectivity indicates resilience both with respect to different percentage overlap of locations between successive time sections and various magnitude of these sections (**Figure 4B**). Thus, the difference between continuous-time and frequency-based sampling in the I(N) scatter plot (stronger divergence in the medium-N range) is due to the autocorrelation that follows from the drifting pattern of site fidelity. However, the result showing similar magnitude of both the power exponent z and the intercept c reflects stability with respect to how the individual distributed its space use over the range of scales, whether the site fidelity was stable of temporally variable during the given time span.

A condition of a partly retained site fidelity leads to a tendency for a "drifting home range" (Doncaster and Macdonald, 1991), with some degree of locking toward previous patch use, similar to the condition that was simulated and discussed in Gautestad and Mysterud (2006). Behaviorally, punctuated site fidelity illustrates an animal that is faithful to its environment in landscape-scale terms, but occasionally is developing partly new local habitat utilization as time progresses. For example, this scenario could in model-simplistic terms illustrate GPS sampling of an ungulate that occasionally is changing its space use in accordance to changing food distribution during the season (Gautestad and Mysterud, 2006; Bischof et al., 2012). Punctuated site fidelity could also illustrate an intrinsic predator avoidance strategy, whereby fitness may improve by occasional abrupt changes of patch use, and this may under specific conditions be more advantageous than the cost of occasionally giving up utilization of familiar patches. It could also illustrate patch deterioration with respect to a critical resource; energy profit in utilized patches may deteriorate owing to foraging, and thus trigger a "reset" of patch use in conceptual compliance to the marginal value theorem (Charnov, 1976).

Consequently, for wildlife management and conservation biology it should be of great importance to clarify whether individual space use under influence of spatial memory tends to follow the dynamic principles of scale-free or approximately scale-free (complex) or a scale-specific (non-complex) networks. Either way, the emergence of a network of actual and potential nodes requires that the animal is utilizing a memory map for occasional, non-random returns.

Model Feasibility

To my knowledge MRW is at present the only model developed explicitly for GPS relocation sampling scale that has been shown to reproduce three crucial statistical-physical aspects of individual space use with properties in accordance to our analyses of empirical GPS data (*op. cit.*); power law compliant and non-trivial sample size dependence on observed home range area I(N), power law distribution of step lengths F(L) and power law space use dispersion, as expressed by the fractal dimension D. Our results from empirical analyses have been coherent with theory developed for the relationship between these three aspects, based on the MRW properties (Gautestad and Mysterud, 2010a,b; Gautestad and Mysterud, 2013; Gautestad et al., 2013; Gautestad, 2021). In the present report we extend the MRW framework by studying a fourth aspect of the model; the topology of network nodes.

Owing to the return events, space use becomes very constrained relative to movement with no site fidelity. Consequently, the total energy expenditure for a return step is not expected to be substantially different on average from an exploratory step. Complications with respect to modeling energetic cost of short and long steps may thus be ignored in the present context (**Figure 10**), a property that is consistent with some recent empirical studies (Merkle et al., 2014; Marchand et al., 2017; Merkle et al., 2017). Thus, the energetic aspect lends additional weight to the feasibility of the MRW framework. Memory utilization is energy-efficient, relative to the standard space use paradigm, where the animal is implicitly assumed to obey the general statistical-physical principles of Markovian dynamics (see below).

It should be emphasized that MRW locations that are returned to regard exact geometric positions relative to their first occurrence in the series. However, the present results do not depend on such exact position. The crucial point is that each simulation makes an intrinsic distinction between true return targets (even if these are geometrically rounded to a coarser-defined site) and exploratory steps that just happen to land at a given previous site.

Regardless of strength of connectivity, since return steps in statistical terms may target any previously visited location irrespective of previous revisits, physical patch distances and virtual network distances are in this manner set to be independent *a priori*. The model choice to return to a randomly picked location under the given strength of connectivity may be considered consistent with general principles of statistical mechanics of movement in a homogeneous environment.

Heterogeneity and deterministic behavior are under this approach implicitly confined to finer resolutions (for example, from varying local strength of site fidelity as a function of local habitat attributes, as expressed by a in Eq. 1), and averaged out in the distribution results from the complete set of fixes. This implicit fine-grained heterogeneity may thus be replaced by a homogeneous environmental property in the model for the sake of simplicity.

MRW builds on a non-mechanistic (non-Markovian) kind of statistical mechanics, as a consequence of implementation of memory as defined by the model's premises of "parallel processing" rather than "serial processing" (Gautestad, 2021). In order to embed "non-mechanistic" processes, the framework of mechanical dynamics have been extended to allow for the originally "peculiar" aspects of animal movement, under which some specific paradoxes have been theoretically resolved. The MRW conjecture of non-Markovian processing rests on the memory property where returns happen independently of temporal interval since previous visit to a given location. This property makes the time domain scale-free: a given location has—on average—a geometrically declining probability for a revisit due to the maturing of space use over time ("longer path"). Simultaneously, multiplying this declining revisit probability to a given location with the number of potential nodes as a path is growing will compensate this decline. Thus, this product reflects a uniform (constant) next-step return probability pr. unit time.

From another perspective, the mechanistically unfamiliar MRW property of Eq. 2, where observed area expansion is a function of N rather than time as such, also violates a basic property of a mechanistically driven system. Adding new fixes may be performed in a time-incremental manner (continuous sampling; a sample size that is proportional with sampling time) or by increasing sampling frequency 1/t within the total time period T (including every n^{th} fix within T, by increasing n until n = N). This statistical-physical property, originally termed "The Home range Ghost" (Gautestad and Mysterud, 1995), makes the process time-independent (and thus non-mechanistic) but temporally *scale-range* dependent of the ratio T/t. In other words, a similar change of both T and 1/t gives a similar change of the expectancy of I(N) when averaging over the two sampling schemes. The present study lends additional empirical and simulation-based results in this respect; the power law in Eq. 2 not only regards serially non-autocorrelated sets of fixes, but—crucially and non-trivially—also autocorrelated sets. The latter regards the geometric averaging of continuous and frequency-based sampling, which (as shown in **Figures 4–7**) restores compliance with Eq. 2.

In contrast, in a Marovian system, a given return is a function of current or recent conditions (first- or n-order Markov, respectively). Thus, "infinite" memory influence on next-move decisions (the core of the parallel processing conjecture) is computationally dismissible. However, mechanistic implementation of memory-based site fidelity as alternatives to MRW has also been proposed and explored by others (Morales et al., 2005; Dalziel et al., 2008; van Moorter et al., 2009; Boyer and Walsh, 2010; Nabe-Nielsen et al., 2013; Boyer and Romo-Cruz, 2014; Boyer and Solis-Salas, 2014; Bracis et al., 2015). It will be interesting to see which of the two theoretical directions to understand the observations of complex movement as expressed by Eq. 2 gain further support in the time ahead; parallel processing under scale-extended statistical mechanics, or scale-specific (Markovian) processing under standard biophysical premises.

Characteristic Scale of Space Use: Expressing the Balance of Exploratory Moves, Return Frequency and Preferential Connectivity

In addition to exploring topological aspects of memory-influence in general terms, the second main part of this report reveals important properties of various degree of drifting site fidelity in the Euclidean realm. In particular, I describe how the divergence between I(N) from continuous and frequency-based sampling appear as a feasible method to reveal such instability of site fidelity. Crucially, under a given condition of connectivity strength, unit step length a and constant average return frequency t_{ret}, both c and z from the total series (Eq. 2) are on average similar to c and z that are estimated from each of the ten separate time sections (**Figure 4B**). This result holds even when estimating these parameters under subsections of a given section; i.e., by reducing N within an interval with absence of forced drift of site fidelity (not shown). This property follows from the model independence between c, z and N. Hence, when averaging over spatio-temporal heterogeneity, the results confirm that the overall property of c and z is maintained. Even when temporal heterogeneity is further increased within the same total time span by using 50 sections with 2% overlap of potential nodes for return step locations, the averaging of time-continuous and frequency-based sampling verifies the power law with a consistent slope and intercept (**Figure 5B**). The drift effect on site fidelity is most strongly increased when historic locations are abandoned at every punctuation event (**Figure 6**). However, this report also shows that CSSU, as expressed by c, is not only a function of unit step length a of exploratory steps and t_{ret} for return events, but also influenced by the strength of preferential connectivity. Stronger preference leads to smaller CSSU; i.e., a more condensed space use (**Figure 7**).

However, under a given node connectivity regime, despite the added complexity of space use under the punctuated site affinity, a similar magnitude of c and thus CSSU is found. This is a non-trivial and important statistical-physical result: averaging over spatial and temporal heterogeneity of space use shows a similar result with respect to estimating c. The parameter c is thus confirmed to be very resilient with respect to finer-scaled heterogeneity relative to the chosen scales in time and space for the analysis.

The general recognition of spatio-temporal memory as a crucial aspect of animal space use is currently forcing a rapid extension of the theoretical foundation of animal movement modeling, in particular for vertebrates. In the present report I have deepened our own multi-decennial quest in this regard, by drilling into the topology aspect of memory-based site fidelity and how early-phase return events to previously visited locations tend to lock habitat utilization into the emergence of a home range. Contrary to the classic paradigm, under the present MRW model the concept of home range size becomes imprecise, due to the intrinsic scaling property of the mixture of exploratory bouts and return events. Incidence, I(N), describes a power law under changing N, in violation of the traditional expectation of an asymptotic approach toward a stationary home range size with increasing N. Consequently, the Characteristic Scale of Space Use, CSSU, is for statistical fractal-compliant fix patterns here (as in our previous papers) advocated as an alternative expression for size; i.e., "area pr. square root of N" (Eq. 2) rather than area *per se*. Under the MRW framework, the instability of I(N) under a change of N is not a trivial function of small-sample error (as under the paradigmic assumptions of a home range utilization), but is the result of varying observation intensity on a given multi-scaled and non-Markovian space use process. Obviously, this statement needs further validation, both theoretically and not at least empirically.

Figure 7 shows that space use drifts toward becoming more fine-gained in unit-scale CSSU terms as connectivity drifts from neutral toward preferential. This is quite logical and to be expected *a priori*, since constraining returns to a subset of previously visited locations by necessity also increases the relative connectivity to early-phase emergence of nodes. Consequently, I(N) for a given N becomes more constrained relative to neutral connectivity conditions. However, the stability of z when shifting from neutral to preferential connectivity is perhaps more surprising and supports the broad versatility of the MRW model as a parsimonious model for memory-influenced habitat utilization.

Black Bear Data Under the I(N) Analysis

While the previously published analysis of black bear movement (Gautestad et al., 1998) applied Rescaled Range analysis (R/S) (Mandelbrot, 1983; Feder, 1988) to test for MRW compliance, the present result confirms a similar pattern under the I(N) method where continuous and frequency-based sampling are averaged. Most relevant for the present context, the separation of these two fix sampling schemes scatter plots indicate that on average these individuals expressed some (un-quantified) magnitude of drifting site fidelity. The present re-analysis of a sample of black bear telemetry series, albeit very limited and prone to statistical uncertainty, provides important support for several aspects of the MRW approach. First, this pilot study shows that the power law of N-dependence of observed space use (Eq. 2) holds when shifting from Rescaled Range analysis (Gautestad et al., 1998) to an I(N) analysis (**Figure 8**). Second, independence between key parameters of the MRW model are supported (**Figure 9**), and third, the present result invites to further explorations of the ecological aspect of drifting site fidelity using the method that has been presented here.

In general, when analyzing real data; as long as sampling rate of fixes, t_{obs}, is larger than the average return rate, t_{ret}, and the movement behavior satisfies MRW, neither z nor c are influenced. In real data, a verification of this property is thereby indirectly achieved by finding stability of both parameters in I(N) as grid scale k is "zoomed" over a scale range. Too small k leads to $z > 0.5$ (as described in **Supplementary Material 1**), and too large k leads to $z < 0.5$. Where z approximates 0.5, the actual k-scale squared gives an estimate of CSSU.

CONCLUSION

As always, scientific progress is achieved by the dual development of theory and empirical tests. In this report a specific model, MRW, is applied to propose a novel direction to explore the evolution of two complementary aspects of animal space use under memory influence, the topological property of network graphs and whether the simulation-revealed property of node popularity may be revealed indirectly by studying Euclidean dispersion of fixes. The latter approach depends in the MRW model, which embeds several testable predictions. These properties come under further scrutiny here, as a side-effect of exploring topological properties of spatial memory and spatio-temporal properties of drifting site fidelity. First, the modern view of home range as an emerging object from occasional returns to popular sites is gaining additional support. Traditionally, home range theory has been based on individuals that are expressing independent local returns within a spatially constrained area (e.g., demarcations due to physical borders or territorial behavior). For example, many statistical methods in tests of habitat selection rest on an assumption of random and non-intentional self-crossing of the animal's path, leading to "re-discovery" of profitable sites (i.e., a Markovian process). Second, verification of a MRW-like fix pattern (for example, compliance with Eq. 2) both supports a cognitive capacity for long term utilization of a memory map, and also a specific statistical-physical class of movement: a mixture of scale-free movement in tandem with occasional returns. Third, an acceptance of MRW-like behavior in statistical-physical terms has as a consequence that local space use intensity should preferably be quantified by CSSU and not by local density of fixes. Thus, two sections of a home range may express different magnitude of CSSU, despite a similar magnitude of fix density; or *vice versa*. Fourth, empirical support for scale-free and memory-influenced movement means a new direction to study to what extent an animal is distributing its habitat utilization effort over a scale range. In Eq. 2, a power exponent close to 0.5 rather than close to zero implies that—in statistical and over-all terms—the effort has been quite evenly distributed over this spatial range. Further, empirical support for long term memory and return events quite independent of the time span since last visit gives weight to the hypothesis of scale-free habitat utilization also in the time domain. Fifth, the MRW framework lends support to the quest to scrutinize the biophysical aspect of movement, rather than just taking the classic assumptions of a mechanistic, Markovian-compliant kind of process as granted.

To conclude, under the present approach site fidelity from memory utilization under the MRW conjecture should either be tested using methods that are available for this purpose (Gautestad, 2012, 2021), or this kind of behavior could be applied as a premise for analysis of complex habitat utilization if sufficient empirical support has accumulated.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because Pilot study regarding statistical analysis of previously published data (Gautestad et al., 1998).

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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SUPPLEMENTARY MATERIAL

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Seeing Is Be-Leaving: Perception Informs Migratory Decisions in Sierra Nevada Bighorn Sheep (*Ovis canadensis sierrae*)

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Seasonal migration is a behavioral response to predictable variation in environmental resources, risks, and conditions. In behaviorally plastic migrants, migration is a conditional strategy that depends, in part, on an individual's informational state. The cognitive processes that underlie how facultative migrants understand and respond to their environment are not well understood. We compared perception of the present environment to memory and omniscience as competing cognitive mechanisms driving altitudinal migratory decisions in an endangered ungulate, the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) using 1,298 animal years of data, encompassing 460 unique individuals. We built a suite of statistical models to partition variation in fall migratory status explained by cognitive predictors, while controlling for non-cognitive drivers. To approximate attribute memory, we included lagged attributes of the range an individual experienced in the previous year. We quantified perception by limiting an individual's knowledge of migratory range to the area and attributes visible from its summer range, prior to migrating. Our results show that perception, in addition to the migratory propensity of an individual's social group, and an individual's migratory history are the best predictors of migration in our system. Our findings suggest that short-distance altitudinal migration is, in part, a response to an individual's perception of conditions on alterative winter range. In long-distance partial migrants, exploration of migratory decision-making has been limited, but it is unlikely that migratory decisions would be based on sensory cues from a remote target range. Differing cognitive mechanisms underpinning short and long-distance migratory decisions will result in differing levels of behavioral plasticity in response to global climate change and anthropogenic disturbance, with important implications for management and conservation of migratory species.

Keywords: memory, perception, culture, facultative migration, partial migration, ungulates, reintroduction, cognitive movement ecology

INTRODUCTION

Seasonal migration is defined as a regular movement between two or more discrete seasonal ranges separated in space and time (Avgar et al., 2014; Berg et al., 2019). Seasonal migration allows individuals inhabiting environments with temporally predictable variation to track resources, like forage and mates, avoid risks associated with predation and parasitism, and mediate exposure to adverse climatic conditions (Fryxell and Sinclair, 1988; Mysterud et al., 2011; Avgar et al., 2014). Migratory behavior contributes to the increased growth, survival, and reproduction of migratory individuals (Hebblewhite and Merrill, 2011; White et al., 2014). Across a population, the improved demographic performance of migrants contributes to larger equilibrium population sizes than could be achieved through resident behavioral strategies (Fryxell et al., 1988; Fryxell and Sinclair, 1988).The influence of migrants also spans ecosystems as they transport nutrients, disperse seeds, serve as vectors for parasites and disease, and participate in trophic interactions, bridging disjunct habitats (Bauer and Hoye, 2014; Shaw, 2016). The ecological services and ecotourism industries supported by migration generate considerable economic value for the public (Shaw, 2016; Kauffman et al., 2021). The conservation of migratory behavior is important not only to maintain sustainable populations of migratory species, but also to protect the ecological and economic benefits migration confers.

The size of migratory populations and prevalence of migratory behavior has declined globally across terrestrial herbivores, particularly among ungulates (Harris et al., 2009; Tucker et al., 2018; Kauffman et al., 2021). The loss of migrants is primarily attributed to anthropogenic disturbance and global climate change (Lendrum et al., 2013). In species such as mule deer (*Odocoileus hemionus*) (Sawyer et al., 2019) and caribou (*Rangifer tarandus*) (Dalerum et al., 2007), migration is a fixed, innate behavior arising from genetics or maternal effects (Møller et al., 2011; Pulido, 2011). However, migration can also be a conditional strategy with individuals exhibiting behavioral plasticity in response to changes in their internal state and external environment, as observed in moose (*Alces alces*) (Ball et al., 2001; Singh et al., 2012), roe deer (*Capreolus capreolus*) (Cagnacci et al., 2011), pronghorn (*Antilocapra americana*) (White et al., 2007), and bighorn sheep (Spitz et al., 2018; Denryter et al., 2021b). Behaviorally plastic migrants make a series of choices with respect to their migratory movements. First individuals decide if they will migrate or remain resident on their present range. If migrating, they also choose when to leave and where to go. We consider only the initial decision to migrate in this manuscript, and refer to this event as a "migratory decision". Our objective is to understand why individuals choose to migrate, rather than where they go or how they get there. Understanding why terrestrial herbivores decide to migrate is necessary to predict the conditions under which migratory behavior may disappear, allowing for the implementation of proactive, rather than reactive conservation measures.

Plastic migratory behavior is hypothesized to be a response to the physical environment, conditional on an individual's internal state and social environment. Individuals may decide to migrate to follow ephemeral resources, or avoid risks and unfavorable conditions in portions of their physical environment. The forage maturation hypothesis posits that migrants track phenological gradients of plant growth across the landscape to maximize energy and nutrient intake (Fryxell and Sinclair, 1988; Hebblewhite et al., 2008; Berg et al., 2019). Conversely, the predator avoidance hypothesis states that individuals migrate to escape or mitigate consumptive risk, including predation, parasitism, and hunting pressure (Bergerud et al., 1990; Barten et al., 2001; Skov et al., 2011). Migration may also allow individuals to avoid adverse conditions they cannot tolerate including extreme temperatures, drought, and precipitation events (Ketterson and Nolan, 1976; Sabine et al., 2002; Brinkman et al., 2005). Resources, risks, conditions, and the interactions of these elements are presumably evaluated by an individual, in the context of its internal state and social environment, as it decides whether or not to migrate. Relatively fixed (like age class, sex, or life history strategy) and continuously variable (like body fat or lactation status) attributes of an individual's physical condition may influence its migratory propensity (Lundberg, 1987; Grayson and Wilbur, 2009; Chapman et al., 2011; Pulido, 2011; Berg et al., 2019). The terminal investment hypothesis predicts that older individuals will be more likely to accept mortality risks associated with migration to access resources that increase the likelihood of successful reproduction, compared to younger individuals who should invest in their future reproductive potential, and hence, their long-term survival (Clutton-Brock, 1984). These hypotheses suggest that migration is a behavioral adaptation to optimize fitness in variable physical environments, and that behavioral plasticity is a response to shifts in the risk-reward tradeoff over the lifetime of an individual.

An individual's internal state is also shaped by its social environment – here defined as all intraspecific interactions – through density dependent effects and transmission of information between individuals. The dominance or competitive release hypothesis predicts that less dominant individuals will migrate to avoid intraspecific competition for resources when populations reach high densities (Gauthreaux, 1982; Nelson, 1995; Mysterud et al., 2011). On the other hand, positive density dependence (Allee effects) may influence migratory propensity when remaining part of a group confers a fitness advantage (Borrello, 2012) through increased predator vigilance (many eyes) (Lima, 1995; Rieucau and Martin, 2008), reduced predation risk via dilution and confusion effects (Pulliam, 1973; Krause and Ruxton, 2002; Chapman et al., 2011), or transmission of knowledge from experienced migrants (Heyes, 1994; Mueller et al., 2013; Jesmer et al., 2018; Lowrey et al., 2020). The migratory behavior of an individual may mirror the migratory tendencies of its social group – what we term migratory "culture" – because behavior matching maintains group cohesion. These hypothesized mechanisms underpinning migratory plasticity are heavily focused on external drivers, while an individual's knowledge of its internal state and environment are given little consideration.

An implicit assumption of most research into the environmental drivers of migration is that individuals are omniscient, possessing complete and perfect knowledge of their surroundings near and far [as approximated by remotely-sensed environmental covariates, but see cultural transmission (Jesmer et al., 2018)]. However, behaviorally plastic migrants, particularly long-distance migrants, are likely making migratory decisions with less than complete knowledge of the habitat at their destination. Cognition, the processes concerned with the acquisition, retention, and use of information (Dukas, 1998, 2004; Kashetsky et al., 2021), is the lens through which an individual comes to understand its physical environment. Therefore, migratory behavior arises from an individual's 'informational state'- knowledge of its current and alternative environments, rather than the attributes of the environment itself (Blumstein and Bouskila, 1996; Avgar et al., 2013; Merkle et al., 2019).

An individual's knowledge of its environment may result from previous experience, which when encoded in the brain and retained over time is called memory (Fagan et al., 2013; Kashetsky et al., 2021). Memory encompasses two forms of information: an individual's experience of its physical environment (attribute memory) and the spatial location associated with that experience (spatial memory) (Fagan et al., 2013). Bracis and Mueller (2017) found that memory was the best cognitive predictor of long-distance migration in zebras. Abrahms et al. (2019) uncovered evidence of blue whale reliance on memory to track algal blooms. Merkle et al. (2019) were unable to replicate the migratory trajectories of mule deer without the inclusion of a spatial memory component in their individual-based simulations. However, all three of these studies focused on the cognitive processes underlying navigation during migration, rather than migratory decision-making. Memory provides behaviorally plastic migrants with a cognitive mechanism to evaluate the profitability of alternative behavioral strategies based on past range conditions. However, memory-driven migration is a response to a predicted state of the migratory range based on past experience, rather than a response to temporally proximate cues. In environments characterized by high interannual variability of resources, risks and conditions, memory-driven migration may lead to a mismatch between the timing of movement and the optimal environmental state of the target range.

Alternatively, individuals could make migratory decisions in response to information gathered about the present state of the physical environment. Individuals perceive their environment through visual, olfactory, auditory, and other sensory cues, but the information available to an organism is constrained by its perceptual range. Therefore, perception may be a more useful cognitive mechanism for guiding local movements and short-distance migrations, than for facilitating long-distance migratory movements (Bracis and Mueller, 2017). Bracis and Mueller (2017), Abrahms et al. (2019), and Merkle et al. (2019) evaluated perception as a mechanism facilitating navigation during migration in their respective systems, but found that individual responses to local forage conditions did not give rise to the observed migratory trajectories. Interestingly, all three studies compared memory and perception as cognitive drivers of migration in species of long-distance migrants (migratory destination outside of the perceptual range of an individual). To our knowledge, a similar comparative analysis has never been conducted in a population of short-distance migrants (migratory destination within the perceptual range of an individual). In focusing on navigation, these previous studies also only included individuals that had previously made the decision to migrate. The cognitive drivers of migratory decision-making have yet to be addressed empirically. Understanding how the cognitive drivers of short and long-distance migration differ will be important for predicting the plasticity of migratory behavior in response to anthropogenic habitat alteration and global climate change.

While cognition likely underpins migratory behavior, particularly in behaviorally plastic migrants, cognitive drivers of migratory decision-making receive much less attention than other hypothesized mechanisms (Kashetsky et al., 2021). Our objective is to determine if cognitive processes – specifically attribute memory and perception – influence the decisions of large herbivores to undertake short-distance, altitudinal migrations. We sought to answer this question by investigating longitudinal location data gathered from Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*, hereafter SNBS), an ideal study species because SNBS exhibit one of the highest rates of individual switching between resident and migratory behavior among ungulates (Spitz et al., 2018). We built a suite of mixed effect logistic regression models with variation in migratory status explained by cognitive and non-cognitive predictors. Our goal was to isolate the contribution of cognitive processes to migratory decision-making by controlling for the non-cognitive drivers with the most explanatory power, and then introducing the effects of cognition. We modeled attribute memory by including lagged environmental covariates reflecting range conditions experienced by an individual in the previous year. Since bighorn are a highly visual species with good long-distance eyesight (Mooring et al., 2003), we integrated perception into our models by quantifying the area and attributes of alternative ranges a bighorn could see at the time it was making a migratory decision using a viewshed analysis (ESRI, 2020). We eliminated covariates from the global and nested models using stepwise model reduction and evaluated model performance using goodness of fit statistics, finding that perception is the most important cognitive process influencing migratory propensity in SNBS.

MATERIALS AND METHODS

Focal Species and Study Site

Sierra Nevada bighorn sheep are a subspecies of partially (not all members of the population migrate) and facultatively (individuals are not fixed in their migratory strategy and may switch between years) migratory wild sheep endemic to the southern and central portions of the Sierra Nevada mountain range in eastern California (US Fish and Wildlife Service, 2007). Due to market hunting and disease transmission from domestic sheep, by the 1970s only three native SNBS herds remained (US Fish and Wildlife Service, 2007). Herds are subpopulations defined by boundaries in geographic space outlined in the 2007 SNBS Recovery Plan (US Fish and Wildlife Service, 2007). Between 1979 and 1988, those three herds were used to expand the geographic range of SNBS throughout much of the species' historic range. There are presently 14 SNBS herds, ranging in size from 9 to 138 animals, for a total population of approximately 600 individuals.

The Sierra Nevada (hereafter Sierra) mountains are 650 km long and between 75 and 125 km wide, with a north-south elevational gradient (Hill, 2006). The tallest peaks, including the highest point in the conterminous United States (Mt. Whitney; 4,421 m), are found in the southern part of the range. The western slope of the Sierra is gentle and mesic in contrast to the steep, xeric escarpment of the eastern slope (Hill, 2006). During the winter, most SNBS herds are found to the east of the Sierra crest in habitat encompassed by the range's rain shadow. Annual precipitation is highly variable, but generally falls in the form of snow between October and May, with snow persisting at high-elevations until late summer (California Department of Water Resources, 2019). Snow accumulation at high-elevations ranges between 500 and 1,500 cm annually (California Department of Water Resources, 2019). Winds near the crest of the Sierra average 43 km/h and scour snow from the alpine ridges, providing snow-free habitat for SNBS (Bair et al., 2015).

Sierra Nevada bighorn sheep summer in the alpine (elevations > 3,300 m) (Spitz et al., 2018), a habitat spanning the crest of the Sierra characterized by sparse vegetation interspersed with meadows. Average temperatures in the alpine range from daily lows of −2°C to highs of 15°C during the summer, and −14 to −1°C during the winter, with snowfall possible year-round (California Department of Water Resources, 2019). SNBS may overwinter in the alpine or at lower elevations (1,525–2,500 m) (Spitz et al., 2018). The low-elevation winter range is characterized by sage brush-steppe (*Artemisia tridentata*) plant communities. During the winter, average daily temperatures on these low-elevation ranges are between −2 and 7°C (California Department of Water Resources, 2019). SNBS may travel through mid-elevation (2,500–3,300 m) pinyon-juniper woodlands, coniferous forests, and subalpine meadows when migrating from summer to low-elevation winter range. The straight-line distance between high- and low-elevation ranges is, however, typically <5 km.

Migratory Delineation

Location data for SNBS are collected by the California Department of Fish and Wildlife (CDFW) via direct capture, ground field surveys, and very high frequency (VHF) and global positioning system (GPS) telemetry (Stephenson et al., 2012). For the purposes of this study, our animal year begins July 1st (post spring migration and lambing) and ends June 30th. Our animal years are further divided into 3-month seasons with summer defined as July–September (months 7–9), fall as October–December (months 10–12), winter as January–March (months 1–3), and spring as April–June (months 4–6). Helicopter net gun captures are conducted in the spring and fall to deploy GPS and VHF collars and for the purposes of translocating individuals between herd units. Annual ground surveys are conducted during the summer or winter seasons for every herd unit (with seasonal variability in survey timing necessary to optimize survey success). Observers undertake a full population census for each herd unit, recording the number, age, and sex of all bighorn, along with the location of marked individuals (Johnson et al., 2010a). Monthly fixed wing telemetry flights gather positional data on VHF-collared bighorn (Stephenson et al., 2012). GPS-collared animals provide between 2 and 24 daily locations, uploaded continuously to CDFW via satellite.

We used these four sources of positional data to classify the migratory behavior of individual SNBS. Migration of SNBS is altitudinal (2,000–2,500 m) over relatively short distances (4–10 km), and its fall bout (from high to low-elevation) can occur any time between November and January of the following year (Spitz et al., 2018). Spitz et al. (2017) developed an altitudinal net squared displacement (NSD) method for classifying the migratory status of SNBS, but the approach is only applicable to individuals with sufficient telemetry data. We developed a new technique to delineate migration in SNBS that can accommodate all forms of positional data, increase sample size, and allow for the fitting of more complex models. We used an elevational cutoff of 2,850 m to demarcate 'migrant' and 'resident' classes of SNBS. We selected a cutoff of 2,850 m because that elevation provided a clear separation between used high and low-elevation winter habitat across herd units based on GPS data. For any given year, animals detected below 2,850 m one or more times during the winter season (January–March) were classified as 'migrant,' while individuals not detected below 2,850 m, but observed at higher elevations were classified as 'resident.' We deemed a single detection below the elevational threshold sufficient to classify an individual as migratory based on a sensitivity analysis of GPS collared individuals. Removing individuals with few positional fixes below 2,850 m did not change the number of migrants. We assigned animals known to be alive, but not detected during a given year an "unknown" migratory status.

Given that multiple types of location data are often collected for a single individual during an animal year, we developed a hierarchical classification structure for migratory behavior based on the uncertainty of observing an individual below 2,850 m. We considered data types with the most positional fixes to provide the most reliable migratory classifications because they minimize the risk of failing to detect an individual on low-elevation winter range, if it was present. In our hierarchy, there are four levels; GPS data provides the most accurate migratory classification, followed by VHF, ground survey, and capture data. We found few conflicts between migratory classifications across levels of the hierarchy so we concluded a migratory designation could arise from any data type. We validated our migratory classification via elevational cutoff for GPS-collared bighorn against NSD classifications of migration and found that our categorizations only differed by our treatment of flexible migrants. Our classifier has an intentional migratory bias because our focus is on drivers of seasonal movements to low-elevation winter range. Our use of realized migration as a proxy for migratory decision-making rests on the assumption that all individuals that decide to migrate complete the migration, and are observed on low-elevation winter range. We believe this assumption is reasonable given that SNBS typically complete their fall migration within the span of a few days.

Range Delineation

We developed a habitat suitability metric to delineate available summer, winter high, and winter low-elevation ranges independent of present SNBS use. We chose to define ranges independent of present use to (1) accommodate individuals without GPS data, and (2) to create a temporally-static set of polygons within which we explore temporally dynamic variables. We defined three range classes (summer, high-elevation winter, and low-elevation winter) using the resource selection functions (RSFs) for SNBS presented in Spitz et al. (2020) (**Figure 1**). RSFs provide a continuous characterization of range-specific habitat based on relative intensity of use. To demarcate summer range, we used ArcGIS (ESRI, 2021) to select the largest 5% of RSF values from a raster describing the relative intensity of summer habitat use, and merged these cells into sub-seasonal range polygons, excluding areas less than 200,000 m^2 (**Figure 1C**). To define the winter ranges, we combined the raw RSF values for high and low-elevation habitat in raster cell x into a single index using the formula:

$$\left[wRSF_{low}(x) + wRSF_{high}(x)\right] \cdot ln\left[\frac{wRSF_{low}(x)}{wRSF_{high}(x)}\right]$$

where $wRSF_{\mathrm{low}}$ and $wRSF_{\mathrm{high}}$ are the winter RSF values for low and high elevation habitats in x. The index describes high and low winter habitat in a single raster with high-elevation winter range having the smallest (negative) values and low-elevation winter range having the highest (positive) values (**Figure 1**). The use of the RSF index, rather than the raw values, ensures that the classifications of high and low-elevation range are mutually exclusive. A raster cell must have both a large combined RSF

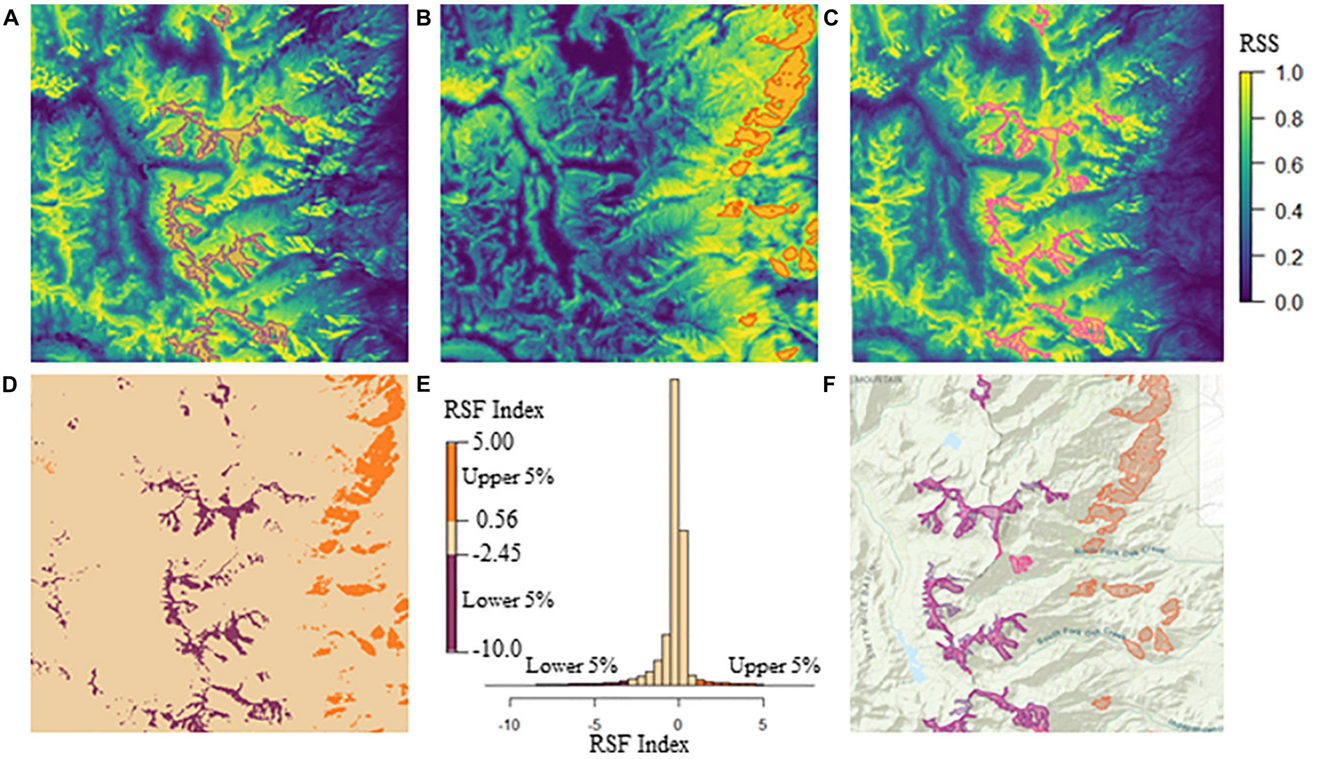

FIGURE 1 | (A) Baxter herd unit high-elevation winter range RSF with blue and yellow colors representing low and high values of relative selection strength (RSS), respectively (RSS colors should be interpreted similarly for panels **B,C**). The purple polygons delineate the Baxter high-elevation winter range considered in our analysis, and encompass the lowest 5% of RSF index values, excluding polygons with areas less than 200,000 m^2. **(B)** Baxter herd unit low-elevation winter range RSF with orange polygons delineating the low-elevation winter range considered in our analysis. Polygon boundaries encompass the highest 5% of RSF index values, excluding areas less than 200,000 m^2 in size. **(C)** Baxter herd unit summer range RSF with pink polygons delineating the summer range considered in our analysis. Polygon boundaries encompass the highest 5% of RSS values, excluding areas less than 200,000 m^2 in size. **(D)** Baxter herd unit RSF index values plotted spatially. Orange low-elevation and purple high-elevation winter range raster cells contain values that fall within the highest 5% or lowest 5% of the RSF index, respectively. Tan raster cells include all index values outside of the most extreme 10% of the data. This index map does not perfectly match the realized range polygons because areas less than 200,000 m^2 are included. **(E)** A histogram of the RSF index raster values. Orange and purple bars represent the highest and lowest 5% of values, respectively (corresponding with low and high elevation range in panel **D**). The tan bars include all values outside of the most extreme 10% of the data (corresponding with the landscape matrix in panel **D**). **(F)** Composite map of Baxter herd unit high and low-elevation winter range and summer range polygons. High-elevation winter and summer range overlap extensively, hence why the pink and purple polygons are nearly indistinguishable.

value ($wRSF_{\text{low}}(x) + wRSF_{high}(x)$), and a large range-specific RSF value (low or high) to be considered a candidate for inclusion in a winter range. We selected the largest and smallest 5% of the values to define the low-elevation and high-elevation winter sub-seasonal ranges, respectively. Both the RSF (summer range) and index (winter ranges) threshold values were chosen because the resultant sub-seasonal ranges encompassed all the GPS points of range resident (non-transient) individuals. Based on this range delineation, each herd unit contains between 1 and 35 sub-seasonal ranges for each combination of season and elevation, that we refer to in aggregate as the seasonal range (summer, high-elevation winter, and low-elevation winter). Given that individuals without GPS data cannot be attributed to a sub-seasonal range polygon, all individual associations are considered to occur at the level of the seasonal range.

Covariates

We attempted to explain variation in migratory status between individuals using cognitive predictors – perception and memory – while controlling for non-cognitive drivers – an individual's internal state and social and physical (conditions, risks, and resources) environment. The physical environment of an SNBS is characterized by forage biomass, shrub cover, snow-free area, distance to steep terrain, lion predation risk, and distance to migratory range. The biological importance and methods used to derive each covariate are explored in detail below. While change in the physical environment may underlie migration, it is unclear if SNBS are pushed from their present range by unfavorable conditions or pulled to an alternate range by favorable conditions. For an individual to be drawn to an alternative range, it must possess some information about conditions at that location. An individual may remember what it experienced at that location in the previous year (memory) or use its senses to gather information about the present state of the alternate range (perception). Memory and perception provide partial information about conditions at a distant location, but an individual may also possess complete information (omniscience), as assumed by many ecological models. An individual's propensity to migrate may also be influenced by its internal state (sex and age, as well as previous migratory history) and social environment. An individual's social environment is comprised of the migratory behavior of its social group (deme culture), the length of time its social group has existed (deme history), and the size of the group (deme size). Our base model encapsulates all the information an individual possesses about itself, its social environment, and present resources, risks, and conditions at the time it makes the decision to migrate. Our three cognitive models (omniscient, perception, memory) represent different degrees and sources of information about alternative ranges, while controlling for important base model covariates. All models and the covariates they include are described in detail below and summarized in **Table 1**.

Physical Environment Covariates

Access to resources, exposure to risks, and experienced conditions may influence migratory behavior by either attracting animals to or repelling them from a seasonal range. For each season in each sub-seasonal range (polygons delineated using the approach outlined in Section "Range Delineation"), we extracted all environmental covariates detailed below and calculated their average values. To aggregate the covariates to reflect seasonal range-level measurements (each seasonal range includes 1–35 sub-seasonal polygons), we took the area-weighted means of these averages across all sub-seasonal polygons in a range. We adjusted the spatial scaling of all means to correspond to an average value per hectare of range, and then multiplied by the aggregated range area in hectares to represent the mean seasonal quantity of the covariate.

Increased availability of forage on winter range during the winter season is a resource expected to attract SNBS, and hence positively affect their tendency to migrate. We quantified standing residual forage using the Rangeland Analysis Platform (RAP) biomass tool which combines field, satellite, meteorological, and land surface data to model vegetation productivity across the western United States (Jones et al., 2018). The RAP modeling framework estimates accumulated primary production according to plant functional type every 16 days at a spatial resolution of 30 m (Robinson et al., 2019; Jones et al., 2021). We calculated cumulative annual herbaceous biomass in kilograms per hectare (kg/ha) by summing the forb and grass biomass estimates across seasons, beginning in the spring of the preceding animal year through the winter of the focal animal year. Although the RAP biomass data suggests new growth occurs on some high-elevation winter ranges during the winter, we chose to exclude these values based on expert opinion. We did include winter biomass accumulation values for low-elevation winter range because green-up can occur as early as January given sufficient precipitation (Wehausen, 1992).

Browse comprised of woody shrubs may serve as an important nutritional resource for SNBS during the winter months when forage access is restricted by snow cover. We estimated the annual shrub cover for each sub-seasonal range using RAP's modeled fractional cover product (Jones et al., 2018; Allred et al., 2021). Our range-aggregated shrub cover index is an estimate of the total hectares of shrub cover within a range based on an area-weighted mean shrub cover across all sub-seasonal ranges. We predicted that increases in forage biomass or shrubs on winter range would increase that range's attractiveness because of an increase in nutritional resources.

While SNBS survive extreme winter conditions in the Sierra, extensive snow cover can impede movement and restrict access to forage and browse, increasing reliance on body fat reserves to stave off starvation (Monteith et al., 2013; Stephenson et al., 2020). We accounted for the potential role of snow-free area as an attractor to SNBS using daily downscaled 30 m fractional snow cover layers (Rittger et al., 2021) aggregated to produce seasonal average percent snow cover estimates per hectare for each seasonal range. Given that SNBS may migrate during either fall or winter seasons, and the seasons are of equal length, we averaged the range-aggregated mean percent snow cover for the fall and winter to encompass snow attributes at all times of the year when SNBS make migratory decisions. Finally, to calculate the total hectares of snow-free area within a range across the fall and winter seasons, we subtracted the mean percent snow cover

TABLE 1 | Covariate structure of our full and trimmed base, omniscient, perception, memory, and global models.

			Base		Omniscient		Perception		Memory		Global	
Category	**Covariate**	**Effect**	**Full**	**Trim**	**Full**	**Trim**	**Full**	**Trim**	**Full**	**Trim**	**Full**	**Trim**
Individual	Sex	0	X		▨	▨	▨	▨	▨	▨	▨	▨
	Sex: age	0	X		▨	▨	▨	▨	▨	▨	▨	▨
	Migratory history	+	X	X	*	*	*	*	*	*	X	X
	Translocation status	−	X		▨	▨	▨	▨	▨	▨	▨	▨
Social envio.	Deme culture	+	X	X	*	*	*	*	*	*	X	X
	Deme history	−	X	X	*	*	*	*	*	*	X	X
	Deme size	+	X		▨	▨	▨	▨	▨	▨	▨	▨
Physical envio.	Fall biomass WH	−	X		▨	▨	▨	▨	▨	▨	▨	▨
	Snow-free area WH	−	X		▨	▨	▨	▨	▨	▨	▨	▨
	Dist. steep WH	−	X	X	*	*	*	*	*	*	X	X
	Winter biomass WL	+	▨	▨	X		▨	▨	▨	▨	▨	▨
	Snow-free area WL	+	▨	▨	X	X	▨	▨	▨	▨	X	
	Dist. steep WL	−	▨	▨	X							
	Lions WL	−	▨	▨	X							
Cognitive	View area WL	+	▨	▨			X		▨	▨	▨	▨
	View biomass WL	+	▨	▨	▨	▨	X		▨	▨	▨	▨
	View snow-free WL	+	▨	▨	▨	▨	X	X			X	X
	View dist. steep WL	−	▨	▨	▨	▨	X	X			X	X
	Snow-free lag WH:Res	−	▨	▨	▨	▨	▨	▨	X		▨	▨
	Snow-free lag WL:Mig	+	▨	▨	▨	▨	▨	▨	X		▨	▨
	Biomass lag WH:Res	−	▨	▨	▨	▨	▨	▨	X		▨	▨
	Biomass lag WL:Mig	+	▨	▨	▨	▨	▨	▨	X		▨	▨
	Dist. steep WH:Res	−	▨	▨	▨	▨	▨	▨	X		▨	▨
	Dist. steep WL:Mig	−	▨	▨	▨	▨	▨	▨	X		▨	▨
	Lions lag WL:Mig	−	▨	▨	▨	▨	▨	▨	X		▨	▨

Symbols in the effect column represent predictions of how larger covariate values will influence migratory propensity (0 = no prediction, + = positive effect, − = negative effect). In the covariate names, WH and WL are abbreviations for "winter high-elevation range" and "winter low-elevation range" respectively. "Res" and "Mig" are indicator variables representing an individual's resident (Res = 1) or migratory (Mig = 1) status. Detailed descriptions of covariates can be found in the text. Within the model descriptions 'X' demarcates covariates that were considered in the full model and retained in the trimmed model. An asterisk (*) denotes a covariate carried over from the trimmed base model, and not subjected to stepwise model selection. Gray shading indicates that a covariate was not considered in a model.

from 100% to get the mean percent snow-free area per hectare, and multiplied by the total range area. We anticipated that as a range's snow-free area increased, SNBS attraction to the range would increase because of access to nutritional resources and reduced costs of locomotion.

Physical characteristics of high-elevation terrain may facilitate snow scouring by strong winter winds, improving forage access for SNBS. Resident SNBS [i.e., those wintering on high-elevation alpine range have been observed to use large, flat windswept plateaus (Stephenson et al., 2020)]. Large plateaus provide access to forage and allow SNBS to distance themselves from precipitous terrain where avalanches and falls down icy slopes result in mortality events (Conner et al., 2018). In contrast, on low-elevation winter range, quick access to steep terrain is important to permit migratory SNBS to escape predators not commonly found at higher elevations (Spitz et al., 2020). Hence, we expect migratory propensity to be negatively associated with increasing distance to steep terrain on both the high and low-elevation winter ranges. We calculated distance to steep terrain in meters for each 30 m DEM pixel in each sub-seasonal range, where steep terrain was defined as any pixel having >31° and <70° slope (Johnson et al., 2007; Spitz et al., 2020). We averaged the distance to steep terrain across each sub-seasonal range and calculated the area-weighted mean of the sub-seasonal ranges to produce a range-aggregated distance. Since our interest was in the amount of a range close to (low-elevation winter range) or far from (high-elevation winter range) steep terrain, we multiplied linear distance in meters by range area in hectares. Given that our seasonal ranges are similar in size and geometric configuration across herd units, large values of our proximity to steep terrain metric represent land area far from escape terrain, while smaller values characterize ranges with land close to steep terrain.

Predator density on low-elevation winter range may also drive SNBS migratory decisions in avoidance of predation risk. SNBS share their low-elevation winter range with mule deer which serve as the primary food source for mountain lions (*Puma concolor*) in the Sierra (Dellinger et al., 2020). Lions consume migratory SNBS as an alternative prey source on common winter range, making lion depredation one of the primary causes of adult mortality in SNBS (Davis et al., 2012; Conner et al., 2018). As an index of predator abundance, we used annual counts of adult lions (≥18 months) obtained following the methods described in Gammons et al. (2021). Lion counts were conducted at a recovery-unit scale, which encompasses multiple herd units. We assumed that the index applies to each herd unit within the recovery unit, an assumption supported by the extensive home ranges of lions in the Sierra. To account for noise in total lion counts arising from changes in survey effort across time, we used a 5-year moving average to smooth counts. We replaced missing years with linearly interpolated values, except if the missing year was at the beginning or end of the time series, in which case we repeated the first or final value. We approximated predation risk by calculating the predator density of each herd unit, dividing the lion count by the area of the low-elevation winter range with the expectation that predation risk should have a negative effect on SNBS migratory propensity.

The distance SNBS travel between summer and winter range also captures a form of risk incurred moving through unfamiliar or infrequently used portions of the landscape. While high-elevation winter range is a subsection of an SNBS's summer range, reaching low-elevation winter range requires traversing areas SNBS do not normally inhabit. The landscape matrix between summer and low-elevation winter ranges may contain land cover that SNBS avoid, snow that impedes movement, treacherous topography, predators, or lack resources. We used the straight-line distance, corrected for change in elevation (using the Pythagorean theorem), between the centers of summer range and low-elevation winter range as a proxy for travel-related migratory risk. We expected that larger inter-range distances would have a negative effect on SNBS migratory propensity.

Social Environment Covariates

The social environment, as it is defined here, encompasses all information an individual possesses about itself, its previous behavior, and intra-specific interactions with members of the same social group (deme) or herd unit.

SNBS sexually segregate into demes of rams and ewes, although both may migrate (Schroeder et al., 2010). Males remain with their mothers in ewe demes until they are 2 years of age when they are pushed out of their maternal group and join a ram deme (Geist and Petocz, 1977; Ruckstuhl, 1998; Pelletier, 2005; Schroeder et al., 2010). To account for ram behavioral variation between adolescence and sexual maturity, we included sex as a predictor in our models, with females serving as the reference category, and an interaction of sex and age for males.

An individual's migratory history may inform its future behavior through knowledge of the location of migratory winter range (spatial memory) and previous range conditions (attribute memory), as well as its innate inclination to migrate. We included a migratory lag covariate to account for past behavior. Bighorn that displayed resident behavior in the previous observation period (within 2 years of the focal animal year, if unobserved the prior year) were assigned a value of −1. Migrants were assigned a value of 1, and individuals previously unobserved were designated 0. We expected this variable to reflect individual behavioral persistence, and hence have a positive effect on the propensity to migrate.

Individuals translocated between ranges during the summer or fall do not possess spatial or attribute memory of migratory winter range in their adopted herd unit. If migration is facilitated by an individual's prior knowledge of the presence, location, or attributes of low-elevation winter range in their current environment, in the absence of cultural transmission of information, the behavior of translocated animals may be constrained by a lack of information. We accounted for the absence of spatial and attribute memory in translocated individuals in a novel environment by including a binary translocation covariate, with individuals receiving a value of 1 in the year they were placed on summer range in a new herd unit, and a 0 otherwise, with the expectation that this covariate will negatively affect propensity to migrate.

The behavior of an individual's social group (deme) may dictate the behavior of the individual, particularly if group membership confers a fitness advantage (Festa-Bianchet, 1991). We classified demes through a combination of expert opinion and visual review of mapped positional data for individual bighorn relative to conspecifics and prominent landscape features. In herd units with small populations where only a single social group was present, we replaced the deme designation with the herd unit identifier. To capture group influence on individual behavior, we included a 'deme culture' covariate that represents the proportion of migrants in a deme during a given animal year (excluding the focal individual), with the expectation that this covariate would positively affect an individual's propensity to migrate.

The propensity of a deme to migrate likely changes with time since establishment (typically in a previously unoccupied area) as collective knowledge of available resources, risks, and conditions is accumulated, and deme culture solidifies. We indirectly accounted for this temporal shift by including an inverse time on the landscape covariate for each deme, which we will refer to as 'deme history.' We recorded the first year a deme was detected as part of our deme classifications. Any demes present in our reference year, 1978, were assigned a value of 0. Demes emerging later than 1978 were assigned a value equal to the difference between the year they were first documented and the reference year. We anticipated that the length of time a deme has existed on the landscape would be positively correlated with member propensity to migrate due to the cultural transmission of knowledge (Jesmer et al., 2018; Lowrey et al., 2020).

Theory suggests that deme size (equivalent in our systems to local population density) should increase member migratory propensity, as it increases competition for forage (primarily on high-elevation winter range) and decreases per-capita predation risk (primarily on low-elevation winter range) (Avgar et al., 2020). Counts of female SNBS are conducted annually, although the season (winter vs. summer) during which the surveys take place varies between herd units and years. Winter counts are pre-birth pulse surveys and summer counts are post-birth pulse surveys, meaning they are not directly comparable because counts differ by the number of female lambs, assuming adult female mortality is negligible (Johnson et al., 2010b). We adjusted all winter counts to approximate summer counts by adding half of the lamb count (assuming a 50/50 sex ratio given that lambs are not identifiable as male or female) to the female winter count and shifting the count year to reflect the subsequent animal year (because our animal year begins in July). To account for noise arising in total female counts due to changes in survey effort across time, we used a five-year moving average to smooth counts. We replaced missing years with linearly interpolated values, except if the missing year was at the beginning or end of the time series, in which case we repeated the first or final value. To create our deme size index, we divided our smoothed annual female counts for each herd unit by the number of demes present during a given year. We assumed all demes were of equal size because we did not have positional data for all females in a herd to assign them to a deme. We expected deme size to have a positive effect on the propensity of its members to migrate.

Modeling

We built a suite of four binomial generalized linear mixed models ('base,' 'omniscient,' 'perception,' and 'memory'; detailed below) using Laplace approximations of maximum likelihood in the R package lme4 (Bates et al., 2015). We conducted all analyses described in the methods in R (Version 4.1.1, R Core Team, 2021), unless otherwise noted. Our response variable was the binary classification of whether a given individual migrated in a given year, with our random effects accounting for herd- and individual-level variability in the model's intercept (the basal migratory propensity). Our model inputs included 1,298 animal years of data, which encompassed 460 unique individuals across 14 herd units. We centered the means of all continuous population-level covariate values at 0 and scaled them in units of standard deviation from the mean to improve convergence and facilitate interpretation. The physical environment experienced by an individual is characterized by cumulative biomass, snow-free area, and distance to steep terrain. We excluded shrub cover and migratory distance covariates from all four of our models because their effects were highly correlated with other covariates that we deemed of greater biological importance in our study system.

We trimmed all four models using stepwise AIC model selection. Beginning with the full models, we excluded a single covariate during each iterative model run and re-calculated the AIC score of the model with a reduced fixed effects structure. The reduced model that received the lowest AIC score served as the starting model for the next step. We continued the stepwise reduction until all remaining models scored at least two $\triangle$AIC points higher than our starting model for the step, which we designated our best model.

Base Model

Our base model fixed-effects structure captures information an individual possesses about itself, its social environment, and its present physical range at the time it makes the decision to migrate. As such, this base model excludes the effects of perceptual or memorized information about the low-elevation winter range, and hence serves as an appropriate null model. The base model includes sex, an interaction of sex and age, migratory history, and translocation status as covariates representing the state of an individual (**Table 1**). The social environment experienced by an individual is comprised of deme culture, deme history, and deme size covariates. We assumed that at the time it makes the decision to migrate, an individual is located on its high-elevation winter range (a subsection of its summer range). Therefore, the individual has perfect information about the physical environment on high-elevation winter range at that point in time (i.e., the fall season). After trimming our base model, we carried the remaining fixed effects (and the random-effects structure) forward in our three other models to reflect information an individual possesses in the absence of our cognitive processes of interest. The trimmed base model covariates were not subject to stepwise model reduction in any of the cognitive models.

Omniscient Model

The omniscient model represents a common, but likely unrealistic, ecological assumption – that individuals have perfect knowledge of their environment (near and far) when making decisions about habitat use. While SNBS in our base model had perfect knowledge of the physical environment on high-elevation winter range, individuals in the omniscient model also had perfect knowledge of the low-elevation winter range environment they would experience as migrants in the coming winter. Our omniscient model thus includes all covariates from the trimmed base model, in addition to cumulative biomass, snow-free area, proximity to steep terrain, and predator density on low-elevation winter range for the focal animal year (**Table 1**).

Perception Model

Sierra Nevada bighorn sheep likely do not have perfect information about the conditions on low-elevation winter range when making migratory decisions, but may possess partial information based on the amount of migratory range they can see. While little is known definitively about the eyesight of bighorn sheep, their visual acuity is much to the chagrin of North American hunters who have compared it to a man aided by eight-powered binoculars (Geist, 1971). Bighorn have been observed to react to predators at distances of over 1 km (Geist, 1971). Bighorn also forage more efficiently in habitats with greater visibility, presumably because these landscapes permit early sighting of predators (Risenhoover and Bailey, 1985; Valdez and Krausman, 1999). While bighorn are traditionally considered to be reliant on their vision (which may also reflect a human-centric bias, as we are visual creatures), auditory and olfactory cues may also influence SNBS migratory decisions. However, non-visual sensory cues are difficult to quantify retroactively and cannot be meaningfully interpreted on the seasonal timescale of our data. Although our perceptual model only explicitly accounts for visual information available to SNBS, it generally reflects partial knowledge of the present environment, encompassing non-visual cues indirectly.

We quantified the visibility of low-elevation winter range from the summer range in each herd unit using ESRI's ArcMap Viewshed Analysis tool (ESRI, 2020) (**Figure 2**). The tool calculates the visibility of cells in a raster surface from a designated point location given line-of-site barriers imposed by topographic relief, as captured by a digital elevation model (DEM). We assumed that land cover did not restrict line-of-site, which is reasonable in our system given the low profile most vegetation and steepness of the terrain. From our summer range sub-seasonal polygons, we randomly sampled observation

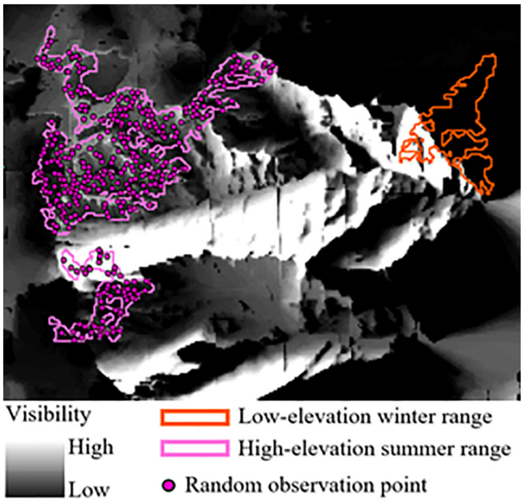

FIGURE 2 | Viewshed analysis performed on a subsection of the Olancha Peak herd unit. Pink high-elevation summer range polygons encompass a series of random observation points on which a hypothetical bighorn stands, looking out over the landscape in all directions (evaluating 360 degrees of visibility). The landscape is represented as a raster, with each raster cell receiving a binary designation of 1 (seen) or 0 (not seen). This process is repeated for every random point, with raster cells being assigned a value that represents the total number of 1 s and 0 s accumulated across all observations. Higher totals (more 1 s) represent greater visibility and are depicted in colors closer to white on the gray scale raster. Lower totals (more 0 s) indicate low visibility and are represented by colors closer to black. Bighorn on the summer range looking down at the orange low-elevation winter range polygon have good potential visibility (unobstructed by topography) of attributes on the left-most edge of the range, but visibility declines moving toward the right-most edge.

points at a density of one point per hectare (**Figure 2**). Random observation points characterize locations individuals could occupy on their summer range and look down-slope at potential low-elevation winter range. We assumed the eyeline of an SNBS was 1.75 m above the ground, ArcGIS's default observer height, because we did not have a good estimate of true eyeline height for bighorn. Although an eyeline of 1.75m may overestimate visibility given that SNBS stand, on average, 1 m at the shoulder (CDFW, 2021), the bias is consistent across herd units and should not influence our final results. It is also likely that bighorn use local high-points for visual observation which our overestimate of eyeline may represent. From a random observation point, we assigned all raster cells in our low-elevation winter range polygons a binary classification of 1 (seen) or 0 (not seen). We repeated this classification procedure for each observation point, and calculated a total visibility score for each raster cell by summing the binary classifications. We then summed the visibility score of all raster cells across an entire seasonal range. To account for differences in range size, we created a visibility index that scales between 0 and 1, with 1 indicating all raster cells on low elevation range were visible from every observation point, and 0 representing no visibility of raster cells from any observation point. We calculated our visibility index by dividing a range's total visibility score (sum of all cell visibility scores) by the total number of raster cells in a range multiplied by the total number of observed points (representing the possibility that every raster cell is seen from every observation point). The visibility index captures the relative variation in visibility between herd units, but given our numerous assumptions may not accurately represent what SNBS actually see. We expected visibility to have a positive effect on migratory propensity as a main effect (SNBS more likely to migrate when they can see more of the low-elevation range), but also to enhance the effects of other low-elevation range attributes.

In our perception model, the covariates characterizing the low-elevation winter range during the migratory window – cumulative biomass, snow-free area, and proximity to steep terrain – are multiplied by the visibility index (before scaling and centering) to represent visual information about the migratory range available to SNBS at the time they make a migratory decision. We also included (in addition to the trimmed base-model covariates) a range visibility covariate for each herd unit, taking the product of the herd unit visibility index and the area of the low-elevation winter range in hectares to capture the importance of seeing potential migratory range in the absence of specific information characterizing range attributes (**Table 1**).

Memory Model

While our first three models sought to capture an individual's knowledge of the present and/or future physical environment, individuals may also remember attributes of the ranges where they overwintered previously, and this information is expected to influence their present migratory behavior. We modeled the influence of attribute memory on migratory behavior by including interactions between last year's range-specific environmental covariates on either high-elevation (for last year's resident) or low-elevation range (for last year's migrants), and migratory history indicator variables. Animals translocated over summer/fall were assumed to rely on attribute information from their natal range. Because this model formulation necessitates excluding animal years where the migratory status of the individual in the previous year was unknown, we fit the memory model using a reduced data set (779 animal years). The memory model includes lagged cumulative biomass, snow-free area, and proximity to steep terrain covariates for both high and low-elevation winter range. We also included a lagged predator density covariate on low-elevation winter range, as well as all covariates from the trimmed base model (**Table 1**). We trimmed the memory model by removing the high and low-elevation representations of the same environmental covariate in pairs because each pair represents a single hypothesized behavioral driver. We expected that memory of a range would increase range affinity if the conditions experienced last year were good, or encourage the opposite behavior if experienced conditions were poor.

Global Model and Model Goodness of Fit

We then combined the covariates from the trimmed base, perception, omniscient, and memory models into a global model which we again trimmed using stepwise AIC model selection to determine which cognitive processes most strongly influenced migratory behavior (**Table 1**). We calculated conditional and marginal pseudo-R^2 goodness of fit statistics for all trimmed models using the MuMIn package (Barton, 2020). To evaluate the predictive capabilities of the trimmed models, we split our data into five folds based on individual ID, trained our trimmed models using four folds of the data, tested our trained models on the remaining fold, and fit ROC-AUC curves in the R package pROC (Robin et al., 2011) to both the trained and tested models. A higher ROC-AUC value (range 0–1, with 0.5 representing random chance) represents better model performance. We repeated this process until each fold had served as both testing and training data and reported the mean ROC-AUC values across all training and testing iterations. Model predictions on test data arise from the population-level estimates of the fixed effects because the testing data is an out of sample prediction containing new levels of the random effect (unique individuals) not encountered during model training.

RESULTS

The annual percentage of migratory SNBS across the species' range varied from 56 to 100%, with a mean of 81.6% (*SD* = 13.6%) (**Figure 3A**). The percentage of individuals that changed behavioral strategies between subsequent years ranged from 0 to 39.3% with a mean of 15.5% (*SD* = 10.1%) across years (**Figure 3B**). We note here that while our study sought to address the drivers of migratory behavior rather than migratory switching, Spitz (2015) considers the latter.

The base model covariates retained after stepwise model selection included migratory history, deme culture, deme history, and distance to steep terrain on high-elevation winter range. Individuals that migrated in the recent past were more likely to migrate in the focal animal year. The propensity of individuals to migrate increased as the proportion of migrants in an individual's social group increased. Individuals that were part of demes with longer histories on the landscape were more likely to migrate than those belonging to 'younger' demes. Lastly, increasing distance to steep terrain on high-elevation winter range, capturing the presence of plateaus, had a negative effect on SNBS migratory propensity. These effects all agree with our a-priori expectations based on the ecology of the system.

All cognitive models included the four retained base covariates (to capture variability unexplained by cognitive processes) and the suite of cognitive covariates kept after stepwise model reductions. The only covariate retained in the trimmed omniscient model was the snow-free area on low-elevation winter range. As expected, SNBS were more likely to migrate as the snow-free area on their migratory range increased. The trimmed perception model included visible snow-free area and visible distance to steep terrain on low-elevation winter range. SNBS were more likely to migrate if they could see a greater percentage of snow-free area and shorter distances to escape terrain on their potential migratory range. No cognitive covariates were retained in the trimmed memory model (in addition to the base covariates).

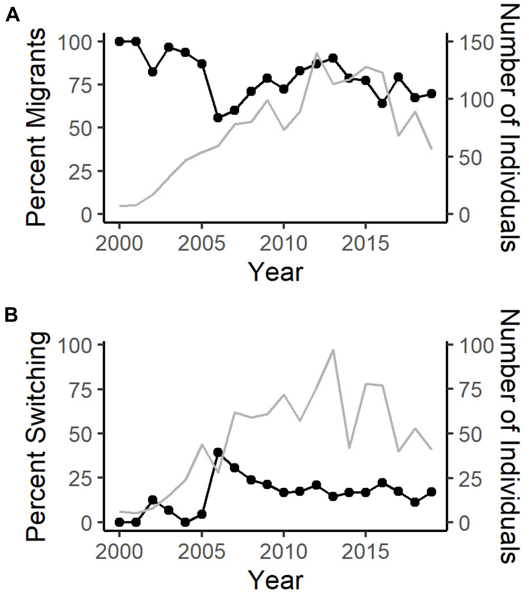

FIGURE 3 | (A) The annual percentage of migratory (detected below elevations of 2,850 m) Sierra Nevada bighorn sheep from 1998 to 2020 based on capture, ground survey, VHF, and GPS telemetry data (black line). The number of individual bighorn monitored each year varies with time and population size (gray line). **(B)** The annual percentage of Sierra bighorn that switch behavioral strategies (previous resident, present migrant or previous migrant, present resident) between years (black line). The number of individual bighorn with longitudinal data (migratory classification in the previous and present year) varies with time and population size (gray line).

The results of our trimmed global model indicate that perception is the most important cognitive process underlying SNBS migratory decision-making. The omniscient snow-free area covariate was eliminated from the global model during the stepwise model reduction process, resulting in identical trimmed global and perception models. Overall, the trimmed global model reveals that SNBS are more likely to migrate if they recently migrated (**Figure 4A**), if their social group includes a high percentage of migrants (**Figure 4B**), and if they are able to see larger amounts of snow-free area on low-elevation winter range (**Figure 4E**). SNBS are less likely to migrate if they are part of a social group that has existed for a shorter period of time (**Figure 4C**), if they have access to high-elevation habitat far from steep terrain (**Figure 4D**), and if they observe a lack of habitat close to steep terrain on potential migratory range (**Figure 4F**). Lastly, innate differences between individuals explain a considerable amount of residual variability in migratory propensity, as evidenced by the magnitude of our random effects (**Table 2**).

A comparison of model performance and goodness of fit statistics across our suite of trimmed models supports perception as the cognitive process that explains the most migratory variability in SNBS (**Table 3**). However, comparing the marginal R^2 values of the perception and base (excluding cognitive covariates) models, cognitive covariates only explain ~4% of the variation in SNBS migratory behavior compared to

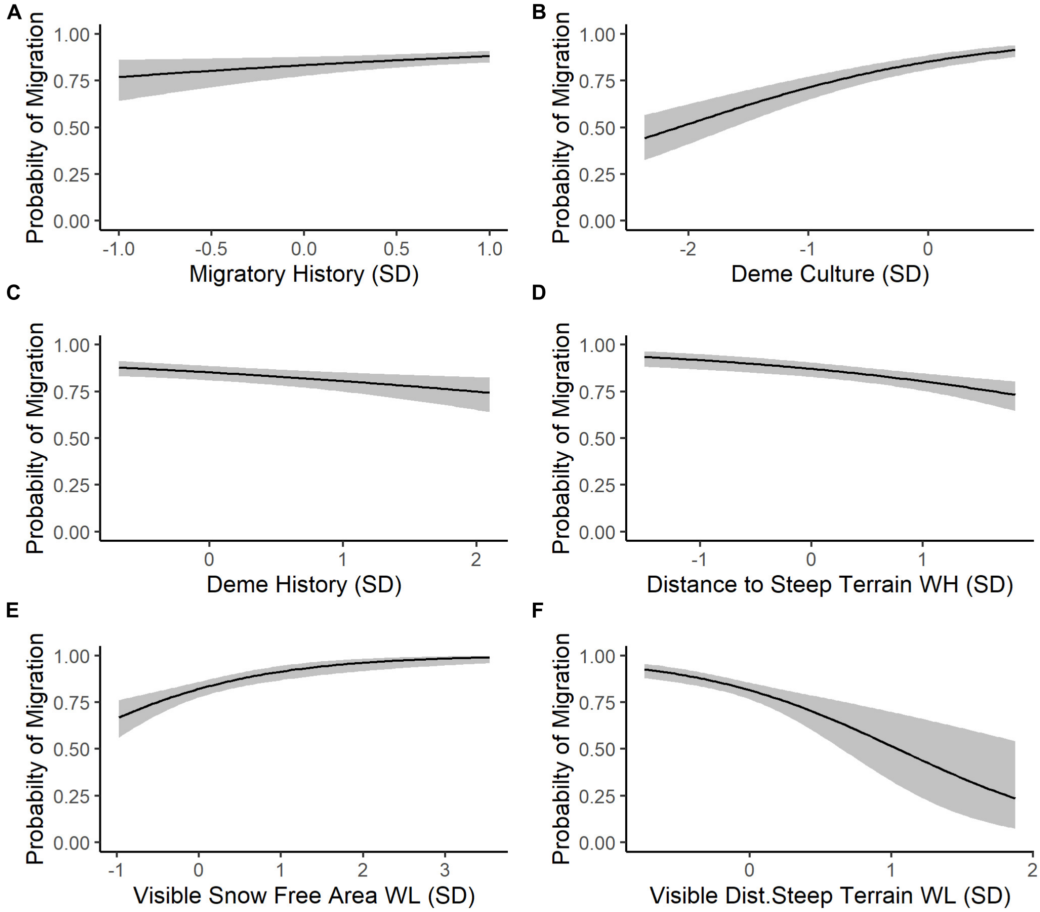

FIGURE 4 | (A) The predicted probability (black line) that an individual SNBS will migrate (with 1 representing certainty that migration will occur) given an individual's migratory history represented in units of standard deviation (SD) away from mean 0 on the odds ratio scale (back transformed from the logit scale) with the values of all other covariates held at their population mean. Predictions are made only using population-level fixed effects based on coefficient values from our trimmed global model to allow for out of sample predictions (random effect variance is excluded). The gray ribbon represents a 95% confidence interval around the prediction. We allowed each covariate to vary in turn while holding all others at their population mean so **(B)** captures the probability of migration based on the proportion of migratory individuals in the subpopulation, **(C)** depicts the probability of migration given the inverse of the length of time that an individual's subpopulation has existed on the landscape (larger values represent a shorter time on the landscape), **(D)** represents the probability of migration given the distance to steep terrain on high-elevation winter range, **(E)** captures the probability of migration based on visible, snow-free area on low-elevation winter range, and **(F)** shows the probability of migration given the visible distance to steep terrain on low-elevation winter range.

TABLE 2 | Binomial linear mixed effect model results for our trimmed global model, predicting migratory behavior (0 = resident, 1 = migrant) of Sierra Nevada bighorn sheep using a suite of base and cognitive (perceptual) fixed effects and a (1| Herd Unit:Individual) random effect structure in the the R package lme4 (Bates et al., 2015).

Model	Covariate	Coefficient	95% CI	*p*-value
Trimmed global fixed effects	Intercept	1.276	0.901, 1.650	< 0.001*
	Migratory history	0.400	0.077, 0.723	0.015*
	Deme culture	0.835	0.617, 1.052	<0.001*
	Deme history	−0.328	−0.549, −0.107	0.004*
	Distance to steep terrain WH	−0.494	−0.753, −0.235	<0.001*
	Visible snow-free Area WL	0.839	0.463, 1.215	<0.001*
	Visible dist. steep terrain WL	−1.416	−2.096, −0.736	<0.001*
Random Effect Variance	1 | Individual:Herd Unit	1.072	**Marginal R^2**	0.384
	1 | Herd Unit	0	**Conditional R^2**	0.535

*We estimated marginal and conditional pseudo-R^2 values using Nakagawa and Schielzeth (2013) method implemented in the MuMIn package (Barton, 2020). * indicates a statistically significant p-value at an alpha level of 0.05.*
Marginal and conditional R^2 values appear to the right of the bold text in the body of the table.

TABLE 3 | Model performance (AIC_C) and goodness of fit statistics (pseudo-R^2 and ROC AUC scores) for the trimmed base and cognitive models.

Trimmed model	AIC_c	ΔAIC_c	Marginal R^2	Conditional R^2	Train ROC AUC	Test ROC AUC
Perception (global)	1018.061	–	0.384	0.535	0.918	0.830
Omniscient	1022.194	4.133	0.378	0.501	0.906	0.832
Base	1027.993	5.799	0.345	0.477	0.896	0.834
Memory	–	–	0.368	0.391	0.857	0.847

We calculated AIC_C scores and marginal and conditional pseudo-R^2 values using functions implemented in the MuMIn package (Barton, 2020). The memory model cannot be directly compared to the other candidate models because it was fit using a reduced data set. We computed ROC AUC scores using the R package pROC (Robin et al., 2011) and calculated the mean ROC AUC estimate across 5 combinations of test and training data. The model uses population-level means to predict the migratory status of test individuals not encountered during model training.

~34% captured by the base model covariates (**Table 3**). While our study highlights the influence of cognitive processes on migratory decision making in SNBS, an individual's previous experiences, and present social and physical environment explain the preponderance of behavioral variation. All models had strong out-of-sample predictive capacity (**Table 3**).

DISCUSSION

Our study is the first to evaluate cognitive processes that underpin migratory decision-making in a population of short-distance, altitudinal migrants. Our results demonstrate that short-distance altitudinal migration of SNBS is, in part, a behavioral response to an individual's perception of present environmental conditions on available, low-elevation (migratory) range. An individual's sensory informational state (perception model) explained more variation in migratory behavior than memorized information (memory model) or perfect environmental knowledge (omniscient model), illustrating that individuals make migratory decisions with only partial information about their target range. While the addition of cognitive processes to our base model improved model performance, the availability of high-elevation winter habitat, an individual's social environment, and intrinsic factors explained the greatest amount of behavioral variation within the population. We refer to SNBS as perceptually-informed migrants to reflect the limited influence (or our limited ability to detect the influence) of cognitive drivers on migratory decision-making. We believe that our findings are encouraging with respect to the future persistence of SNBS. Perceptually-informed migration may result in greater behavioral plasticity in response to changes in resource phenology and distribution arising from global climate change, while migrants reliant on prediction of future environmental conditions given past experience may exhibit a lagged response to climatic variability.

Perception and Memory

Perception of present conditions on low-elevation migratory range, rather than memory of past conditions or omniscience, was the strongest cognitive predictor of short-distance altitudinal migration in SNBS. SNBS migration occurs over large changes in elevation, but short geographical distances. Steep elevational gradients in the Sierra likely favor perceptually-informed migratory decisions because visual range increases with altitude. Large changes in elevation also give rise to a condensed ecological gradient where resources, risks, and conditions shift drastically over short geographic distances (Lomolino, 2001; John and Post, 2021). Unlike long-distance migrants tracking gradual resource changes over considerable distances, SNBS can likely see a large proportion of the ecological gradient spanning their migratory route to destination range, and assess the profitability of movement. While our model may not accurately represent what bighorn can see, it captures partial sensory information about the present state of alternative ranges, which may include sensory inputs (smell and sound) that we did not explicitly represent. Our findings support our expectation that perception would be the cognitive mechanism favored by short-distance migrants because it is biologically realistic, unlike omniscience, and matches the timing of movement with changes in the environment.

The spatial scale of migratory movement limits the cognitive mechanisms available to support migratory decision-making. By our definition, long distance migrants cannot use perception of alternative range to make a migratory decision because they are moving to a location outside of their perceptual range. Long distance migrants may perceive that the environment is unfavorable on their present range and decide to migrate, but they are being pushed from their current location rather than pulled to a more favorable location, like the SNBS. Long-distance migrants may also use perception to follow a resource gradient to an alternate range (Holdo et al., 2015; Merkle et al., 2019). However, long-distance migrants cannot decide to move to a specific target destination without invoking non-perceptual cognitive processes. Individuals could rely on memory to return to a range they visited previously (Bracis and Mueller, 2017; Abrahms et al., 2019; Merkle et al., 2019), cultural transmission of knowledge from past migrants (Jesmer et al., 2018; Lowrey et al., 2020), or an innate encoding of the migratory destination (Mouritsen, 1998; Kashetsky et al., 2021). None of these cognitive mechanisms provide long-distance migrants with information about the present conditions on their destination range. Global climate change causes phenomenological shifts in events like green-up that may disproportionately impact long-distance migrants because they do not possess the information to match the timing of their movements to environmental changes on their target range.

The spatial and temporal predictability of resources, risks, and conditions may also determine which cognitive mechanisms are used by migrants. Memory-informed migrants make predictions about the present/future state of their target range based on past experience (Bracis and Mueller, 2017; Abrahms et al., 2019; Merkle et al., 2019). Effective prediction relies on consistency in the location and timing of environmental variation. High-altitude environments along steep elevational gradients, like those found in the Sierra, are not characterized by predictable variation. Birds, frogs, skinks, snails, and freshwater shrimp have all been found to adjust their life history strategies at high altitudes, producing fewer, but larger offspring partially in response to increased climatic unpredictability (Badyaev and Ghalambor, 2001). Perceptually-informed migration may be an adaptive cognitive response to environmental variability within and between years. The Sierra has the highest variability in snow events of any mountain range in the western United States, low correlation of interannual snowpack, and no discernible directional trend in snow accumulation over a 71-year time series (Cayan, 1996). If the SNBS attraction to snow-free areas observed in our system was a memory-informed response to the previous year's snow cover, individuals would likely experience a mismatch between the expected timing and location of snow-free area and present snow conditions. The timing of the first major precipitation event that drives green-up on low-elevation winter range also is highly variable between years, ranging from early autumn to mid-winter (Wehausen, 1992). If migrants depart for low-elevation winter range in advance of green-up, they face increased predation risk and are not compensated with greater forage availability. Migration in response to a past state of the environment confers fewer fitness advantages than a behavioral response to present environmental cues when environmental variability is unpredictable.

Variation in the timing of SNBS migration between years (Spitz et al., 2018) suggests that SNBS are responding to inter-annual environmental variability based on proximate cues. The existence of vacillating migration in SNBS, where individuals undertake 2–4 movements between seasonal ranges during the migratory window (Denryter et al., 2021b), also suggests that migration is a response to observed intra-annual variability. Memory may be the cognitive mechanism that underlies migration in predictable environments, while perception facilitates migration when the timing and location of resources, risks, and conditions is variable.

Habitat

An individual's migratory status is partially determined by the quality and availability of high and low-elevation winter habitat. Our results corroborate the findings of Spitz et al. (2020) who observed that habitat selection by migrant and resident SNBS was predictive of the local prevalence of migratory behavior. Similar to our study, Spitz et al. (2020) found that resident bighorn selected habitats twice as far from steep terrain as migrants. While our top model included a perceptual contextualization of low-elevation range attributes, in concurrence with Spitz et al. (2020) we found that migration is more prevalent in habitat with less snow near escape terrain. However, Spitz et al. (2020) also observed that forage availability on both high and low-elevations ranges helped to explain the frequency of migrant and resident behaviors. They concluded that migrant SNBS prioritize access to forage at the cost of increased predation risk, while residents minimize predation risk but incur increased energetic costs imposed by limited access to forage and greater thermoregulatory demands (Johnson et al., 2013; Spitz et al., 2020; Denryter et al., 2021a). While our results suggest that avoidance of snow may be of greater importance for migrants than access to forage, discrepancies between studies may result from our quantification of vegetative biomass. We used an annual measure of forage biomass on each range. Spitz et al. (2020) did not have access to these new remotely sensed products to incorporate temporally dynamic habitat attributes, and instead relied on 11-year averages of forage and snow cover. Observed habitat selection in response to long-term averages of temporally variable covariates may indicate that bighorn migration has some dependence on memory that we did not capture looking at range conditions experienced only in the previous year. In long-lived species like SNBS, complex, non-Markovian representations of memory merit further evaluation.

One habitat attribute that we did not quantify, but warrants further exploration is connectivity between high and low-elevation ranges. The distance covariate included in our model does not capture resistance to movement based on land cover attributes. Mid-elevations in the Sierra are characterized by pinyon-juniper scrub and coniferous forests. SNBS avoid forested landscapes presumably because tree cover conceals predators and increases predation risk. Contiguous mid-elevation forest cover may restrict migratory movements. However, the migratory corridors of Sierra sheep are difficult to delineate because individuals can move between seasonal ranges within a few hours. The temporal resolution of GPS fixes from collars is often too coarse to capture SNBS mid-migration. Establishing a measure of migratory connectivity in our system is an important step toward understanding the residual variation in migratory behavior between herds.

Culture

Our results show that membership to a social group with a large proportion of migrants is the strongest predictor of migratory behavior in SNBS, but time since establishment of the group determines the group's propensity to migrate, in line with the findings of Jesmer et al. (2018) and Lowrey et al. (2020). While time since establishment may also capture behavioral variation resulting from changes in group size and experienced density, the independent group density covariate in our analysis did not receive support. The increase in migratory propensity over time has been hypothesized to arise from social learning, a process grounded in shared memory across generations (Jesmer et al., 2018). When SNBS colonize or are translocated to a new area of the landscape, they possess no knowledge of migratory ranges or routes accrued from experience on their new range, other than a general awareness of previously overwintering at a high or low elevation in their natal range (migratory history). As individuals explore new habitat, they accumulate information about their surroundings, which if retained, becomes memory (Fagan et al., 2013). The strong group cohesion of SNBS permits dissemination of information within social groups between individuals. The group's collective knowledge of the landscape is a compilation of individual knowledge, and increases over time with the contribution of subsequent generations. Social learning provides a form of collective memory that is not represented in our individualistic characterization of memory.

While attribute memory did not inform SNBS migratory decision-making, the importance of a deme's history on the landscape (representative of collective memory) suggests memory is necessary to support migration. Similar to Bracis and Mueller (2017), Abrahms et al. (2019), and Merkle et al. (2019) who found memory underpinned navigation of migratory mule deer, whales, and zebras, respectively, SNBS may rely on memory to navigate to low-elevation winter range, particularly over longer geographic distances. Although we did not explicitly consider drivers of the navigation process, navigation is implicit in our model. We used an individual's migratory status in a given year as our response variable which encompasses both halves of the migratory process – decision-making and navigation. By treating a completed migration – a realization of a migratory decision – as representative of a migratory decision, we don't account for individuals who decide to migrate, but fail to navigate to an alternative range. However, it is possible that SNBS migration in a novel landscape requires numerous failed attempts before enough knowledge is accumulated to permit successful navigation to low-elevation winter range. Translocated bighorn with an abbreviated history on the landscape are less migratory than native populations, a behavioral trend attributed to an absence of collective memory (Lowrey et al., 2020). Given the prevalence of translocation as a management strategy in our system to establish SNBS in historic habitat, further study of the importance of memory for navigation between migratory ranges is warranted.

We sought to represent deme culture by quantifying the proportion of migrants in each social group in the absence of the focal individual, which may serve as a proxy for accumulated knowledge or opportunities for social learning if each migrant individual has previous experience. However, an increase in an individual's probability of migration as the migratory propensity of the group increases may simply represent the importance of remaining part of a group. Predator vigilance is important for SNBS survival, particularly while foraging, and being part of a group with "many eyes" confers a safety advantage (Lima, 1995; Rieucau and Martin, 2008). Group membership also reduces predation risk through confusion and dilution effects (Pulliam, 1973; Krause and Ruxton, 2002). While there is limited predation risk on high-elevation range during the winter, mountain lion predation events on low-elevation range are the greatest source of adult mortality for SNBS (US Fish and Wildlife Service, 2007; Johnson et al., 2013; Gammons et al., 2021). Migration to low-elevation range may become safer as the number of migrants increases for which proportion of migrants serves as a proxy. However, our deme culture covariate captures all factors common to a migratory or resident portion of a social group that explain some behavioral variation. The cultural effect size from our analysis should be interpreted with caution.

In agreement with Lowrey et al. (2020), our findings indicate that individual variability and the social environment are stronger determinants of migratory behavior than attributes of the physical environment. Our base model covariates capture 47.7% of the variability in our system and the addition of cognitive mechanisms only slightly improves model performance (pseudo-R^2 0.535). When translocating animals to establish new herds or augment existing populations, wildlife practitioners should be mindful of who they are moving if the emergence of migratory behavior is a priority. The identity of a translocated individual and migratory proclivity of its new deme are stronger determinants of migratory behavior than habitat. However, a limited understanding of the structure and composition of the social groups in our system means that changes in social dynamics when adding or removing individuals to a herd are unpredictable. If a single dominant individual is responsible for initiating migration, the behavior of a group may change with augmentations made to the social hierarchy. Translocated individuals may adopt or disrupt the social hierarchy of their new herd. Improving our understanding of SNBS social structure and migratory initiation will allow resource managers to optimize their selection of individuals for translocation to achieve desired behavioral outcomes.

Individual History

Our results agree with the findings of Spitz et al. (2018) that migratory behavior in SNBS is highly plastic. Compared to Spitz et al. (2018), we detected a higher frequency of migratory behavior (with an average of 81% vs. 63% of individual SNBS migrating each year) and a lower facultative switching rate (with an average of 15.5% vs. 25% of individuals changing migratory strategies between years). Discrepancies between studies likely arise from differences in the types and quantity of data used, as well as migratory classification techniques. Spitz et al. (2018) analyzed 262 animal years of GPS data collected between 2005 and 2016. Our study incorporated 1,298 animal years of data spanning from 1999 to 2020. We integrated multiple sources of positional data into our analysis including GPS, VHF, visual survey and capture information. Spitz et al. (2018) also used elevation-based net squared displacement to classify migration and chose to categorize individuals that exhibit vacillating or abbreviated migration (Denryter et al., 2021b) as residents. These same individuals are classified as migrants in our study because of their presence below the elevational cutoff during the migratory window. We may have detected a lower migratory switching rate than observed previously because non-traditional migrants who may more readily adopt conventional migratory strategies are already classified as migrants in our study. Our classification would indicate that no behavioral switching occurred. It should be noted that embedded in our data is an inherent migratory bias because visual counts and captures during the migratory window most often take place on low-elevation winter range where all observed individuals are migrants. While this may over-represent the prevalence of migratory behavior in the population relative to GPS-based classifications, we believe it does not affect our ability to quantify the drivers of migration.

The migratory switching rate of SNBS is one of the highest known among ungulates (Spitz et al., 2018) and this behavioral plasticity likely arises because migratory decisions are partially informed by perception of conditions on alternative ranges. SNBS may switch between migrant and resident behaviors more often than other taxa because they possess real-time information about alternative ranges that allows individuals to assess the profitability of migration relative to residency on their current range. SNBS should choose to occupy the range that affords the greatest fitness gains if the risk incurred in moving between ranges is negligible (Fryxell and Sinclair, 1988; Mysterud et al., 2011; Spitz et al., 2018). Given the short distance that SNBS travel between ranges, migration may reflect a comparative evaluation of high and low-elevation range quality based on perceptual information. Repeated comparative evaluations of habitat quality during the migratory window may explain the behavior of vacillating migrants. Interannual variation in range quality may also provide an alternative explanation for low-elevation range abandonment observed in SNBS in the 1980s and attributed to predation (Wehausen, 1996). In comparison, long-distance migrants, like caribou (*Rangifer tarandus*), have been observed to exhibit strong range fidelity even in habitat that has undergone extensive anthropogenic alteration (Dalerum et al., 2007). Given that caribou rely on spatial memory to navigate the landscape (Avgar et al., 2015), it is likely that this species' lack of behavioral plasticity in selection of migratory range is due to the predominance of memory as a cognitive driver. Sawyer et al. (2019) also found an absence of migratory plasticity among mule deer, a species reliant on spatial memory to facilitate migration (Merkle et al., 2019). The asymmetry of behavioral plasticity between cognitive drivers means that perceptually-informed migrants will be better able to tolerate the increased climatic variability that accompanies global climate change (assuming no significant loss of habitat). However, additional research is necessary to validate our hypothesized drivers of migratory switching in SNBS because the scope of our study is limited to the drivers of migration.

Our study recorded high migratory switching rates in SNBS in addition to behavioral inertia. Individuals that migrated the previous year were more likely to migrate in the present year. Spitz et al. (2018) also noted that individuals only changed migratory strategies approximately every 4 years. While this periodicity may be driven by environmental factors, it may also be a consequence of an individual's physiological condition or reproductive status. Some species reproduce and migrate in alternate years to compensate for the energetic demands of reproduction (Morrison and Bolger, 2012). Lactating SNBS ewes enter the winter season with lower body fat reserves than females who lost a lamb early or did not reproduce (Stephenson et al., 2020). Lactation may necessitate migration given the high energetic cost of residency on high-elevation range because of a lack of forage and increased thermoregulatory demands. Presently, we have little information on body condition and lambing status that could be explored in relation to migratory behavior for SNBS. However, those data, when available, should be incorporated into future studies of migratory drivers.

Management

Predicting when migratory behavior will arise in novel landscapes is a challenge for wildlife practitioners as they work to re-establish migratory populations via translocation in unoccupied native range. The frequency of facultative migration is predictable in species where perception and habitat attributes explain significant behavioral variability. For SNBS, resource managers can apply the perception and physical environment covariate predictions from our model to areas of the landscape where they are considering translocation to estimate the probability of migratory behavior emerging in an established herd. However, culture and characteristics of individuals are better predictors of migratory behavior than perception or attributes of the physical environment. Known migrants should be placed with individuals from the same social group into habitat with characteristics corresponding to migratory behavior to maximize chances of behavioral continuity in a new environment, if desirable. Re-establishing "lost" short-distance migration (Wehausen, 1996) will be easier to accomplish in species like SNBS, where perception is the primary cognitive mechanism influencing migratory decisions, because individuals (or social groups) are not reliant on prior knowledge of where and when to move. It may prove more challenging to re-establish long-distance migration to low-elevation winter range on the eastern slope of the Sierra in populations of SNBS translocated to the western slope. The Sierra crest prevents SNBS reliance on perceptual cues to evaluate range quality on the opposite slope and collective memory of this historical migration is absent in translocated populations. Environmental drivers and trial and error may be important for recovering migratory movements that span the Sierra crest. Persistent changes in the resources, risks, and conditions that drive migratory behavior, if detectable through a sensory-perceptual mechanism, may still lead to the disappearance of migration in perceptually-informed species. The disappearance of migration is of concern if it decreases a species' fitness or results in the loss of collective memory important for future migratory movements.

Conclusion

Perception is indicated as the primary cognitive mechanism underlying short-distance altitudinal migratory decisions in Sierra Nevada bighorn sheep. Perceptually-informed migrants are behaviorally plastic and able to respond to changes in resource phenology and distribution in unpredictable environments. Migrants that depend on perception will likely be more resilient to climatic unpredictability arising from global climate change than species that must rely on past experience to predict future conditions on migratory range. Perceptually-informed migration allows for the possibility of predicting the emergence of migratory behavior in novel landscapes based on habitat attributes that enhance or limit sensory perception. However, accurate predictions will require a better understanding of the interplay of habitat, culture, and individual behavioral variation and the magnitude of their influence on migratory behavior.

Future studies should focus on cognitive drivers of migratory decision-making across taxa to determine if a sensory perceptual mechanism is unique to short-distance, altitudinal migrants.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because they pertain to an endangered species. Requests to access the datasets should be directed to the Sierra Nevada Bighorn Sheep Recovery Program (asksnbs@wildlife.ca.gov).

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because previously collected data was used.

AUTHOR CONTRIBUTIONS

DB, DG, TS, and TA contributed to the development of ideas. DB, DG, CJ, and RH conducted the analysis. DB wrote the manuscript with input from all authors.

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Hierarchical, Memory-Based Movement Models for Translocated Elk (*Cervus canadensis*)

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The use of spatial memory is well-documented in many animal species and has been shown to be critical for the emergence of spatial learning. Adaptive behaviors based on learning can emerge thanks to an interdependence between the acquisition of information over time and movement decisions. The study of how spatio-ecological knowledge is constructed throughout the life of an individual has not been carried out in a quantitative and comprehensive way, hindered by the lack of knowledge of the information an animal already has of its environment at the time monitoring begins. Identifying how animals use memory to make beneficial decisions is fundamental to developing a general theory of animal movement and space use. Here we propose several mobility models based on memory and perform hierarchical Bayesian inference on 11-month trajectories of 21 elk after they were released in a completely new environment. Almost all the observed animals exhibited preferential returns to previously visited patches, such that memory and random exploration phases occurred. Memory decay was mild or negligible over the study period. The fact that individual elk rapidly become used to a relatively small number of patches was consistent with the hypothesis that they seek places with predictable resources and reduced mortality risks such as predation.

Keywords: memory-based movement models, spatial memory, attribute memory, animal learning, translocated elk, hierarchal Bayesian inference

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1. INTRODUCTION

The use of spatial memory is well-documented in many animal species. For example, humans, non-human primates and other large-brained vertebrates make movement decisions based on spatial representations of their environments (Wills et al., 2010). These representations may allow animals to move directly to important sites in their environment that lie outside of their perceptual range (Normand and Boesch, 2009; Presotto and Izar, 2010), such as resource patches, sites that connect with other high quality sites in space, or safe spots to avoid predators, and may also allow them to estimate the travel cost to reach a particular place (Lanner, 1996; Janson, 2007; Janson and Byrne, 2007; Noser and Byrne, 2007). Another type of memory, described for the first time by Schacter (1992) and retaken by Fagan et al. (2013), encodes the attributes of landscape features under the name of *attribute memory*. While spatial memory allows animals to reduce uncertainty about the location of geographical features, attribute memory reduces uncertainty concerning location-independent features of objects (Fagan et al., 2013). The information stored as attribute memory may be the abundance or types of food, and can be linked to spatial information. For example, food patch quality can be spatially encoded: patch quality is an attribute and its location is spatial information (Fagan et al., 2013). The combination of these two types of information allows animals to choose among alternative movement paths as has been observed in bumblebees (Lihoreau et al., 2011) or large herbivores (Avgar et al., 2013; Merkle et al., 2014). Identifying how animals use memory to make decisions is fundamental to developing a general theory of animal movement and space use (Gautestad and Mysterud, 2005; Morales et al., 2010; Spencer, 2012).

Memory is also critical in the emergence of spatial learning, which results from interactions with the environment and can be detected through changes in movement patterns (Mueller and Fagan, 2008). Adaptive behaviors based on learning can occur thanks to an interdependence between the acquisition of information over time and movement decisions (Falcón-Cortés et al., 2017, 2019). For instance, an animal can make decisions based on past successful experiences, resulting in a change of behavior and improved resource exploitation (Leonard, 1990; Bracis and Mueller, 2017; Jesmer et al., 2018; Merkle et al., 2019). Learning is consistent, for example, with frequent visits to certain locations, or site fidelity (Bonnell et al., 2013; Falcón-Cortés et al., 2017), and with the emergence of home range behavior or preferential travel routes (Van Moorter et al., 2009; Boyer and Walsh, 2010). The capability of learning can also bring other benefits beyond improved foraging; e.g., providing advantage in territorial defense (Potts and Lewis, 2014; Schlägel and Lewis, 2014; Schlägel et al., 2017), more effective escape from predators (Brown, 2001), and improving the route choice in migration (Bischof et al., 2012; Poor et al., 2012). Nevertheless, the connections between memory and spatial learning is not well understood. Theoretical models bring useful insights by predicting, for instance, how often memory should be used for the emergence of recurrent movements to a particular resource patch (Falcón-Cortés et al., 2017; Boyer et al., 2019).

Several theoretical studies have highlighted the role played by memory and cognitive abilities for foraging success (Boyer and Walsh, 2010), home range formation (Börger et al., 2008; Van Moorter et al., 2009; Berger-Tal and Avgar, 2012), and paved the way for inferring individual memory capacities from movement and environmental data (Avgar et al., 2013). The applications of these theoretical approaches to free-ranging animals are varied. For example, predictions of a simple memory model based on linear reinforcement through preferential revisits have been compared with the movements of capuchin monkeys, revealing movement rules found to generate very slow diffusion and heterogeneous space use (Boyer and Solis-Salas, 2014). On the other hand, Merkle et al. (2014) applied a patch-to-patch model to ranging data of American bison, finding that these animals remember valuable information about the location and quality of meadows (spatial and attribute memory) and use this information to revisit profitable locations.

The study of how spatio-ecological knowledge is constructed throughout the life of an individual has not been developed thoroughly. Data analyses that employ memory based models are promising but are often difficult to implement due to the short observation periods available, and the fact that the animals are observed in an environment already familiar to them. If memory is long-ranged, the above limitations may affect the results. To avoid these shortcomings, we used data from relocated animals. This means that the observed animals explored an unknown landscape at the start of their movement trajectories. In this new environment the spatial locations of different environmental features and patches were initially unknown to them. We analyzed the movement data from 21 relocated elk (*Cervus canadensis*) as described in Frair et al. (2007) and Wolf et al. (2009). We expected elk to show an initial exploratory phase in which the animals were getting familiarized with their new environment and collecting information about the location and quality of different habitat patches. We then expected an exploitation phase showing less random space use, eventually leading to the formation of home ranges. Furthermore, as the relocated animals came from three different sources with different degrees of similarity with the release site (see below), it is possible that some animals would show different strategies.

In a recent study, a memory-based movement model similar to the ones that we propose below was fitted to roe deer reintroduced into a novel environment, showing that home ranges in the absence of territoriality could emerge from the benefits of using memory during foraging (Ranc et al., 2020). Here we followed a similar approach, but placed emphasis on comparisons among alternative movement models. This allowed us to reveal possible differences in behaviors across individuals. We also paid special attention to the estimates of certain key parameters characterizing informed movement, such as the rate at which an animal used memory, and whether memory decayed over time and how.

We present four simple patch-to-patch movement models, defined through the probabilities of transiting from one patch to another. The simplest model is memoryless as it assumes that the transition probabilities only depend on the distance between the two patches and on the size of the target patch. For simplicity, we do not consider other patch variables such as patch quality. The remaining three models consider the role of memory. The manner in which we introduce memory in the dynamics is similar to that of Boyer and Solis-Salas (2014) and Falcón-Cortés et al. (2017): the probability to revisit a particular patch is modified by a factor which depends on the accumulated number of past visits to this patch, such that the most visited patches have a higher probability to be revisited. In these memory-based models we assume that animals remember patch locations (spatial memory) and the number of past visits to each patch (attribute memory). The main difference between these three models is the way in which animals use their memory. In the simplest case we suppose that animals have infinite memory, i.e., they can remember all the patches previously visited, and they use their memory at a constant rate. In another model we assume infinite memory but the rate at which the animal decides to use its experience increases with the number of explored patches. In the last model we relax the assumption of infinite memory by introducing a memory decay associated to each patch visit (McNamara and Houston, 1985), whereas the rate of memory use increases as in the previous model.

2. METHODS

2.1. Ranging Data

We used data collected and presented by Frair et al. (2007); see also Wolf et al. (2009). The study area consisted of 15,800 km^2 along the eastern slopes of the Rocky Mountains in central Alberta, Canada. Approximately 2,000 elk inhabited the area during the study period, from December 2000 to September 2002 (Frair et al., 2007). Elevation was 500–1,500 m and the area was largely forested (68.7% of the total area). Dominant tree species included lodgepole pine *Pinus Contorta*, white spruce *Picea Glauca*, and aspen/poplar *Populus Tremuloides* and *P. Balsamea*. Interspersed throughout the forested matrix were wet and dry meadows (7.1%), cutover forest following timber harvest (4.3%), bare soil/rock outcrops (12.3%), rivers and lakes (2.1%), and areas regenerating from wildfire or site reclamation (<1%) (Frair et al., 2007; Wolf et al., 2009).

Over the study period, female elk were translocated to the study area from three source sites within Alberta: (1) Banff and Jasper National Parks, mountainous areas with the full suite of predators present in the study area but protected from hunting, (2) Cross Ranch Conservation Area (ca 20 km southwest of Calgary), a hunted area of foothills and agricultural lands largely without predators, and (3) Elk Island National Park, a flat aspen parkland without predators or hunters, see Frair et al. (2007) for more details about these three sites. Collared animals included six females from the town site of Banff released in February 2001. Nine females were released from the Cross Area, six during December 2000 and three in December 2001, and six females were released from Elk Island between January and February 2002. The animals were captured primarily using corral traps baited with hay. These animals were transported to release areas in livestock trailers that held between 9 and 16 animals depending on the sex and age class composition. Elk were released directly from the trailers into the study area. The animals were released in a number of separate locations to increase independence between results from different individuals (Frair et al., 2007; Wolf et al., 2009).

Prior to release, translocated elk were fitted with GPS collars (LMRT4 and GPS2200, Lotek Wireless, ON, Canada) that collected locations every 2 h for up to 11 months. We used all locations of each collared animal during a season or until radio-contact was lost, the animal died, or GPS collars were retrieved via breakaway device (11 months post-release). All collars were equipped with mortality sensors that activated after 7 h of immobility. Collar tests across the range of cover and terrain conditions encountered within the study area indicated a high fix rate and positional accuracy of ≤50 m 80% of the time (Frair et al., 2007; Wolf et al., 2009).

Foraging patches were defined based on a 27-class landcover grid developed for this region (see Frair et al., 2005). The grid had a 28.5 m cell size, and an overall classification accuracy of 82.7%. Using ArcGIS (Environmental Systems Research Institute, Redlands, California), we combined those classes where elk can find forage [dry/mesic and wet meadows, shrubland, clearcuts, and reclaimed herbaceous (pipeline)] into a single foraging habitat class. Then, we converted the grid to a polygon layer without simplifying lines, which is equivalent to an 8-cell neighborhood rule for patch definition. We eliminated polygons <0.27 ha in size (essentially <3 contiguous pixels), and retained 16,782 patches for analysis. The resulting foraging patches averaged 6.93 ± 29.4 ha in size. For each elk GPS location occurring within a patch, we recorded the unique number for that patch, which allowed us to derive information on the time spent moving between foraging patches, the residency time within patches, and the return time to previously visited patches. Thus, we transformed the original GPS trajectories into a time series of patch to patch visits which included the time spent in each patch and the time traveling between patches. We assumed that most foraging occurred in these high biomass patches. **Figure 1** shows the map of the study area with the distribution of the foraging patches, as well as four representative trajectories during summer and winter for two elk.

2.2. Models

For each model below, we made the following assumptions:

- The animals were moving in a stationary $2d$ environment which consisted of a set of N available patches (resource sites), N is obtained from environmental data as detailed in the previous subsection. Patches were characterized by their area a_n, with n in $\{1, ..., N\}$. The Euclidean distance between the centroids of the patches n and m is denoted by $d_{n,m}$.
- We modeled discrete movement events: at each time step $t \rightarrow t+1$ an animal decides to move to another patch (patch-to-patch movement) following a set of rules that we will explain below. The model does not take into account the actual time spent in a patch or between patches, and consider each trajectory as a whole without making distinction between seasons.
- An animal will go from patch n to patch m with probability $P_{n,m}$. This probability were computed in different ways for each model.
- All the parameters to estimate were positive numbers.

2.2.1. Model I

The first model is Markovian as it assumes that the forager chooses to visit a patch (m) in the environment by considering the distance ($d_{n,m}$) from its current patch (n) and the area (a_m) of the patch m. We define a probability vector $\mathbf{k} = (\mathrm{k}_1, ..., \mathrm{k}_N)$ whose m-th entry denotes the probability that the animal goes to patch m from patch n. Each entry is defined by:

$$\mathrm{k}_m = \mathrm{d}_m * \mathrm{c}_m / \sum_r \mathrm{d}_r * \mathrm{c}_r, \quad r = 1, ..., N \tag{1}$$

with,

$$\mathrm{d}_m = \exp(-(d_{n,m}/\alpha)^{\beta})$$

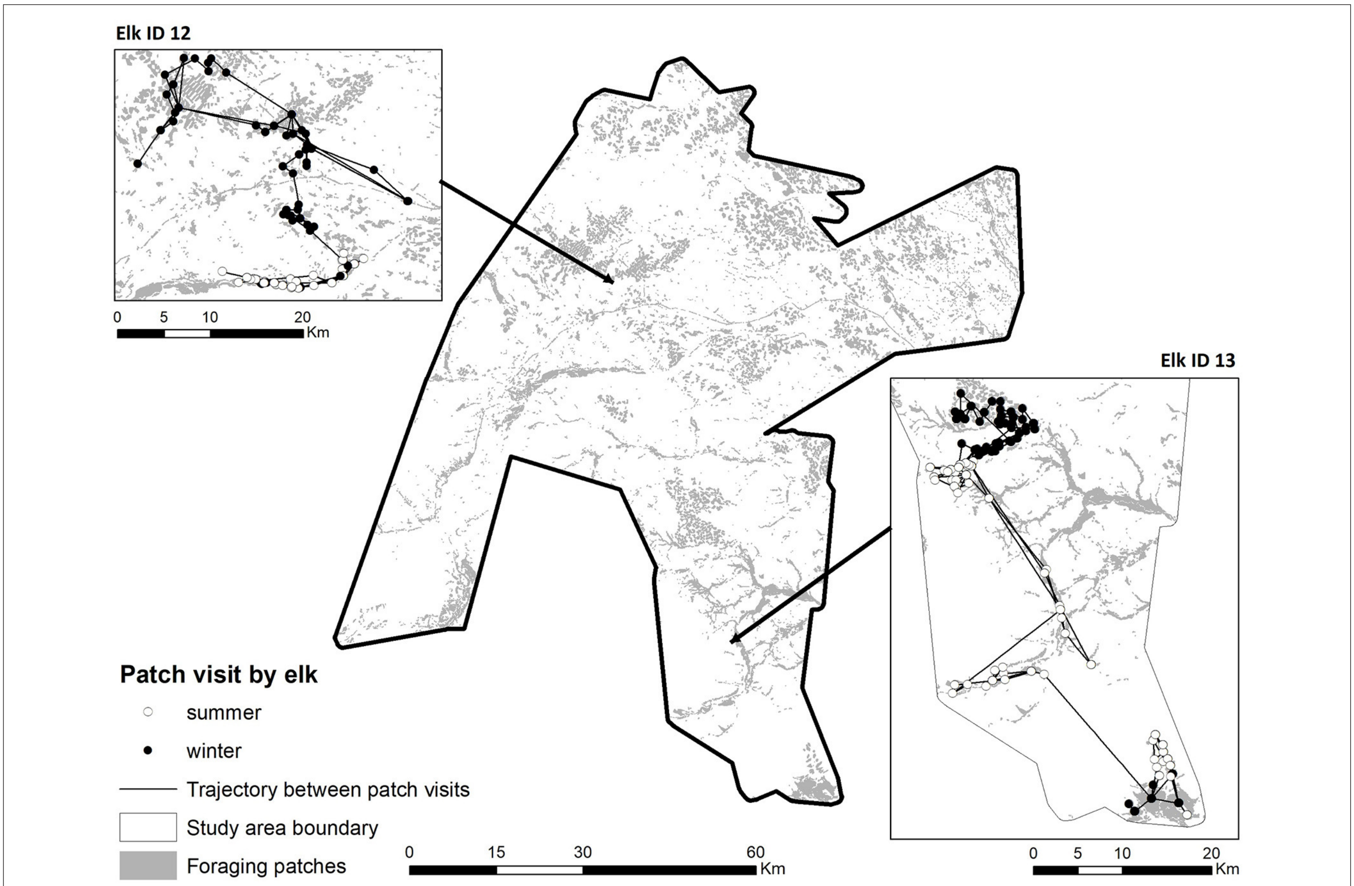

FIGURE 1 | Map of the study area with the distribution of the foraging patches. As an illustrative example, the trajectories between patches of two representative elk are displayed, in summer (white circles) and in winter (black circles).

and

$$c_m = \exp(x_m)/(1 + \exp(x_m))$$

where $x_m = \lambda a_m + \kappa$, i.e., we assume that the probability to visit patch m decays exponentially with the distance to patch n ($d_{n,m}$) and increases with the area of patch m (a_m). This model (as well as the others below) does not specifically consider a variable for the patch quality, but assumes that the animals have a higher probability to cross a large patch than a small one. We aim at obtaining a hierarchical estimation for the parameters α, β, λ, and κ (see **Table 1**).

2.2.2. Model II

We next incorporate memory effects through a parameter $q \in (0, 1)$ that defines the probability with which an animal decides to use its experience to revisit a patch. In this Model II, we assume that the forager has infinite memory, i.e., is capable of remembering all previously visited sites. Linear reinforcement is implemented by setting that the probability to choose a particular site for revisit is proportional to the accumulated number of visits to that site. This model has two types of movement decisions:

- With probability q the forager moves from patch n to patch m considering, besides the distance and area, the number of visits that patch m has received in the past. The entry m of the probability vector k is now defined by:

$$k_m = d_m * c_m * m_m / \sum_r d_r * c_r * m_r, \quad r = 1, ..., N \qquad (2)$$

  with d_m and c_m defined as in (1) and $m_m = n_m$, where n_m is the number of visits at site m until the present time t. Hence, $m_m = 0$ if the animal has never visited m.
- With probability $1-q$ the forager does not use its memory and will choose a patch m using the probability vector k defined in (1). Hence the forager performs an exploratory movement.

2.2.3. Model III

Given that the data trajectories belong to animals that were released in an unfamiliar environment, it is reasonable to hypothesize that movements were dominated by exploration at early times and by memory at later times. In such case, one may allow the memory parameter q to vary with time.

In this model, the memory parameter depends on the number of unique visited sites (UVS) of the forager up to time t. To this end, we define $\mathbf{u} = (u_1, ..., u_T)$ as a vector of length T, with T the

TABLE 1 | Prior distributions.

Parameter	Prior distribution	Interpretation
α	Normal (0, 10)	Scale parameter for the exponential function that defines the probability decay with distance.
β	Normal (0, 1)	Shape parameter for the exponential function that defines the probability decay with distance.
λ	Normal (0, 1)	Slope parameter for the logit function that defines the probability increase as function of patch area.
κ	Normal (0, 1)	Intercept parameter for the logit function that defines the probability increase as function of patch area.
q	Beta (1, 1)	Parameter that defines the memory use frequency.
ρ	Normal (0, 10)	Scale parameter for the exponential function that defines the increase of probability memory use as function of the number of unique visited sites.
ϵ	Normal (0, 1)	Shape parameter for the exponential function that defines the increase of probability memory use as function of the number of unique visited sites.
ν	Normal (0, 10)	Scale parameter for the exponential function that defines memory decay as function of time since last visit for each patch.
θ	Normal (0, 10)	Shape parameter for the exponential function that defines memory decay as function of time since last visit for each patch.

trajectory length and u_T the number of distinct patches visited by the forager up to time T ($u_1 = 1$). This vector is an observed data and q will depend on it as follows:

$$q(u_t) = 1 - \exp(-(u_t/\rho)^{\epsilon}) \tag{3}$$

In this model the total number of parameters to estimate is six, four of them already considered in Model I, plus two parameters for the increase of memory use as function of the UVS (ρ and ϵ, see **Table 1**).

2.2.4. Model IV

So far we have considered in Model II and III that foragers possess infinite memory. Besides, we have considered that reinforcement is linear, i.e., that an animal chooses a site for revisit with probability proportional to the total number of visits to that site. To incorporate memory decay, we assume in Model IV that the weight of any visit decays exponentially in time, from the value unity. Hence, the animal will forget those visits that are far away in the past and will remember very well those that are recent. Therefore, the recently visited sites have a larger probability to be visited again.

The memory factor defined in Model II now takes the form:

$$\mathrm{m}_m(t) = \sum_{i=1}^{n_m} \exp\{-[(t-t_i)/\nu]^{\theta}\} \tag{4}$$

with n_m the number of visits to patch m until time t, and t_i the time at which the i-th visit to this patch occurred. It is important to note that m_m defined in Equation (4) will be characterized by an exponential memory decay for $\theta = 1$, a stretched exponential decay for $\theta < 1$, and a super-exponential decay for $\theta > 1$. In this model, one needs to estimate eight parameters. The six parameters already considered in Model III and two more describing memory decay (ν and θ, see **Table 1**).

We fitted these four models to the data and then we performed a model comparison. We used two different tools to perform this comparison: a Posterior Predictive Check (PPC) to asses the model's ability to "predict" the data used to parameterize it, and the Watanabe-Akaike Information Criterion (WAIC) (Watanabe and Opper, 2010) as an approximation for out of sample predicting capacity of each model. These two tools help us to compare the four models above. Specifications about fitting and comparison are shown in the next sections.

2.3. Model Fitting

For some parameters such as q, the frequency of memory use, we used non-informative priors while for other parameters we used weakly informative priors (**Table 1**). All priors were truncated to take only non-negative values.

The models were fitted by using a two-stage approach as proposed by Hooten and Hefley (2019). Such fitting procedure was necessary because fitting the hierarchical level in only one stage would have been intractable computationally, regarding both memory and execution time. The first stage involves fitting the set of individual-level models independently using placeholder priors for all model parameters. Each individual has its own set of parameters for each model. This first-stage was achieved using Hamiltonian Monte Carlo (HMC) techniques implemented within the software Stan (Carpenter et al., 2017) and accessed via RStan (Stan Development Team, 2018). For all models we ran three HMC chains with 5,000 iterations for Model I and II, 10,000 iterations for Model III and IV. We discarded the first half of the iterations for warm-up, and obtained a Rhat < 1.1 and a reasonable number of effective samples (n_eff), from which the posterior distribution of all parameters were obtained. For each animal, the starting point of the fitting simulation was taken as the first visited patch observed. More details about how we performed the simulations are given in **Supplementary Material** (A Guide Example).

The second stage involved a simple MCMC algorithm to fit the full hierarchical Gaussian model using the posteriors from the first stage as priors (Hooten and Hefley, 2019). This second stage ran only one chain with 7,500 (15,000) iterations (the union of the three chains from the first stage) with 3,750

(7,500) iterations for warmup, a p—value $p_v > 0.05$ for the Geweke's statistic and a reasonable n_eff for all the relevant parameters in the different model dynamics. With this second step, we obtained the posterior distributions at the individual-level for the parameters of each animal (this fit takes into account the variability between individuals) as well as the posterior distributions of the parameters at the population-level.

2.4. Model Assessment and Comparison

In order to assess and compare the descriptive and predictive capacity of the different models, we use two kinds of tools: one qualitative and the other quantitative.

As qualitative assessments, we performed PPC on the number of unique patches visited by the animals through time. That is, for each animal we determined the number of unique patches visited (or UVS) as a function of the number of between-patch movements and compared this quantity with the predictions of simulated trajectories from the different models. For each simulated trajectory, we used parameter combinations sampled from the joint posterior of each of the corresponding model. For each model and individual animal, we simulated 1,000 trajectories, with initial position as same as the observed one, and we checked whether the observed change in number of UVS fell within the credible interval of the simulated ones. We thus could asses whether the observed pattern was consistent with the parameterized model.

As a quantitative assessment of model predictive capacity we used WAIC (Watanabe and Opper, 2010). This quantity is computed from the log-pointwise-predictive-density of each model, which was calculated from the posterior distributions obtained from the second-stage algorithm. This quantity helped us to suggest the best model for each individual: we say that a model is the best when it obtained the lowest WAIC and when the difference between this and other model's WAIC were >2.

3. RESULTS

3.1. Model Comparison

Considering the PPC for all individuals and models (**Supplementary Figure 9**), we found that six trajectories (out of the 21 individuals) were contained within the 95% credible interval (CI) of Model I, while 17 did so for Model II, 10 for Model III and 15 for Model IV.

The WAIC comparisons displayed in **Table 2** show us that Model I was not the best model for any individual, i.e., the calculated WAIC for Model I was never the smallest one for any animal. Model II had the smallest WAIC for 12 individuals. Model III was the best for nine animals, and Model IV was not the best for any individual. Therefore, in most cases, a constant rate of memory use and a linear reinforcement without memory decay provided a good description of their trajectories. These results agree qualitatively with those of the PPC.

To illustrate these general results, we present a closer analysis of the PPC and WAIC for four representative individuals that portray different kinds of behaviors on a trajectory. **Figure 2** displays the PPC for each model and animals 1, 7, 11, and 17. **Table 2** shows WAIC for all models and the same four representative animals in gray. The lowest WAIC between models for each individual is indicated in bold. We denoted as δ the difference between the WAIC of each model and the lowest one, and P_W as the effective number of parameters.

Figure 2-first Row shows the PPC results for individual 1 from Banff. Model I fitted well only the first steps of the trajectory, indicating that the animal was probably in exploration phase. Later on, the trajectory is no longer contained within Model I credible interval. Model II fitted well the final steps of the trajectory from this animal, suggesting that it followed an exploitation phase with $q = 0.68$ (from here on, all reported parameters values are the mean from their correspond posterior distribution). However, like Model I, neither Model II OR IV described the entire time series. Thus, Model III was the only acceptable model for animal 1, indicating that this particular individual increased its memory use as it explored the environment. In agreement with this finding, Model III had the lowest WAIC for this animal (**Table 2**).

Figure 2-second Row displays the PPCs for animal 7 from Cross Ranch. Here, Models I and III fitted well just the first trajectory steps, indicating a exploration phase, but overall, they were not acceptable for animal 7. In contrast, Model IV contained all the observed trajectory within its CI, suggesting that this particular individual increased its memory use as it explored the space and its memory decayed over time. Model II was also acceptable for animal 7, with a constant rate of memory use of $q = 0.38$. Therefore, animal 7 had two possible acceptable models. However, the lowest WAIC for individual 7 was for Model II, and the δ for Model IV was quite large (**Table 2**).

Figure 2-third Row corresponds to animal 11, also from Cross Ranch. Models I, III, and IV fitted well only the first steps of the observed trajectory. Model II contained within its CI the entire observed data, indicating that this particular animal used its memory at a constant and very high rate ($q = 0.80$), being most of the time visiting known patches. **Table 2** indicated the lowest WAIC for Model II, confirming the conclusion drawn from the PPC.

Figure 2-fourth Row corresponds to animal 17 from Elk Island. Model III fitted well just the first steps of the trajectory and it was not acceptable for this individual. Otherwise Models I, II, and IV contained within their respective CI all the observed trajectory. This give us three possible interpretations for animal 17: (i) The animal was always in exploratory phase. (ii) The individual used its memory at constant rate $q = 0.25$. (iii) The animal increased its memory use with time and its memory decayed over the time. **Table 2** shows that Model II actually had the lowest WAIC. Therefore, Model II can be considered as fairly good to describe and predict the trajectory of animal 17.

Table 2 summarizes models fit to each elk by their source population. Elk from 1 to 6 belong to the Banff and Jasper Source, animals from 7 to 15 to Cross Ranch, and elk from 16 to 21 to Elk Island. Models having the lowest WAIC are bolded. We can see that for all animals from Banff and Jasper, Model III was the best according to WAIC. For animals from Cross Ranch, Model II was the best for most of them. And for 66% of elk from Elk Island, Model II was the best. This suggests that animals from different source populations reacted differently to the new environment.

We discuss in the following the different parameters obtained from the fits.

TABLE 2 | WAIC from the pointwise log-likelihood for each model and each individual.

Source	ID	Model I			Model II			Model III			Model IV		
		WAIC		P_W	WAIC		P_W	WAIC		P_W	WAIC		P_W
		Est	δ	Est	Est	δ	Est	Est	δ	Est	Est	δ	Est
	1	916.51	148.28	12.06	788.51	20.28	7.27	**768.23**	**0.00**	**7.05**	801.51	33.28	11.23
	2	1864.50	221.87	8.50	1645.72	3.09	8.46	**1642.63**	**0.00**	**9.50**	1724.00	81.37	13.08
	3	2751.13	342.30	5.60	2410.23	1.40	5.73	**2408.83**	**0.00**	**10.16**	2499.04	94.21	14.99
Banff and Jasper	4	295.62	38.37	13.92	263.21	6.32	7.25	**256.89**	**0.00**	**5.80**	267.09	10.20	6.98
	5	611.20	57.11	21.75	561.77	7.68	33.43	**554.09**	**0.00**	**29.81**	653.32	99.23	76.39
	6	1161.61	169.74	21.04	994.70	2.83	31.52	**991.87**	**0.00**	**29.74**	1031.30	39.43	33.59
	7	1670.40	70.08	8.93	**1600.32**	**0.00**	**11.42**	1654.73	54.41	18.34	1689.76	89.44	24.60
	8	398.77	33.54	8.78	370.41	5.18	2.83	**365.23**	**0.00**	**1.70**	372.14	6.91	2.32
	9	846.68	54.29	11.59	**792.39**	**0.00**	**9.40**	812.27	19.88	9.68	834.13	41.74	11.40
	10	793.78	21.14	10.00	**772.64**	**0.00**	**5.81**	857.71	85.07	16.11	846.62	73.98	9.43
Cross Ranch	11	3406.23	677.88	6.71	**2728.35**	**0.00**	**7.34**	2755.67	27.32	5.99	2868.43	140.08	18.11
	12	1259.08	98.78	7.88	**1160.30**	**0.00**	**11.72**	1193.49	33.19	18.01	1223.01	62.71	15.93
	13	1732.02	160.37	7.32	**1571.65**	**0.00**	**10.58**	1577.72	6.07	9.88	1627.82	56.17	14.03
	14	1020.30	102.70	7.39	**917.60**	**0.00**	**7.29**	921.85	4.25	7.55	951.79	34.19	9.45
	15	2561.35	213.99	7.37	**2347.36**	**0.00**	**5.49**	2394.94	47.58	18.72	2467.82	120.46	23.22
	16	289.98	3.03	13.39	**286.95**	**0.00**	**15.68**	295.28	8.33	16.24	296.51	9.56	18.12
	17	499.80	34.65	27.65	**465.15**	**0.00**	**10.51**	468.45	3.30	8.85	469.82	4.67	10.55
Elk Island National Park	18	1604.57	118.75	6.80	**1485.82**	**0.00**	**7.30**	1485.86	0.04	5.80	1540.36	54.54	10.08
	19	130.98	106.86	53.14	27.41	3.29	2.84	**24.12**	**0.00**	**1.40**	26.20	1.21	1.81
	20	23.02	5.18	0.78	18.05	0.21	0.69	**17.84**	**0.00**	**0.24**	18.92	1.08	0.27
	21	241.79	72.34	50.91	**169.45**	**0.00**	**12.35**	176.70	7.25	13.92	178.27	8.82	15.73

Table shows point estimates (Est) for information criterion WAIC, the effective number of parameters (P_W), and difference between WAIC's models as δ. In bold the lowest WAIC for each individual.

3.2. Spatial Parameters

The spatial parameters α, β, λ, and κ are present in all models. The estimated values for these parameters do not vary too much between the four different models. We present here a common interpretation for these parameters. From now on the analysis focuses on the individual-level estimate of each parameter [say p_j $(j = 1:21)$] as well as on the population-level parameter p.

Parameter α, which controls the scale of the exponential decay with distance between patches (see **Supplementary Tables 6–9**) fluctuated little among individuals and across the four models [$0.60 \leq \alpha_j \leq 2.57$ (km)], with a population average between models of $\alpha = 1.71$. Parameter β, which controls the shape of the exponential decay, varied between 0.64 and 1.50 among individuals, with a population average of $\beta = 1.09$, i.e., close to the exponential shape. These values mean that distance played an important role in patch selection; the animals did not choose patches beyond one or two kilometers from their actual positions (maybe due to the patchiness of the environment) as shown by the posterior curve in **Figure 3** (Top). These results highlight the importance of "distance discounting" in movement choices, even when memory was involved.

Parameter λ, which controls the slope of the logit increase with patch area, also fluctuated little among individuals and models [$2.34 \leq \lambda_j \leq 3.70$ (ha)], with a population average of $\lambda = 2.90$. Whereas, parameter κ, which controls the intercept of the logit increase, had fluctuations between 0.02 and 0.42 among individuals, and a population average of $\kappa = 0.14$. We conclude that patch area played a significant role during patch use: the probability increased rapidly for patches of area around 1 ha, and saturated for patches with area >2 ha as shown by the posterior curve in **Figure 3** (Bottom).

3.3. Memory Use

Figure 4 displays the marginal posterior distributions of the parameter q, that defines the probability of memory use in Model II. As mentioned earlier, this model was considered the best for 12 individuals. For these individuals q had a minimum value of 0.18 and a maximum of 0.80, but most of them had a $q \approx 0.5$. Hence, according to this model, roughly half of the moves from patch to patch performed by most of the animals are informed by memory, while the other half can be considered as exploratory. For those animals with values of q far from 0.5, the trajectories are either dominated by memory (e.g., ID 11) or by exploratory movements (e.g., ID 10 and 21) .

Model III assumes that q grows from zero with the number of UVS at time t (u_t), as defined by Equation (3). **Figure 5** (Top) displays the marginal posterior distributions of the parameter ρ. This parameter defines the number of visited sites needed for the onset of important memory effects. For those individuals for which this Model III was considered

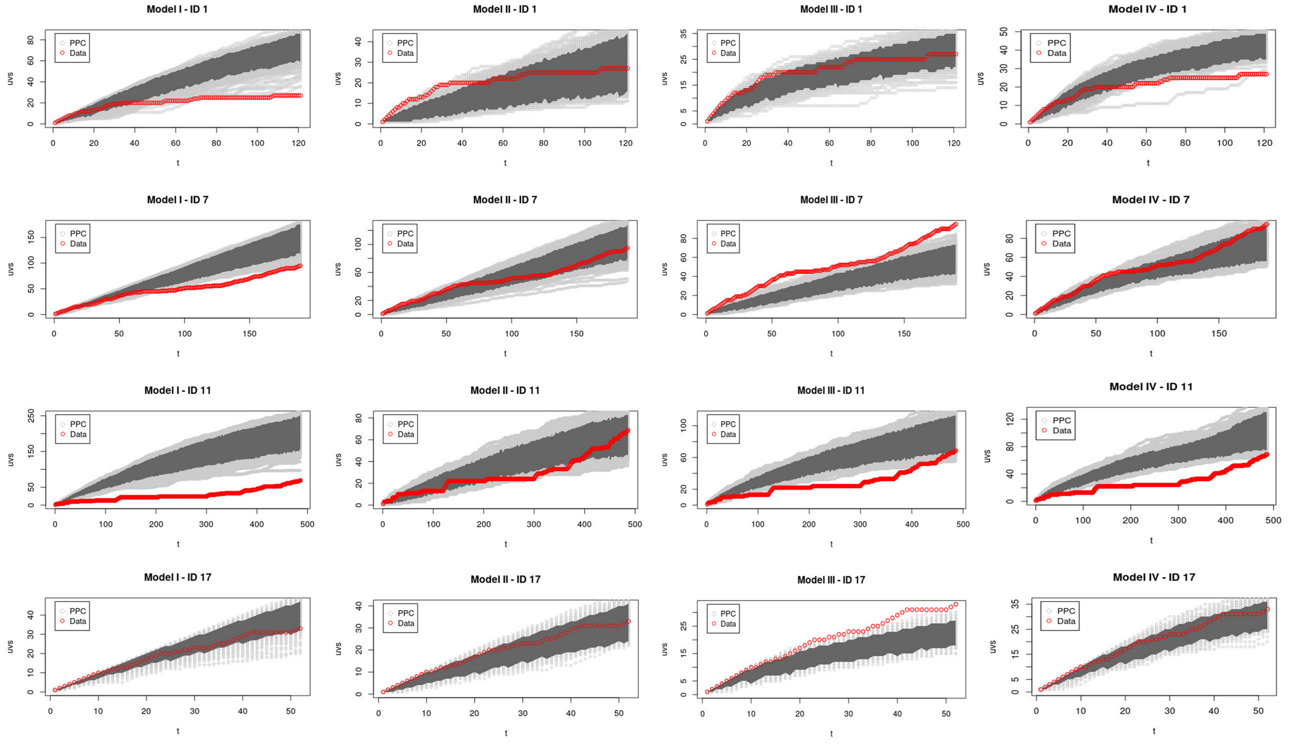

FIGURE 2 | Posterior predictive check (PPC) of models I–IV for elk with ID 1 (1st row), 7 (2nd row), 11 (3rd row), and 17 (4th row). The number of unique patches visited (UVS) is shown as a function of time. The PPC curves (obtained from simulating movement using parameters sampled from their posterior distributions) are in light gray, with the 95% CI in dark gray. The red curves were obtained from the real trajectories. The y-scale for each graph in the same row is different in order to clearly show which parts of the observed trajectory are inside of the CI.

the best ρ had values between 12.87 and 12.93. Likewise, the shape parameter ϵ **Figure 5** (Center) of the exponential ranged between 0.03 and 0.86. **Figure 5** (Bottom) displays the growth of memory use as a function of **u** at the population-level. Memory use increased rapidly to 0.5 when the unique visited sites were between 5 and 10, before slowly tending to its asymptotic value.

3.4. Memory Decay

Model IV takes into account all the assumptions of Model III, with the addition of a decay in memory. **Figure 6** (Top) displays the marginal posterior distribution of the scale parameter ν that defines the time scale of memory decay. For the population-level this parameter was estimated as $\nu = 10.78$. The mean shape parameter θ was estimated as $\theta = 0.30$, thus, memory decayed on average more slowly than exponentially, namely, as a stretched exponential [**Figure 6** (Center)]. Actually, **Figure 6** (Bottom) reveals that the weight of a visit to a patch (whose initial value is 1) often decayed very slowly in time. In many realizations, this weight remained significant (> 0.2) even after a number of steps ($t \sim 100$) much larger than the mean half-time (estimated as ~ 5 steps, or ~ 30 h in physical time). Therefore, the half-time of memory decay is not very meaningful here.

4. DISCUSSION

We have presented four simple models to fit a set of movement data collected in western Canada for 21 elk relocated into a new environment. In a first stage, Bayesian estimates were carried out at the individual-level using Hamiltonian Monte Carlo sampling. A hierarchical analysis was next implemented following the algorithm proposed in Hooten and Hefley (2019), allowing us to infer how the population as a whole is adapting to a new environment. All the results obtained at the individual-level can be found in the **Supplementary Material**. To compare and evaluate these four different models we used two tools, one quantitative the other qualitative. We used, on the one hand the Watanabe Akaike Information Criterion (WAIC) and on the other hand, a Posterior Predictive Check (PPC) based on the number of unique patches visited by the animals. The results obtained by these two tests were in agreement. We found that the trajectories of all animals were far from being described by a memoryless random walk and rather exhibited patterns of recurrent revisits to patches. Although it is possible that some unquantified patch feature makes them more attractive to the animals and hence more likely to be revisited, it is unlikely that the pattern of patch use described by the time series of unique patches visited can result from memoryless movement. In other words, unobserved patch features will have to have a

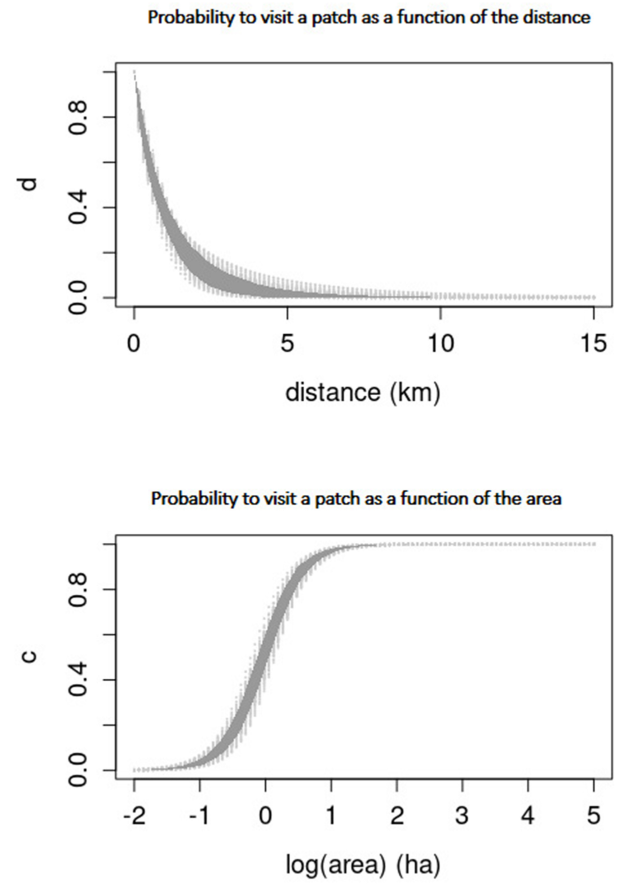

FIGURE 3 | Probability weights (see Equation 1) for choosing a patch as a function of distance **(Top)** and area **(Bottom)** at the population-level for Model I. The curves (obtained from sampling the parameters posterior distributions) are in light gray, with the 95% CI in dark gray. Very similar results were obtained for Models II–IV (see **Supplementary Figures 6–8**).

very particular distribution in order to match observed changes in patch use with time.

Our Models II and III, that consider an infinite memory capability (with constant and dynamic rate of use, respectively) combined with a linear reinforcement of the visited patches, fitted and predicted well all the trajectories. This is consistent with the results exposed by Wolf et al. (2009) in which a thorough statistical study of habitat selection found that elk had a strong tendency to select the most recently visited locations to forage instead of selecting locations only by their quality. Moreover, the values of our spatial parameters, and the dispersion curves that they defined, corresponded well with resident elk movement scales reported in Frair et al. (2005). Foraging movements were of the order of hundreds of meters and relocating moves of the order of 1.6 km. Our fourth model, that considered a dynamic use of memory as well as memory decay, was not considered as the best model for any individual. That model therefore seems too sophisticated for this population over the observation period.

The exploitation-exploration paradigm is a well known concept in ecology. There are several models that have focused on identifying and predicting these two phases from single animal trajectories (Morales et al., 2004; Jonsen et al., 2007) but they are often based on memoryless dynamics and the exploitation-exploration phases are the result of different types of random walks movements. Our Model II is memory-based and the use of memory is governed by a constant parameter q. While the exploration phase corresponds to random decisions unrelated with experience, the exploitation phase is ruled by the use of memory and the reinforcement learning acquired by experience. These simple assumptions were enough to adequately represent the temporal changes in the number of unique patches visited (**Supplementary Figure 9**) by twelve animals and therefore to identify the presence of these two phases. It is important to note that those twelve individuals for which Model II was considered the best model, as well as the nine animals for which Model III gave the best results, had a high value of q (near 1/2, typically). This suggests that these animals used memory intensively, instead of performing pure random walks (which correspond to the limit $q \to 0$). A previous study on capuchin monkeys that used a similar model found a value of q near 0.12 over a 6-month period (Boyer and Solis-Salas, 2014). In that model the environment was represented as a regular discrete lattice in which each point was a site to visit. The high values of q observed in our study could be explained by frequent decisions to return to high-resource patches or safe places, for instance those where the predation risk (by wolves or humans) is lower. The movement patterns produced by these high values of q is also consistent with the scale movement results exposed in Frair et al. (2005) that shows that elk make use of certain patches and do not explore beyond them, possibly to reduce their mortality rate and predation risk.

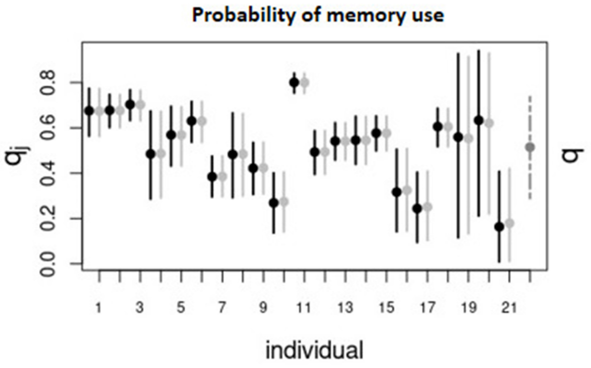

FIGURE 4 | Mean marginal posteriors (points) and 95% CI (vertical lines) for individuals (denoted by ID number) and the population (denoted by "pop") for the parameter q of Model II which controls the probability of using memory when making a movement decision. The black intervals correspond to the results of the first-stage algorithm and the solid light gray intervals correspond to the results of the hierarchical, second-stage algorithm across all animals. Dashed gray interval correspond to the population-level.

We also found that animals from the same source population tended to behave similarly: for most of the animals relocated from Banff and Jasper, Model III was considered the best model, whereas most of the elk coming from Cross Ranch and Elk Island

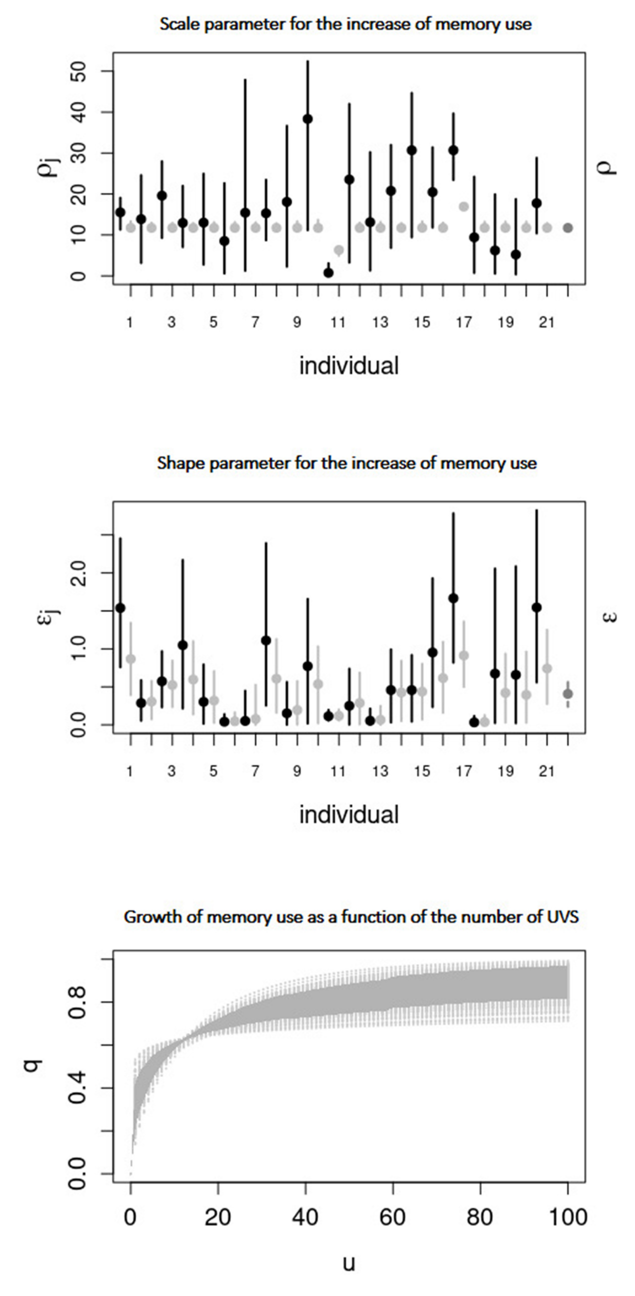

FIGURE 5 | (Top and middle) Same as **Figure 4** but for parameters ρ and ϵ (resp.) of Model III. **(Bottom)** Increase of the probability of memory use q as a function of the number of unique visited sites u at the population-level. The curves (obtained from sampling parameters from the joint posterior distributions) are in light gray, with the 95% CI in dark gray.

were best described by Model II. These results might be explained by the experience animals had before translocation: we speculate that if the original environment was similar to the new one or the animal was not naive to predators, the animal relied more heavily on memory as they visited new patches (Model III). Conversely, if the original environment was very different or the animals naive to predators, then the they kept high rates of exploration (Model II). This hypothesis stems from the fact that Banff and Jasper are mountainous with similar kinds of valley meadows as the new habitat, and that the animals were familiar with predators, while Cross Ranch and Elk Island have quite different habitat backgrounds, mostly wide-open areas dominated by agriculture and flatland, respectively, and with animals naive to predators.

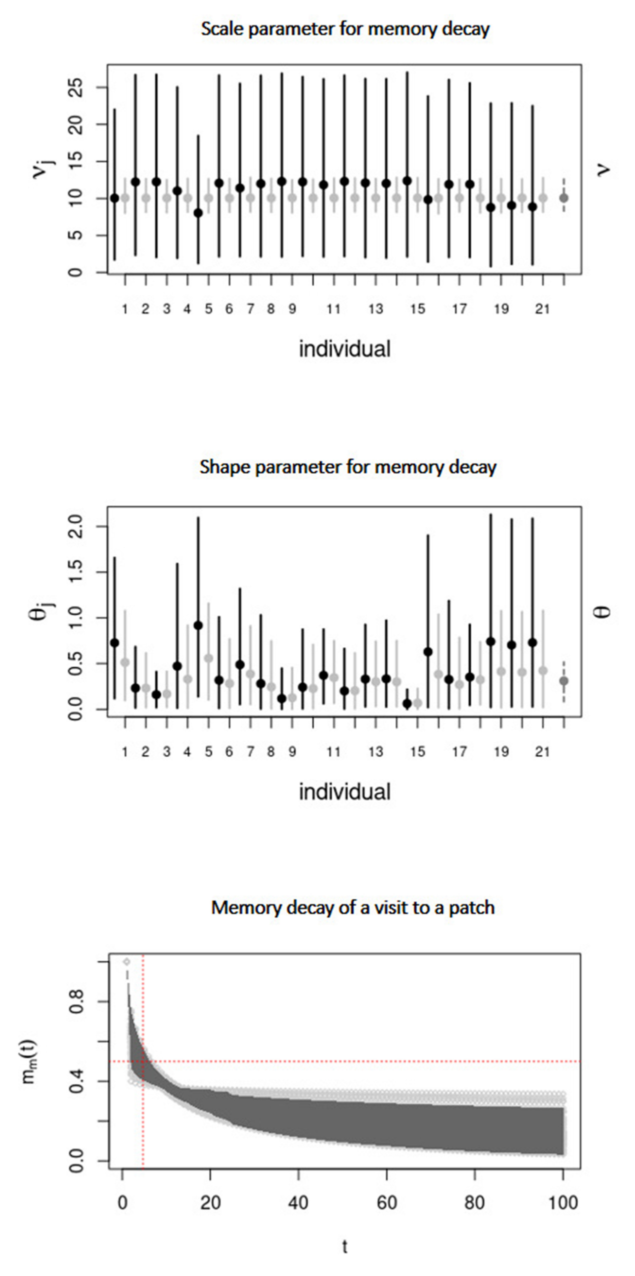

FIGURE 6 | Same as **Figure 4** for the parameters ν **(Top)** and θ **(middle)** of Model IV. **(Bottom)** Decay of the weight of a visit to a patch, $\exp\{-[(t-t_i)/\nu]^{\theta}\}$ vs. t, with , $t_i = 1$, sampled from the joint posterior distribution of ν and θ.

It is noteworthy that the model in which memory decays with time (Model IV) was not supported as the best model for any of the animals during the period of this study. This suggests that elk remember very well the places they have visited at least within

1 year. Similar findings have been reported for other species such as American bison (Merkle et al., 2014), sheep (Gautestad and Mysterud, 2005), woodland caribou (Avgar et al., 2015), or chimpanzees (Janmaat et al., 2013). These works reported evidence of long-term or very slowly decaying memory, with individuals having the ability to return sometimes to locations which had not been visited for months, or even years.

Studying the movement trajectories of translocated animals provides a promising way to understand how animals use memory. Our findings are qualitatively consistent with those recently reported by Ranc et al. (2020) on reintroduced roe deer. The movements of those animals were described by a model including both memory and resource preferences, somehow similarly to ours in the memory mode, with a reinforcement that saturated to a limiting value instead of growing linearly as here. Their fitted model was able to predict the dynamics of home range formation observed in roe deer, thus bringing support to the hypothesis that memory constitutes an important mechanism for home range emergence (Börger et al., 2008; Van Moorter et al., 2009). Although not analyzed in detail here, it is very likely that the models that we have fitted would also predict several movement properties indicative of limited space use and home range behavior in elk, but it would be important to have longer observation periods to verify this.

Our models and data analysis show a clear effect of distance and patch area on the probability of a patch being used in the next move. Thus, the configuration of patches in the landscape will affect how space is used and how memory is built. Several extensions would make these models more realistic and complex. For example, the probability of moving from one patch to another could be affected not only by distance and patch area but also by more realistic estimates of movement costs due to topography and other landscape variables such as different habitat types and predation risk between patches. Furthermore, it would be interesting to include properties of patches that would make them more or less attractive, and also to consider potential seasonal changes in these attributes.

Compared to previous work that studied habitat selection in these animals (Frair et al., 2007), our model is quite coarse as we are only considering moves from patch to patch without taking into account how animals go from one patch to another or how they move inside patches. It would also be possible to consider continuous time modeling taking into account the time that an animal spend going from one patch to another, as well as the residence time within patches. The residence time is a key movement component, which can exhibit high variations within home ranges due to a higher selectivity among habitat types (Van Moorter et al., 2016). Our modeling approach also ignored the fact that in a network of patches, nearby patches can compete as possible destinations due to their spatial configuration (Ovaskainen and Cornell, 2003). This effect can be approximated by considered all possible ways in which an individual leaving a particular patch can eventually reach another patch in the network, although the computational costs are substantial (Morales et al., 2017).

Our models could capture features of the movement patterns of the study animals with a minimum number of parameters and rather simple dynamical rules. Such simplicity is advantageous if one wishes to apply the same models to other data sets. Particularly, a single parameter q quantifies the behavior of an animal memory-wise, and can serve as a basis for comparisons between individuals or between species. Substantial variations of this parameter among individuals of a same species and in a same environment, as observed here, indicate that the movement strategies employed are quite flexible.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: please contact Prof. Evelyn Merrill (emerrill@ualberta.ca) for dataset details. Requests to access these datasets should be directed to Prof. Evelyn Merrill.

ETHICS STATEMENT

The animal study was reviewed and approved by Animal capture, handling, and transportation procedures were approved by Province of Alberta (permit No. 1432GP) and University of Alberta (permit No. 300401).

AUTHOR CONTRIBUTIONS

AF-C, DB, and JM provided the original idea and developed models. EM and JF provided the real trajectory data used in the paper. All authors discussed the general outline, the theoretical framework of the article, and contributed to comments and revisions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/full#supplementary-material

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Some Memories Never Fade: Inferring Multi-Scale Memory Effects on Habitat Selection of a Migratory Ungulate Using Step-Selection Functions

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Understanding how animals use information about their environment to make movement decisions underpins our ability to explain drivers of and predict animal movement. Memory is the cognitive process that allows species to store information about experienced landscapes, however, remains an understudied topic in movement ecology. By studying how species select for familiar locations, visited recently and in the past, we can gain insight to how they store and use local information in multiple memory types. In this study, we analyzed the movements of a migratory mule deer (*Odocoileus hemionus*) population in the Piceance Basin of Colorado, United States to investigate the influence of spatial experience over different time scales on seasonal range habitat selection. We inferred the influence of short and long-term memory from the contribution to habitat selection of previous space use within the same season and during the prior year, respectively. We fit step-selection functions to GPS collar data from 32 female deer and tested the predictive ability of covariates representing current environmental conditions and both metrics of previous space use on habitat selection, inferring the latter as the influence of memory within and between seasons (summer vs. winter). Across individuals, models incorporating covariates representing both recent and past experience and environmental covariates performed best. In the top model, locations that had been previously visited within the same season and locations from previous seasons were more strongly selected relative to environmental covariates, which we interpret as evidence for the strong influence of both short- and long-term memory in driving seasonal range habitat selection. Further, the influence of previous space uses was stronger in the summer relative to winter, which is when deer in this population demonstrated strongest philopatry to their range. Our results suggest that mule deer update their seasonal range cognitive map in real time and retain long-term information about seasonal ranges, which supports the existing theory that memory is a mechanism leading to emergent space-use patterns such as site fidelity. Lastly, these findings provide novel insight into how species store and use information over different time scales.

Keywords: short-term memory, movement ecology, mule deer, step-selection functions, space use, *Odocoileus hemionus*, cognition, long-term memory

INTRODUCTION

Animal movement is a fundamental process that underpins the relationship between species and their environment (Nathan et al., 2008; Morales et al., 2010). For decades, the study of animal movement has informed our understanding of important ecological processes, including patterns of distribution and abundance (Turchin, 1989, 1991), optimal foraging (Owen-Smith et al., 2010; Middleton et al., 2018), species interactions (Schlaegel et al., 2019), and habitat selection (Byrne et al., 2014; Avgar et al., 2016). By quantifying the factors that drive animal movement, we can better understand these ecological processes and improve predictions of when and where we observe species, which has important applications for species management and conservation (Jeltsch et al., 2013; Berger-Tal and Saltz, 2014; Allen and Singh, 2016; Tucker et al., 2018). Thus, the study of animal movement is central to both basic and applied ecology.

Animal movement is the direct result of the complicated interplay between the physiological state of the animal, the influence of abiotic and biotic environmental factors, and the constraints of the cognitive and physical capacities of the individual (Nathan et al., 2008). Animals move to fulfill basic biological needs that promote fitness (e.g., finding a mate, locating forage, avoiding risk, etc.), and these movements are directly influenced by environmental conditions (e.g., the locations of conspecifics, distribution of resources, predator abundance etc.; Nathan et al., 2008; Avgar et al., 2013b). Although the influence of environmental factors has been a primary focus of movement ecology, in recent years, studies have increasingly recognized the importance of quantifying the influence of cognition on animal movement (Schmidt et al., 2010; Avgar et al., 2013a; Fagan et al., 2013; Bracis et al., 2015; Spiegel and Crofoot, 2016). Cognitive processes, such as learning and memory, are the mechanisms that allow species to store and use information about their environment (Shettleworth, 2001). By tracking experience with their environment, animals can adjust their movements to better exploit local environments to fulfill biological needs (Benhamou, 1994). Thus, accurate explanations and predictions of movement depend on appropriately quantifying the cognitive capabilities of animals and accounting for the influence of cognition on movement decisions.

Due to advancements in field technology and analytical techniques, our ability to infer memory and its effect on movement of free-ranging animals has improved in recent years (Fagan et al., 2013). Research integrating cognitive processes into studies of animal movement has yielded important discoveries about space-use behavior, habitat selection, and foraging theory (Van Moorter et al., 2009; Wolf et al., 2009; Avgar et al., 2015; Bracis et al., 2015). This work has demonstrated that species use memory to follow annual migration routes (Bracis and Mueller, 2017; Merkle et al., 2019), and generate and maintain home range boundaries (Boerger et al., 2008; Van Moorter et al., 2009; Spencer, 2012). Further, memory can reinforce territoriality through routine patrolling of territory boundaries (Schlaegel et al., 2017). Cognition allows species to remember locations of resources (i.e., spatial memory) and their relative quality (i.e., attribute memory; Fagan et al., 2013; Merkle et al., 2014). Species that use memory optimize resource gain by increasing access to high quality forage and reducing the energetic costs associated with movement (Mcnamara and Houston, 1985; Mitchell and Powell, 2012; Merkle et al., 2014; Bracis et al., 2015; Polansky et al., 2015).

Despite the documented benefits of using memory in making movement decisions, theory suggests that memory only provides an adaptive advantage under specific environmental contexts and the use of memory is limited by physiological constraints (Dukas, 1999; Riotte-Lambert and Matthiopoulos, 2020). Species are more likely to use memory to make movement decisions in semi-heterogeneous and semi-predictable environments (Barraquand and Benhamou, 2008; Boyer and Walsh, 2010; Esposito et al., 2010; Bracis et al., 2015). When environments are highly predictable or unpredictable, there is little benefit to memory, and other factors are more likely to guide movement decisions including reliance on ingrained behaviors and the transfer of socially acquired information (Mcnamara and Houston, 1987; Riotte-Lambert and Matthiopoulos, 2020). Furthermore, processing and storing information in memory induces an energetic cost, therefore, memory is limited by storage capacities, and the accuracy and availability of information decays over time (Dukas, 1999; Burns et al., 2011). Species are regularly exposed to an abundance of information; therefore, the information that gets stored in memory must be prioritized by its relevance and how long it is useful to the individual. Memory can be compartmentalized into different memory types: short-term (or working) memory and long-term (or reference) memory (Howery et al., 1999; Cowan, 2008). Information in short-term memory decays quickly, meaning new information can be processed without reaching storage capacity. In contrast, long-term memory has minimal decay, but exacts a greater physiological cost for retaining the accuracy of information (Cowan, 2008). Although uncommon in the animal ecology literature, a few empirical studies have demonstrated that species can rely on different memory types when making movement decisions (Mettke-Hofmann and Gwinner, 2003; Oliveira-Santos et al., 2016; Vergara et al., 2019).

The above suggests that the influence of memory on animal movement will depend on the environmental and physiological constraints on cognition, and therefore it is important that we account for how these constraints might limit or promote how species use memory to make movement decisions. Within and among species, individuals are likely to rely on memory differently depending on life stage, season, life history strategies, internal state (e.g., hunger, reproduction), other animals (e.g., conspecifics, predation risk), and current environmental conditions (Mettke-Hofmann and Gwinner, 2003; Sulikowski and Burke, 2011; Morand-Ferron et al., 2019; Snell-Rood and Steck, 2019). Furthermore, given these conditions, species are likely to use memory differently depending on their physiological capacity, for example relying on different memory types or experiencing accelerated or slowed decay of information (Mettke-Hofmann, 2014). Therefore, by studying the conditions and constraints that influence how and when species use memory when making movement decisions, we can deepen our understanding of how animal cognition has evolved and gain a more mechanistic understanding of how cognition drives habitat selection, optimal foraging theory, and gives rise to emergent space-use patterns.

Our objective was to assess the influence of short- and long-term memory on habitat selection of a migratory mule deer population (*Odocoileus hemionus*) when occupying seasonal ranges. Memory typically cannot be directly observed from animal movement data, but in several past studies, memory was inferred by measuring the influence of past experience on current movement decisions (e.g., return to previously visited locations; Fagan et al., 2013; Merkle et al., 2014; Oliveira-Santos et al., 2016; Jakopak et al., 2019). To address our objectives, we inferred short- and long-term memory effects on habitat selection from utilization distributions (UDs) measured from recent (e.g., short-term) and past (e.g., long-term) space use of deer. We incorporated the UDs, which represented landscape experience, and current environmental covariates into step-selection functions, which provided inference to habitat selection by comparing locations used by animals to those deemed immediately available to them in a spatially restricted area (SSF; Fortin et al., 2005; Thurfjell et al., 2014). First, we aimed to establish if experience with the landscape, relative to environmental covariates, was an important driver of mule deer seasonal range movement. Then we assessed the degree to which covariates representing recent and past experience (i.e., use) with the landscape influenced mule deer habitat selection within and between seasons. From these results, we can gain insight to the underlying cognitive processes driving seasonal range movement. Mule deer were ideally suited for this analysis because they display strong fidelity across multiple spatial scales (e.g., return to locations, repeat migration routes, and return to seasonal ranges), which supports the likely role of memory in driving seasonal habitat selection (Northrup et al., 2016; Jakopak et al., 2019; Merkle et al., 2019; Sawyer et al., 2019). Furthermore, mule deer in this system migrate annually between summer and winter ranges, which divides the experience an animal has with the landscape and allows for assessment of the degree to which deer rely on recent compared to past experience when selecting habitat.

If memory is an important driver of habitat selection, then covariates representing previous experience should show stronger effects on habitat selection compared to environmental covariates alone in both seasons. Further, we can infer the relative influence of short- and long-term memory on deer habitat selection based on how deer select for recent experience (e.g., short-term memory) and past experience (e.g., long-term memory) with a location. We also expected that deer would demonstrate stronger selection for familiar locations in the summer compared to winter because during the summer deer birth and raise fawns and must maximize forage intake to cope with a comparatively resource-poor environment on winter ranges. Thus, we expected that the value of selecting familiar locations would be greater when there is increased pressure to maximize access to forage and offspring are most vulnerable to predation. Further, we expected that past experience would be more important in the summer based on past work showing higher fidelity on summer ranges (Northrup et al., 2021; see **Figure 1**).

MATERIALS AND METHODS

Study Area

This study took place in the Piceance Basin of northwestern Colorado, United States, near the town of Meeker (**Figure 2**). This area is topographically diverse, and the dominant vegetation consists of big sagebrush (*Artemisia tridentata*), and a pinyon pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) shrubland complex at lower elevations and a mix of mountain shrublands, quaking aspen (*Populus tremuloides*), big sagebrush and a variety of coniferous trees at higher elevations. The region experiences warm, dry summers and cold winters, with most of the moisture falling as snow during the winter. The area is popular for hunting and over the last 15 years has seen extensive exploration for and development of natural gas resources (Northrup et al., 2021). Mule deer in this area are migratory, moving between low elevation winter range and high elevation summer range. Deer typically occupy winter ranges between October and April and occupy summer ranges between May and September, though this time can vary substantially (Lendrum et al., 2014; Northrup et al., 2014b).

Mule Deer Data

Adult female mule deer were captured as a part of a larger research program that took place between January 2008 and April 2018. Throughout this time, deer were captured during December and March for a variety of project objectives. For initial captures, winter range study area boundaries were flown in a helicopter and deer were captured opportunistically using net gunning (Krausman et al., 1985). Upon capture, deer were blindfolded, hobbled, and administered 0.5 mg/kg of midazolam and 0.25 mg/kg of Azaperone. Deer were then transferred to a central processing site, where a suite of standard measures and samples were taken, deer were fit with global positioning

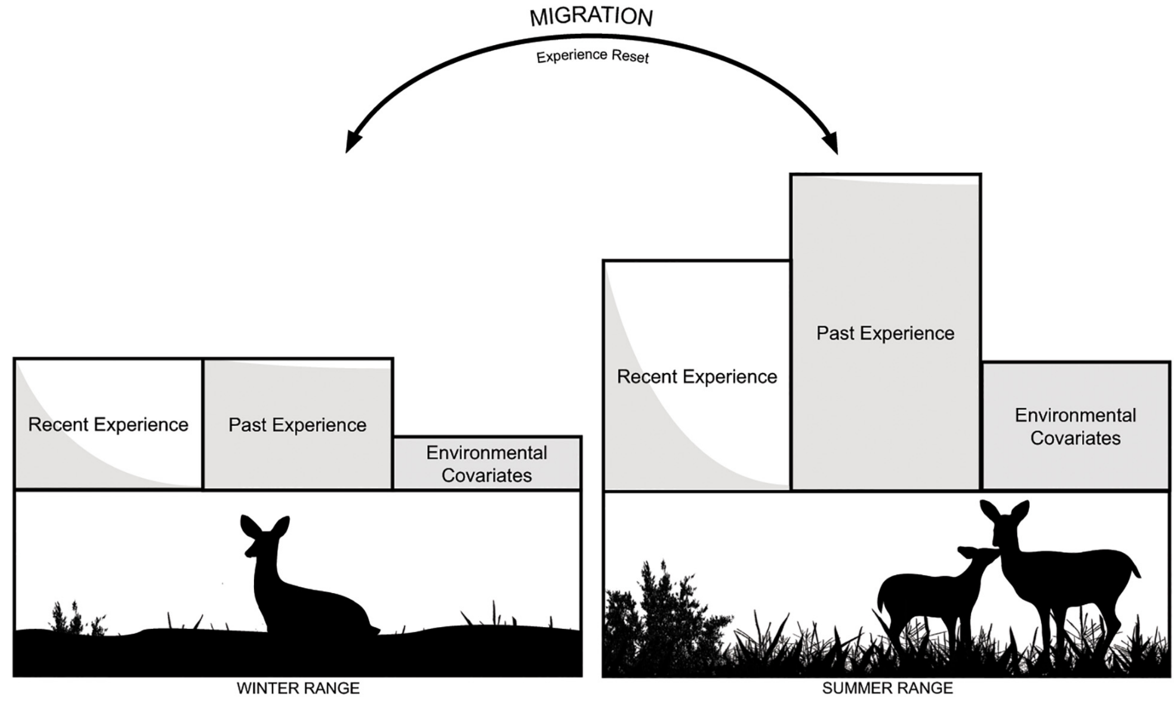

FIGURE 1 | Annual migration between seasonal ranges effectively resets the experience an animal has with the landscape, allowing for an assessment of the relative effects of previous spatial experience across multiple scales (i.e., recent experience, measured from current season space use, and past experience, measured from previous season space use) on current season habitat selection. From the influence of covariates measuring spatial experience and current environmental conditions, we infer how mule deer store and use information in both their short-term (i.e., recent experience) and long-term (i.e., past experience) memory. We expected that if memory is an important driver of habitat selection, covariates measuring both types of experience would show stronger effects on habitat selection than environmental covariates. Summer rangers have greater resource availability than winter ranges, and deer birth and raise fawns during the summer months. Accordingly, we expected that deer would demonstrate stronger selection for covariates measuring experience in the summer compared to winter, and the influence of past experience would be greater in the summer.

system radio collars (G2110D Advanced Telemetry Systems, Isanti, MN, United States) and released on site. Northrup et al. (2014a) provide more in-depth detail on the capture procedure and the suite of measures and samples taken. All procedures were approved by the Colorado Parks and Wildlife Institutional Animal Care and Use Committee (protocol numbers 17-2008 and 01-2012) and followed the guidelines of the American Society of Mammalogists (Sikes, 2016).

Between 2010 and 2013, we aimed to track individual deer over multiple years by recapturing them and replacing collars. In the years following the initial capture, 40 previously captured deer were located using very high frequency (VHF) radio telemetry and captured using net guns. All procedures described above were followed, but collars were replaced each December. For this current analysis, we focused on data collected between October 2011 and September 2013. During this time, collars were set to attempt a relocation every 30 min between October and April and every hour between May and September. We divided data into summer or winter range based on a visual assessment of the migrations of each individual deer because mule deer sometimes demonstrate irregular movements that other standard methods of defining migrations, such as net square displacement, would not accurately capture. We determined that a deer had left their summer or winter range when they made consistent movement away from their established range and did not return until the following season. We similarly determined that a deer had arrived on their winter or summer range when, after migration initiation, they showed localized movements in an area that eventually became part of their range. For the below analyses, we excluded all locations deemed to be during migration.

General Statistical Framework

We examined the habitat selection patterns of mule deer on their winter and summer ranges using step-selection functions. Following Avgar et al. (2016), we generated random movements by drawing step lengths (the distance between relocations) from a gamma distribution with mean and standard deviation for each individual equal to the empirical mean and standard deviation of step lengths. We drew turn angles (i.e., the difference in bearing between the previous and current movement) from a uniform circular distribution. For each used location, we drew 10 available locations and intersected them with the below environmental and memory covariates.

Environmental Covariates

Past research on mule deer in this area has found deer to respond to a number of natural and anthropogenic factors when selecting habitat (Northrup et al., 2015, 2021). Because our intent was to understand how previous experience, quantified through previous space use, influenced deer habitat selection

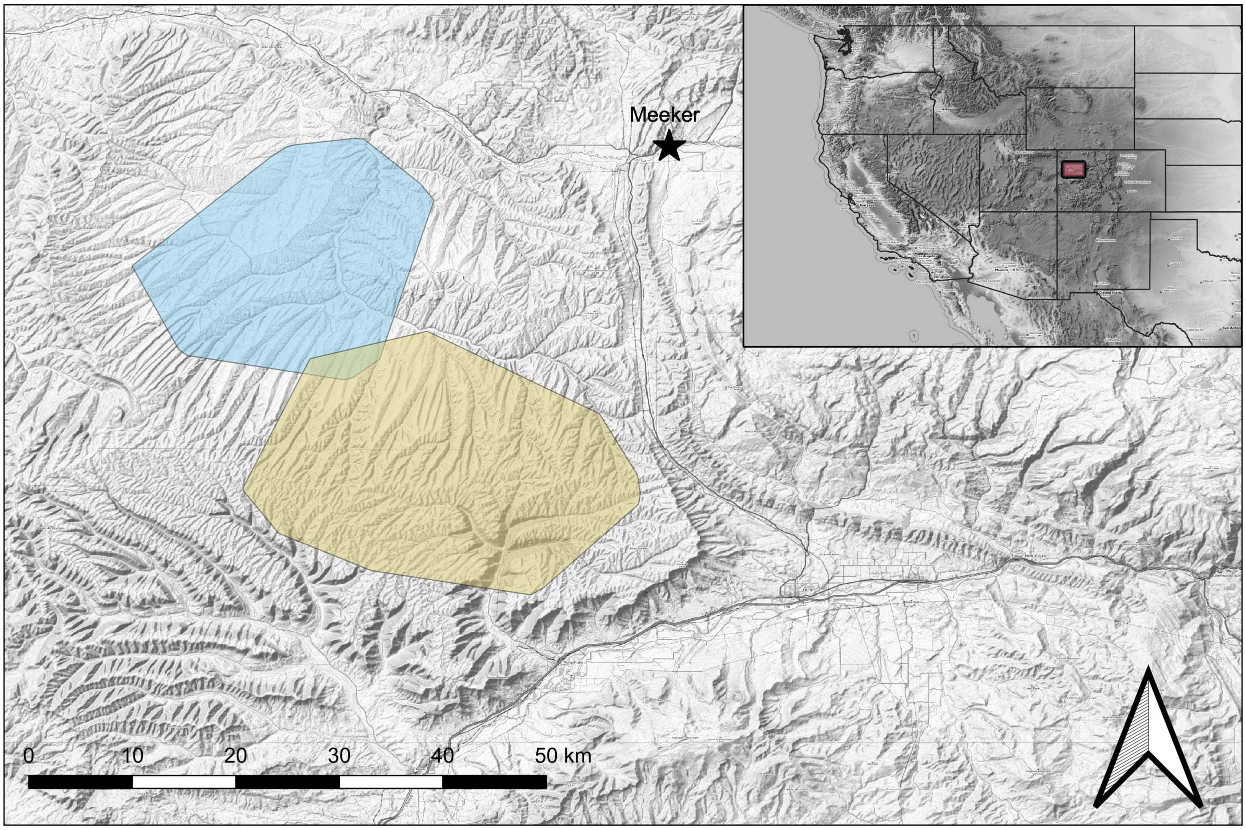

FIGURE 2 | Winter (blue) and summer (yellow) ranges for mule deer in the Piceance Basin, Colorado, United States. Map was produced using QGIS 3.6.3 (QGIS Development Team, 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://www.qgis.osgeo.org/). Base map by OpenTopoMap (Kartendarstellung: © OpenTopoMap; http://www.opentopomap.org) under creative common license CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0/).

while accounting for other environmental factors, we chose covariates based on these analyses. Specifically, for winter models, we assessed habitat selection relative to a terrain ruggedness index (*TRI*), elevation (*elev*), distance to treed edges (*edge*), snow depth (*snow*), and the land cover categories representing barren land (*barren*), shrublands (*shrub*), and grasslands (*grass*) with treed land cover as the reference category. For summer models, we examined habitat selection relative to *TRI, elev,* and *edge* as in the winter models, but also examined the normalized difference vegetation index (*NDVI*). Further, because there was little barren land cover, we combined *barren* and *grass* into a single category (*open*). In addition, because this area had ongoing active natural gas exploration and development, we also assessed the response of deer to the distance to well pads (*dpads*) and the distance to roads (*drds*) for models fit to both seasons.

Covariates Representing Recent and Past Spatial Experience

To meet our objectives, we aimed to quantify covariates representing recent and past experience with a location. Previous analysis of the deer movement data (Northrup et al., 2016) derived a UD for each individual in our sample by fitting continuous time correlated random walk models using the "crawl" package (Johnson et al., 2008; Johnson and London, 2018) in the R statistical software (R Core Team, 2020). These UDs were calculated at a 5 m × 5 m resolution and provide an estimate of the probability that an animal had been within a given 5 m × 5 m cell during the previous year, which we assumed equated to the relative amount of experience each deer had with that cell. Because deer migrate each year, the previous year's UD should capture their past experience with each seasonal range. We used UDs fit to winter range data for winter 2011/2012 as a representation of past experience for habitat selection models (see below) fit to data from winter 2012/2013 and UDs fit to summer range data for summer 2012 for habitat selection models fit to data for summer 2013. We extracted these UD values for every used and available location and termed this covariate *prev_ud*.

To quantify recent experience, we undertook a procedure that calculates metrics equivalent to a daily UD. To do this, we estimated the probability that a deer had been at a given used or available location for every day during the current season prior to the day the focal fix was taken on. To do this, we followed the same general approach as Northrup et al. (2016). Using the "crawl" package (Johnson et al., 2008; Johnson and London, 2018), we fit continuous time correlated random walk models to data from each individual and season. Next, we used these models to predict the location of each animal for every minute they were on their seasonal range. Under this approach, for each minute, the model produces a bivariate normal distribution, which can be used to calculate the probability that the animal was at any location in the study area at that minute. By summing over every distribution for each minute prior to the focal location, we can obtain the probability that the animal had been at that location previously. We thus calculated this probability for each used and available location. To avoid overly weighting very recent experiences, we excluded distributions from the 24 h prior to the focal location from these calculations. Further, to ensure that our results were robust to our choice of the amount of time to exclude, we conducted a sensitivity analysis by also fitting our models excluding locations from the previous 7 days. We termed the covariate representing recent experience *curr_ud* to indicate that it represents the current year's UD to that point in time.

Model Fitting

Previous research in this area has shown mule deer to have strong differences in habitat selection patterns by time of day (Northrup et al., 2015). Thus, we split data by summer and winter range and time of day, with nighttime determined to be the time between sunset and sunrise. Sunrise and sunset were calculated using geographical position and time of day. We then took a tiered approach to model fitting. We expected recent experience should decay over time because, presumably, recent experience should be stored in short-term memory, which has a limited capacity and the availability and accuracy of information decays quickly (Cowan, 2008; Merkle et al., 2014). To estimate decay of recent experience, we followed the general approach of Merkle et al. (2014), who used the following decay function for memory: $\frac{1}{1+k \times t}$ where k is the decay coefficient, with larger values equating to faster decay of memory, and t representing the time since the animal was at a location. For each used and available location, we applied the decay function to discount the probability that the animal had been at a given location for each minute previous to that location. These probabilities were calculated as described above and after applying the decay function, we aggregated these discounted probabilities. For a given used or available location, this approach provides the probability that the animal had been there previously during that season, discounted according to the decay function such that more recent experience could be weighted more. To find the optimal k value for each individual, we fit individual models including all of the environmental and experience-based covariates outlined above, iterating through all possible values of k between 0 and 1 following the general approach of Merkle et al. (2014). We estimated k using maximum likelihood in a two-stage process with the Broyden-Fletcher-Goldfarb-Shanno (BFGS) optimizer in R. First, a k value was chosen, the probability values were discounted using the decay function above, and models were fit using maximum likelihood for the current value of k (see below for model specification). Then, "optim" was used to iterate through this process to estimate the value of k corresponding to the maximum likelihood. In this approach, k and the selection coefficients are estimated separately. We attempted to estimate these parameters simultaneously but were unable to achieve convergence. k parameters were estimated using this approach separately for each individual animal, with step-selection functions fit using conditional logistic regression in the "survival" package in R (Therneau and Grambsch, 2000; Therneau, 2015). In addition, we were interested in understanding how the importance of both recent and past experience changed throughout the season. Thus, we fit the models with an interaction between the landscape experience covariates and the time since the animal arrived on their summer or winter range, which provides inference to whether and how their selection for areas they were familiar with changed over the season.

After determining the optimal k value for each individual, we recalculated the recent experience covariate using this value, which should more appropriately represent a deer's ability to remember recently visited locations, and we fit a hierarchical SSF where all coefficients (i.e., slopes) were allowed to vary by individual. Prior to model fitting, we calculated pairwise correlations among all covariates to ensure they were below 0.7 (see **Supplementary Information**). We fit models using integrated nested Laplace approximation (INLA) in R (Lindgren and Rue, 2015) with the addition of the PARDISO solver (Bollhöfer et al., 2019, 2020; Alappat et al., 2020) to reduce computation time and followed the guidance and coded examples in Muff et al. (2020). For comparison, we fit additional models: one excluding both recent and past experience, one excluding only recent experience, one excluding only past experience, and one excluding the environmental covariates. We compared models using Bayes Factor (Gelman et al., 2013), which we derived from the marginal likelihood by taking the difference between complex models and a reference model where no covariates were included (Gomez-Rubio, 2020). Bayes Factor represents the strength of evidence provided by the data in favor of one theory among two competing theories (Kass and Raftery, 1995). All continuous covariates except *curr_ud* were centered and scaled by subtracting the mean and dividing by the standard deviation. Covariates were scaled using means and standard deviations calculated over all used and available locations for all individuals. We refit the model with both experience types and all environmental covariates, but using the curr_ud covariate calculated excluding the most recent 7 days of experience to assess the sensitivity of our results to the most recently experienced locations (note that the entire model fitting process including the estimation of the decay parameters k was repeated for these models excluding the most recent 7 days). Due to the computational requirements, we fit all models using the Cedar cluster (computecanada.ca, RRG: hyf-453-ab).

RESULTS

We fit models to 29 individual deer in summer and 31 individual deer in winter that had two complete winters and summers of data to fit our objectives. No pairwise correlations between covariates were >0.5 (see **Supplementary Information**). The results of our sensitivity analysis were nearly identical to when we dropped the most recent 24 h for three out of four models and fourth model didn't converge. The coefficients all were in the same direction, with only minor changes to the magnitude, except in summer the magnitude of decay.currud increased considerably, and there were no changes to whether 95% credible intervals overlapped 0. For these reasons, we report our results from models excluding the previous 24 h from the covariate representing recent experience.

The influence on habitat selection from recent experience decayed for most individuals, with decay being substantially faster during the summer (**Figure 3**). For all combinations of season and time of day, models with both recent and past experience outperformed models with one type of experience or no experience at all (**Table 1**). Across both seasons and time periods, deer displayed strong selection for areas with which they had recent experience (locations visited within the same season) and past experience (locations visited last year), though their seasonal dynamics varied between winter and summer (**Table 2**). During the winter, selection for areas with which deer were familiar over the short- and long-term was generally constant across the season (**Figure 4**). However, during the summer, selection declined throughout the season (**Figure 4**). Both recent and past experience was substantially stronger drivers of selection during the summer, with effects nearly three times those of winter (**Figure 4**).

In both seasons, experience with the landscape appeared to be stronger drivers of selection behavior than most of the environmental covariates, having larger magnitude and less uncertainty than other covariates (**Table 2**). Deer also showed strong selection relative to elevation, but the direction of this effect varied by time of day, with deer selecting for lower elevations during the day and higher elevations at night in both seasons. During the summer, few other covariates had strong influence on selection, but during the winter, at nighttime, deer showed strong selection for numerous anthropogenic and landscape features (**Table 2**). In addition to these selection patterns, there were some major shifts in coefficient magnitudes between models fit with and without experience covariates to the same data. Specifically, in the summer, models with no experience had coefficient estimates for NDVI that were more than 3x larger than models with experience, though 95% credible intervals overlapped in all cases (**Table 2**; see **Supplementary Information** for a table version with credible intervals). There were similar, though weaker, shifts in land cover covariates for summer models, but less evidence of such shifts in winter models.

DISCUSSION

Memory is a fundamental component of animal movement decision-making, and our findings build on the cognitive movement ecology literature by providing evidence that memory is an important cognitive process driving mule deer habitat selection (Merkle et al., 2014; Avgar et al., 2015; Oliveira-Santos et al., 2016; Bracis and Mueller, 2017; Marchand et al., 2017). Our results demonstrate that mule deer select for familiar locations, both from recent and past experience, to a greater extent than most measured environmental factors. Although measuring memory directly in observational studies is difficult, we suggest that these covariates are at least partially representative of memory. Thus, these findings indicate that mule deer store information using short- (defined here as information accrued during the season of analysis) and long-term (defined as information accrued the previous year) memory. If deer had no capacity for memory, we would expect that past experience would only influence habitat selection to the degree to which it was correlated with current environmental conditions. While it is possible that experience could represent temporally static environmental factors not captured in our array of landscape covariates, past research on this species has documented the likely use of memory (Jakopak et al., 2019; Merkle et al., 2019), and thus the re-selection of areas that were previously used is more simply and logically explained by memory than by animals repeatedly randomly encountering the same locations. Further, if deer had a more limited capacity for memory, we expect they would have selected primarily for recently visited locations, which would indicate memory is reset when deer leave seasonal ranges. However, the strong influence of past experience (e.g., last season's UD) and the consistent finding of the importance of memory when excluding the previous week of data suggests that mule deer have a strong capacity for long- and short-term memory.

The strong influence of long-term experience has important implications for our understanding of the evolution of long-term memory and migratory behavior (Mettke-Hofmann, 2014). Species migrate to access seasonally variable resources and being able to remember information about the location of resources on seasonal ranges, despite periodic absence, would be critical for exploiting them efficiently (Aikens et al., 2020). Migratory species have been shown to have greater capacity to store and utilize long-term memory, underscoring its importance in informing long distance movements (Mettke-Hofmann and Gwinner, 2003; Pravosudov et al., 2006; Mettke-Hofmann, 2014). Conversely, other research comparing short- and long-term memory found evidence that resident species (e.g., non-migratory) rely more on short-term memory (Oliveira-Santos et al., 2016; Vergara et al., 2019). Our results support these past findings and suggest that both short and long term memory are critical for allowing migratory species to exploit local resources. Further assessments of the relationship between memory types and movement strategies, such as long-term memory and migration, will provide insight to how cognition and movement phenomena have evolved.

The roughly equal influence of both recent and past experience indicates that when mule deer leave seasonal ranges, they retain a certain level of familiarity that influences their detailed movement decisions and thus patterns of space use in the following year. Our findings support several recent papers, which suggest that memory is an important mechanism generating emergent space-use patterns of animals (Van Moorter et al., 2009; Piper, 2011; Spencer, 2012; Avgar et al., 2015). Animals constrain their space use, which results in home range behavior, site fidelity, and recursion (Brown and Orians, 1970; Boerger et al., 2008).

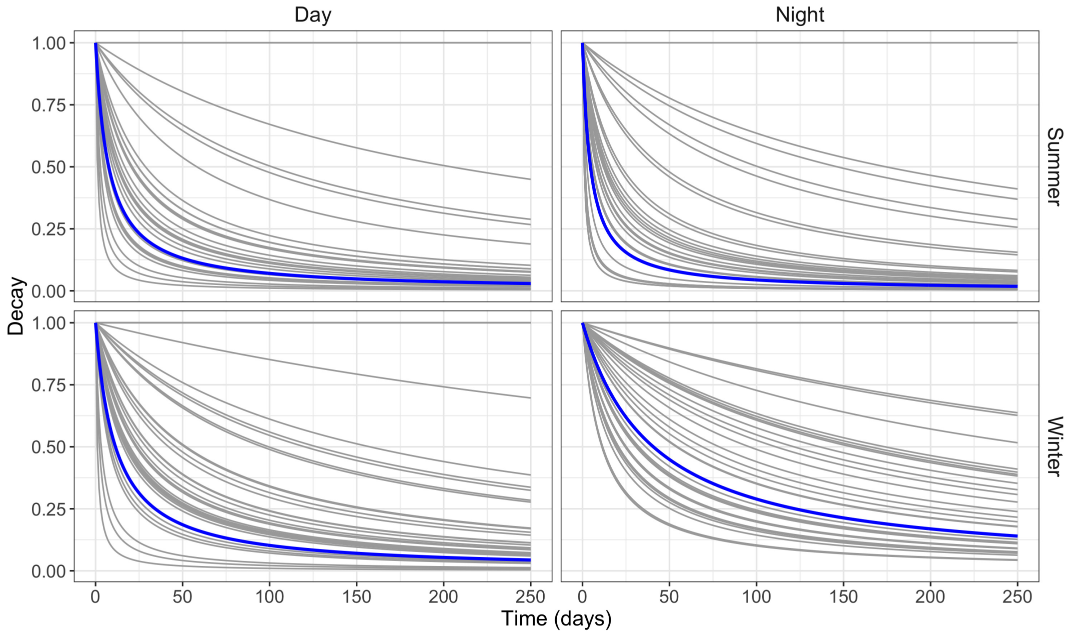

FIGURE 3 | Estimates of short-term memory decay of recently visited locations (i.e., recent experience) for night and day models comparing summer and winter for individual mule deer in the Piceance Basin, Colorado, United States. The blue line indicates the population level mean.

Environmental conditions partially explain why these patterns exist, because species are likely to constrain their space use depending on the availability and quality of habitat and forage (Mitchell and Powell, 2012), population density (Trewhella et al., 1988), breeding status (Gaulin and FitzGerald, 1988), and anthropogenic influence (Martin et al., 2010). However, tracking experience with a landscape allows species to better exploit environmental factors (Wolf et al., 2009; Schmidt et al., 2010; Merkle et al., 2014; Bracis et al., 2015; Forrester et al., 2015). Mule deer in this system exhibit strong fine-scale fidelity to seasonal ranges between successive years, especially in the summer (Northrup et al., 2021). Our results suggest that memory is the mechanistic driver of philopatric behavior in this population. These findings further suggest that general movement paths have been reinforced over successive years and are likely consolidated into long-term memory, which could explain how philopatric patterns emerge at broader scales (Owen-Smith et al., 2010; Merkle et al., 2019). Thus, we propose that long-term memory is likely the mechanism promoting return to seasonal ranges and short-term memory allows for deer to alter their habitat selection based on updated information about dynamic variables in the landscape (Spencer, 2012).

Theory suggests that memory only provides an adaptive advantage when the benefit of reusing information outweighs the cost of retaining it, which occurs most often in environments that have medium levels of heterogeneity and predictability (Mcnamara and Houston, 1987; Barraquand and Benhamou, 2008; Fagan et al., 2013; Bracis et al., 2015; Riotte-Lambert and Matthiopoulos, 2020). As such, we speculate that the stronger influence of previous experience in the summer, both recent and in the past, suggests that memory is more valuable when navigating the summer landscape. This could be a result of a highly predictable landscape related to resource quality and predation risk, in combination with increased pressure to maximize energy stores in the summer. Mule deer birth and raise fawns at this time, and summer ranges have ample forage available (Péron et al., 2018). Contrastingly, deer lose substantial energy stores during the winter due to poor resource availability (Northrup et al., 2021) and likely prioritize energy conservation. Thus, we suspect that good habitat during parturition and areas of high-quality forage are more valuable to remember from year to year on summer ranges, which would support a strong reliance on memory as a strategy for selecting habitat (Péron et al., 2018; Cameron et al., 2020). The lesser influence of experience in the winter suggests it is physiologically more efficient for deer to rely on other informational sources, such as conspecifics or engrained behavior, when moving through a more resource-poor landscape (Riotte-Lambert and Matthiopoulos, 2020). The strong influence of experience in the summer can explain previous observations that deer in this system maintain smaller range sizes in the summer (Northrup et al., 2016), which further supports our interpretation of the strong influence of memory in generating space use patterns. Furthermore, we estimated individuals experience a faster rate of decay of their short-term memory of recently visited locations in the summer compared to winter, which we speculate further supports the stronger reliance on memory in the summer, because when information is valuable, capacity limits of short-term memory may be reached at a faster rate (Spencer, 1992, 2012).

In addition to the above-noted differences between summer and winter, deer selected less often for recently visited locations as the summer season progressed but showed relatively consistent

TABLE 1 | Model comparison using Bayes Factors across season and time of day for hierarchical Step Selection Function models with coefficient estimates (i.e., slopes) varying by individual, fit to adult female mule deer GPS radio collar data from animals in the Piceance Basin of Northwestern Colorado, United States.

<table>
<tr><th>Season</th><th>Time of day</th><th>Model</th><th>Log Marginal Likelihood</th><th>Bayes Factor</th></tr>
<tr><td>Summer</td><td>Day</td><td>use ∼ −1 + env + expR + expP + (1 | Deer) + (env | Deer) + (expR | Deer) + (expP | Deer)</td><td>−558,344</td><td>5,145</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR + expP + (1 | Deer) + (expR | Deer) + (expP | Deer)</td><td>−559,138</td><td>4,351</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + expR + (1 | Deer) + (env | Deer) + (expR| Deer)</td><td>−559,338</td><td>4,151</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR + (1 | Deer) + (expR | Deer)</td><td>−560,161</td><td>3,328</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + expP + (1 | Deer) + (env | Deer) + (expP | Deer)</td><td>−560,528</td><td>2,961</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expP + (1 | Deer) + (expP | Deer)</td><td>−561,551</td><td>1,938</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + (1 | Deer) + (Deer | env)</td><td>−562,310</td><td>1,179</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + (1 | Deer)</td><td>−563,489</td><td>0</td></tr>
<tr><td></td><td>Night</td><td>use ∼ −1 + env + expR + expP + (1 | Deer) + (env | Deer) + (expR | Deer) + (expP | Deer)</td><td>−399,570</td><td>3,945</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR + expP + (1 | Deer) + (expR | Deer) + (expP | Deer)</td><td>−400,243</td><td>3,272</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + expR + (1 | Deer) + (env | Deer) + (expR | Deer)</td><td>−400,395</td><td>3,120</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + expP + (1 | Deer) + (env | Deer) + (expP | Deer)</td><td>−400,885</td><td>2,630</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR + (1 | Deer) + (expR | Deer)</td><td>−401,277</td><td>2,238</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expP + (1 | Deer) + (expP | Deer)</td><td>−401,771</td><td>1,744</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + (1 | Deer) + (Deer | env)</td><td>−402,264</td><td>1,251</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + (1 | Deer)</td><td>−403,515</td><td>0</td></tr>
<tr><td>Winter</td><td>Day</td><td>use ∼ −1 + env + expR + expP + (1 | Deer) + (env | Deer) + (expR | Deer) + (expP | Deer)</td><td>−1,202,517</td><td>1,430</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR + expP + (1 | Deer) + (expR | Deer) + (expP | Deer)</td><td>−1,202,860</td><td>1,087</td></tr>
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<tr><td></td><td></td><td>use ∼ −1 + expR + (1 | Deer) + (expR | Deer)</td><td>−1,203,236</td><td>711</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expP + (1 | Deer) + (expP | Deer)</td><td>−1,203,469</td><td>478</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + (1 | Deer) + (Deer | env)</td><td>−1,203,570</td><td>377</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + (1 | Deer)</td><td>−1,203,947</td><td>0</td></tr>
<tr><td></td><td>Night</td><td>use ∼ −1 + env + expR + expP + (1 | Deer) + (env | Deer) + (expR | Deer) + (expP | Deer)</td><td>−1,354,149</td><td>4,770</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR + expP + (1 | Deer) + (expR | Deer) + (expP | Deer)</td><td>−1,354,937</td><td>3,982</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + expR + (1 | Deer) + (env | Deer) + (expR | Deer)</td><td>−1,354,956</td><td>3,963</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expR+ (1 | Deer) + (expR | Deer)</td><td>−1,355,963</td><td>2,956</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + expP + (1 | Deer) + (env | Deer) + (expP | Deer)</td><td>−1,356,557</td><td>2,362</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + expP + (1 | Deer) + (expP | Deer)</td><td>−1,357,471</td><td>1,448</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + env + (1 | Deer) + (Deer | env)</td><td>−1,357,697</td><td>1,222</td></tr>
<tr><td></td><td></td><td>use ∼ −1 + (1 | Deer)</td><td>−1,358,919</td><td>0</td></tr>
</table>

Covariates are defined as environmental (env), recent experience (expR), and past experience (expP).

selection for these locations during winter. We believe this pattern could best be explained by within season variation in predation risk (Bracis et al., 2018). We believe at the beginning of the summer, when fawns are most vulnerable to predation, deer frequently revisit locations with ample cover to hide their fawns, which likely stays consistent from year to year. As fawns become more mobile as the summer progresses, by rule, deer return to the same location less often (Monteith et al., 2014; Cameron et al., 2020). Additionally, the value of forage declines as the summer progresses, potentially causing the selection of previously visited locations to become less favorable. We did not have sufficient data to test the relationship between environmental predictability, resource depletion and predation risk on selection of familiar locations within and between seasons (Lendrum et al., 2018), but we suspect these are the variables driving observed patterns in memory effects. Furthermore, we acknowledge that because we were unable to incorporate these variables, selection for habitat related to environmental predictability, resource quality, and predation risk could potentially occur absent memory effects. Thus, we encourage future assessments evaluating the role of environmental predictability and understanding how changes in environmental conditions influence when and how species use memory when selecting for habitat.

The strong influence of landscape experience could have negative implications for the ability of deer to respond to landscape change. Previous evaluations of memory suggest that a strong reliance on this process promotes rigid movement behavior that doesn't allow species to respond to change (Merkle et al., 2015; Sawyer et al., 2019). These findings have raised concerns that memory could have maladaptive effects for populations experiencing environmental change related to anthropogenic disturbance (Andersen, 1991; Morrison et al., 2021). Thus, the strong reliance of mule deer on familiarity when selecting habitat suggests that they may not be able to cope well with the accelerated rates of change being documented in natural systems (Sih et al., 2011; Beever et al., 2017; Wyckoff et al., 2018). Alternatively, past work in this system by Northrup et al. (2021)

TABLE 2 | Posterior means of population-level parameters for summer and winter night/day Step Selection Functions when experience coefficients are included or excluded for adult female mule deer in the Piceance Basin of Northwestern Colorado, United States.

Covariates	**Summer**				**Winter**			
	Day		**Night**		**Day**		**Night**	
	No experience	**With experience**	**No experience**	**With experience**	**No experience**	**With experience**	**No experience**	**With experience**
Barren	–	–	–	–	**−0.094**	−0.088	−0.047	−0.039
Dpads	−0.055	0.246	−0.225	−0.147	−0.089	−0.085	0.023	0.022
Drds	0.054	0.042	**0.133**	**0.09**	0.032	0.022	**0.076**	**0.069**
Edge	−0.056	−0.044	0.069	0.06	0.009	0.007	**0.057**	**0.055**
Elev	−0.173	**−0.353**	**0.906**	**0.753**	**−0.214**	**−0.303**	**1.013**	**0.874**
Grass	–	–	–	–	−0.099	−0.078	**−0.243**	**−0.22**
NDVI	0.309	0.083	0.317	0.072	–	–	–	–
Open	**−0.172**	−0.093	−0.075	−0.037	–	–	–	–
Shrub	−0.035	**−0.06**	−0.012	−0.05	−0.008	−0.006	−0.012	−0.007
snow	–	–	–	–	−0.01	−0.012	0.039	**0.043**
TRI	**0.138**	**0.102**	**0.095**	0.029	0.006	−0.006	**0.125**	**0.108**
curr_ud	–	**1.68**	–	**2.394**	–	**1.21**	–	**1.261**
curr_ud time	–	**−0.165**	–	**−0.221**	–	0.004	–	**−0.172**
prev_ud	–	**0.508**	–	**0.546**	–	**0.226**	–	**0.365**
prev_ud time	–	**−0.058**	–	−0.023	–	−0.011	–	0.011

Models were fit with all coefficients (i.e., slopes) varying by individual. Values in bold are significant effects where the lower and upper 95% credible interval does not overlap 0. The lower and upper 95% credible intervals were estimated from the quantiles of the posterior distributions (see ***Supplementary Information****). Parameters can only be compared within season and time of day combinations (i.e., no experience vs. with experience).*

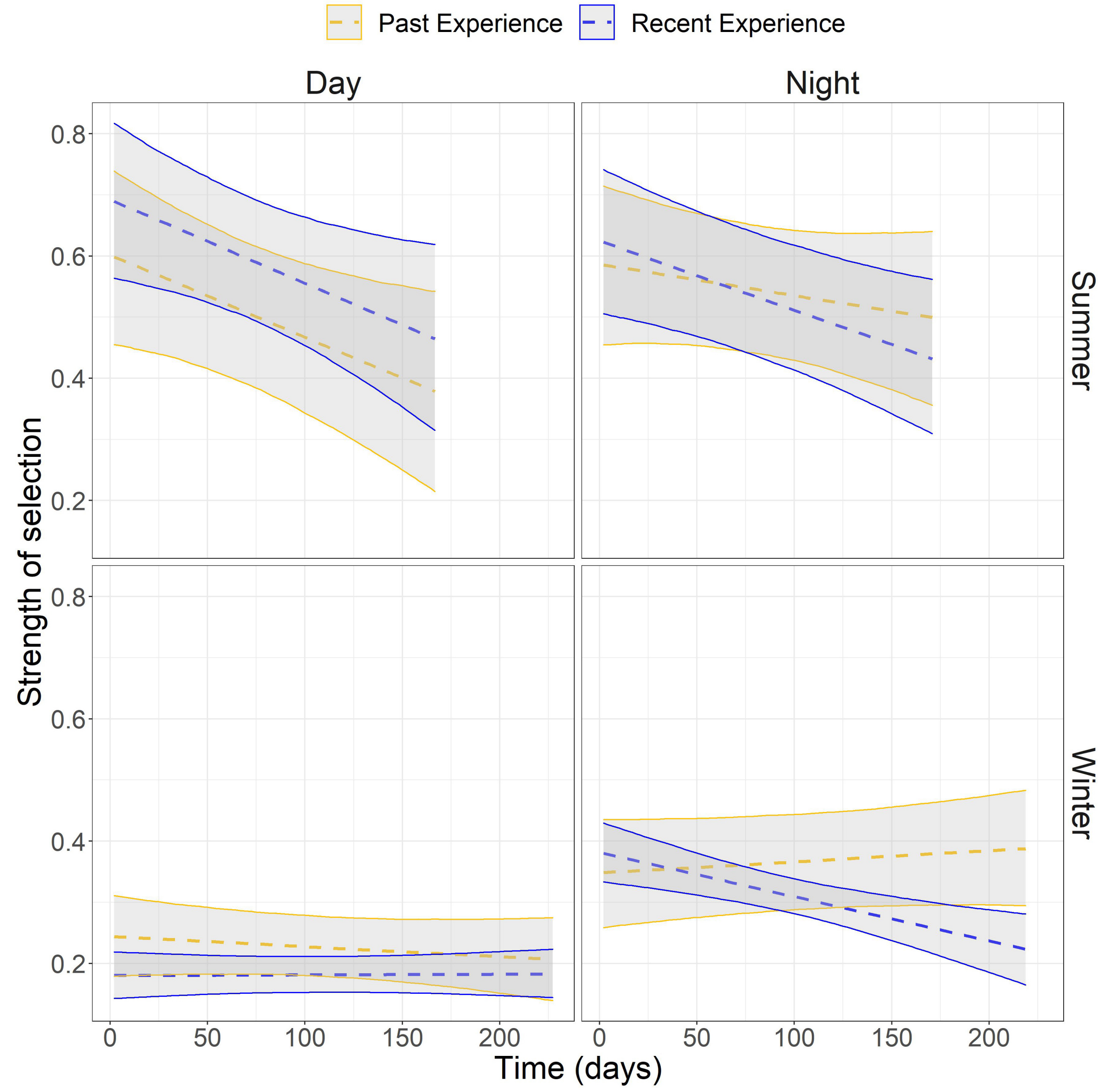

FIGURE 4 | The strength of selection for covariates representing recent- and past experience estimated from population-level parameters from step-selection functions for mule deer within their winter and summer range across time of day in the Piceance Basin, Colorado, United States.

suggests deer potentially can adapt behaviorally to some forms of landscape change with minimal demographic effect, but clearly more research is needed to understand the role of memory in promoting or restricting adaptability to landscape change.

Memory is complex, and thus our methods have limitations in providing inference to this process. First, memory is fundamentally a latent characteristic, and the degree to which it influences animal behavior can only be inferred (Fagan et al., 2013). We inferred memory from selection of areas that had been used in the past, but there are other possible interpretations. As discussed above, the role of memory in informing movement decisions may be confounded by selection of resources absent any significant influence of memory (Oliveira-Santos et al., 2016). If mule deer revisited specific locations based on their moment-to-moment perception of resource quality, we might find similar results, particularly if we were unable to quantify an important environmental resource in our models, such as predation risk. Further, mule deer in our system may also draw on conspecifics (Codling et al., 2007; Jesmer et al., 2018) and ingrained behavior (Riotte-Lambert and Matthiopoulos, 2020) to guide movement decisions. However, we did not sample a sufficiently large proportion of the population to adequately include variables representing conspecific influence, as well as the generally low sample size could have influenced our results.

Further, inclusion of experience tended to reduce the magnitude of environmental covariate coefficients, which could impact interpretation of environmental drivers of space use.

However, we believe our results provide reasonably strong evidence that memory is an important driver of mule deer habitat selection, and mule deer store and use information about their environment in short- and long-term memory. There was little correlation between environmental and landscape experience covariates (see **Supplementary Information**) and models incorporating experience outperformed models with environmental covariates alone, lending additional support to previous research, which showed the inclusion of memory in simulation models was integral for reproducing empirical movement paths (Bracis et al., 2015; Merkle et al., 2019). Further, the annual absence of mule deer from seasonal ranges allowed for more robust inference to the influence of memory type effects based on how deer select for locations experienced recently (e.g., within the same season with decay) or in the past (e.g., the previous season). Lastly, our estimates of the effects of memory should be realistic because they are consistent with previous findings reported for mule deer and other ungulate species, including the capability for long term retention of information (Avgar et al., 2015; Jakopak et al., 2019; Merkle et al., 2019; Cameron et al., 2020) and similar decay rates for short-term memory (Bailey et al., 1989; Laca, 1998).

Our results further demonstrate the utility of including experience in the formulation of step selection functions to infer cognitive drivers of movement (Merkle et al., 2014; Oliveira-Santos et al., 2016). Our findings demonstrate mule deer reliance on recent and past experience varied in accordance with both regional (summer vs winter range) and local (within-range) conditions, lending insight to when memory is advantageous and how the influence of memory can lead to the emergence of space use patterns such as site fidelity. The specific processes driving this temporal and spatial variation in the use of memory, however, warrant further investigation. Therefore, where possible, we encourage future studies to include internal state variables (e.g., reproductive status) and additional external factors, such as resource predictability and predation risk in model formulations to further elucidate processes influencing when and how species use memory to inform movement decisions. Examining how and when species use different types of memory can provide insights to the adaptive advantages of memory-driven movement and the development of emergent space use patterns.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Colorado Parks and Wildlife Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

CA coordinated data collection. GW and CA contributed funding for data collection. JN and RM performed data analyses. RM, TR, and MB developed tables and figures. HR led the drafting of the manuscript with contributions from JN and TR. All authors contributed to the conception and design of the study, manuscript revision, and have read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.702818/full#supplementary-material

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Intraspecific Competition, Habitat Quality, Niche Partitioning, and Causes of Intrasexual Territoriality for a Reintroduced Carnivoran

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Animals exploring a new environment develop cognitive maps using diverse sensory input and, thereby, gain information needed to establish home ranges. Experiencing, and learning information about, resources should be advantageous to the resident of a home range while lack of such information should put invaders into the home range at a disadvantage. Conspecifics, especially, should avoid the home ranges of one another to ensure that they do not experience reduced resource availability caused by resource depression or depletion. Yet, encountering conspecific competitors of different sexes may elicit responses that can lead to spacing on a landscape that has different costs and benefits on males and females. We tested the hypothesis that female fishers (*Pekania pennanti*) avoid competition from both males and female conspecifics whereas male fishers avoid competition only from other males. We reintroduced fishers onto our study site in the presence or absence of competitors' home ranges during late 2009 through 2011. Using satellite transmitters (Argos) and land-based (VHF) telemetry, we monitored fishers and estimated their locations, movements and use of the surrounding landscape during their first 500 days after release. All fishers settled in relatively high-quality habitat but females that encountered the home ranges of conspecifics moved farther, explored larger areas, and settled farther from their release locations than did females that did not encounter a conspecific's home range. Male fishers exhibited diverse responses upon encountering the home ranges of conspecifics. Thus, female fishers avoid conspecific competition from all fishers, but males tolerate, or impose, competition with females, apparently to increase mating opportunities. These observations are consistent with the movements and strategies of other solitary carnivores.

Keywords: carnivore, competition, habitat, home range, intrasexual territory, movements, niche partitioning, territory

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INTRODUCTION

When an animal moves through a new environment, it perceives the characteristics of that environment through its diverse senses and begins to develop a cognitive map of the new area (Heft, 2013; Eichenbaum, 2017). As the animal establishes a home range, its cognitive map becomes more complex. The cognitive map is a multi-dimensional concept of not just the locations of resources but also of the conditions of those resources, their juxtaposition and interspersion, the importance of the resources given the animal's nutritional state and other conditions, the details of travel routes between resources such as ground conditions, exposure to predators, effects of weather patterns, short cuts to other resources, and much more. The cognitive map is not a Euclidean map as seen from above but a concept of an animal's surroundings as seen from the animal's present, or another target location (Heft, 2013). The map includes everything that the animal knows about other animals in the environment, including competitors. Consequently, understanding the development of the cognitive maps is critical for understanding home ranges and how animals learn about their environments (Powell, 2012; Powell and Mitchell, 2012).

Intraspecific competition affects, directly or indirectly, how animals use their environments and how they space themselves. Individuals remove, or deplete, resources, thereby decreasing habitat quality for both conspecifics and competitors of other species (Nunes et al., 1997; Goubault et al., 2005). Individuals may also depress food availability and foraging opportunities by changing prey behavior (Charnov et al., 1976; Jetz et al., 2004; Mitchell and Powell, 2004, 2007; Spencer, 2012). Resource depletion and depression cause individuals to move farther than they would without competition to find patches with abundant resources or to find patches where their ability to acquire those resources has fewer costs (Spencer, 2012).

Resource depletion and depression form a continuum of resource renewal. Depressed resource availabilities, caused by changes in prey behavior, renew over time scales of hours (Jędrzejewski et al., 1993) to a day or more (Ylönen, 1989; Jędrzejewski and Jędrzejewska, 1990). At the extreme, field voles (*Microtus agrestis*) delay reproduction when exposed to odors of weasels (*Mustela nivalis*) and American minks (*Neogale vison*), extending resource depression to a week as an extreme (Koskela and Ylönen, 1995). Depleted resource abundances caused by competitors renew slowly, if at all (Charnov et al., 1976). Although berries eaten by a competitor can renew within days, populations of small mammal prey require weeks to renew, large ungulate prey renew only after the next reproductive cycle followed by another year or more of growth, and minerals removed from a mineral lick may never renew. The consequence is that competitors decrease other animals' abilities to track and to predict resource renewal and, thereby, to forage optimally. Hence, learning the locations, physical attributes, or the time since a competitor last visited an area is crucial to an animal's decisions and, ultimately, to its fitness (Mitchell and Powell, 2007; Spencer, 2012).

Although both intra- and interspecific competitors deplete and depress resources, intraspecific competitors do so most effectively because conspecifics share resources requirements and foraging behaviors (Macdonald, 1983). Thus, sharing a landscape with a conspecific should have a larger effect on an individual's assessment of habitat quality than does sharing the landscape with individuals of other species (Mitchell and Powell, 2004, 2007). If sharing its home range with conspecifics causes a resource for an animal to become limiting, the animal should maintain a territory (a non-overlapping home range; Brown, 1969; Brown and Orians, 1970; Carpenter and MacMillen, 1976). Spatial and temporal patchiness of the limiting resource can change the threshold for maintaining a territory (Powell et al., 1997; Sells and Mitchell, 2020) and for maintaining a shared territory with a mate (Smith, 1968; Powell, 1989, 1994). When conspecifics make resource renewal unpredictable, individuals may avoid areas used habitually by conspecifics, facilitating territoriality without defense (Spencer, 2012). For some species, habitat varies sufficiently across the species' range that members of some populations maintain territories while members of other populations tolerate home range overlap (e.g., black bears, *Ursus americanus*, Powell et al., 1997). Even species for which all populations are generally thought always to maintain territories (e.g., pack territories of wolves, *Canis lupus*), habitat patchiness on landscapes over time can lead to home range overlap (Mech and Boitani, 2003).

Members of many species with large sexual dimorphism in body size maintain intrasexual territories (Powell, 1979b, 1994; Rogers, 1987; Powell et al., 1997; Johnson et al., 2000; Persson et al., 2010; Elbroch et al., 2016). Yurgenson (1947) and then Brown and Lasiewski (1972) suggested that size dimorphism allows resource partitioning by prey size, reducing competition between males and females of the same species. Such reduced competition could, theoretically, allow intrasexual territoriality. This intuitively satisfying niche-partitioning hypothesis has, however, experienced mixed success when tested (Selander, 1966; Schoener, 1967; Husar, 1976; Snyder and Wiley, 1976; Powell, 1981, 1993; Dayan and Simberloff, 1994, 1996, 1998; Holmes and Powell, 1994; King and Powell, 2007; Law and Mehta, 2018; Law, 2019). Resource partitioning by size can only occur when the smaller sex has access to resources not available to the larger (Wilson, 1975; Powell and Zielinski, 1983), a diet requirement that is seldom quantified (for example, Simms, 1979). Sexual size dimorphism does correlate strongly with a carnivorous diet (Powell, 1979b; Law and Mehta, 2018; Law, 2019). Yet, for those mustelids with large sexual size dimorphism, teeth, jaws and other skull structures related to capturing and killing prey are less dimorphic than are the rest of their bodies, indicating similar use of resources between sexes rather than niche partitioning (Holmes and Powell, 1994). Finally, sexual size dimorphism can vary tremendously among successive cohorts in the same place, because males born into food abundance grow to be significantly larger than those born into food scarcity (Holmes and Powell, 1994; Powell and King, 1997: King and Powell, 2007). Thus, even though sexual size dimorphism varies, and the potential for niche partitioning, intrasexual territoriality appears not to vary.

At specific combinations of limiting resource productivity, resource depression, and daily travel distances, dominant and subordinate individuals can maintain overlapping territories (Powell, 1994). Powell (1991, 1994) calculated that dominant individuals that benefit from such an overlap force the subordinate individuals to tolerate the overlap even if the subordinates gain no benefit, a calculation that applies to large males with large territories, each overlapping the smaller territories of several females. Large male black bears with large home ranges monitor the females with small, overlapped home ranges (Seaman, 1992; Powell et al., 1997; Kovach, 1998;

FIGURE 1 | A female fisher (*Pekania pennanti*) wearing a transmitter collar and climbing a log to her den tree, where she has a litter of kits in a cavity. This fisher is a member of a reintroduced population established to investigate the use by fishers of industrial timberlands in northern California (Photo Credit: Fisher Reintroduction in Northern Sierras Project).

Kovach and Powell, 2003) and many mustelids maintain intrasexual territories for years, making such monitoring by males possible (Erlinge and Sandell, 1986; Sandell, 1989; Powell, 1994; Lofroth et al., 2010; Rennie, 2015; Smith et al., 2020; but see Yamaguchi and Macdonald, 2003). Ultimately, even though intrasexual territoriality is well documented, the hypothesis that territoriality is imposed on females by males has never been tested.

Reintroductions of animals provide opportunities to test hypotheses related to what and how animals learn about new environments as they develop new cognitive maps and create home ranges. Biologists can infer how animals perceive and learn through their movements and spacing of new home ranges as more and more animals are released (Linklater et al., 2006; Berger-Tal and Saltz, 2014; Betts et al., 2015; Facka et al., 2016; Facka, 2017; Smith et al., 2020). Thus, reintroductions allow comparisons of the behaviors of individuals released into competition-free zones vs behaviors of those released into occupied zones. If habitat varies across a reintroduction site, the first individuals released should establish home ranges in the first areas of acceptable quality that they encounter. Developing a good cognitive map must be important (Heft, 2013; Eichenbaum, 2017; Lewis et al., 2021). Learning to know where food is located on a new, local landscape and learning how to hunt in those food sites should provide better food security than continuing to explore new sites that may not be better and might have less food. Likewise, individuals released later in a reintroduction benefit from avoiding occupied areas. Colonizers entering an area where conspecifics have established territories should avoid entering or minimize time in those territories (Sjöåsen, 1997). For sexually dimorphic species, females should avoid territories of all conspecifics if intrasexual territoriality is imposed on females by large males but should not avoid territories of large males if niche partitioning exists. Males who find an area without a resident, adult male should establish territories even if (niche partitioning), or because (imposition), the territories overlap the territories of females.

A reintroduction of fishers (*Pekania pennanti*) in northern California (Facka et al., 2016; Facka, 2017) allowed us to test hypotheses about conspecific competition, movements, habitat, and home range establishment. Fishers (**Figure 1**) are medium sized (adult females 2–2$^1/_2$ kg, adult males 3$^1/_2$-6 kg) predatory mammals in the family Mustelidae living only in northern North America. They thrive in large stands of late successional northern forests (Allen, 1983; Powell, 1993; Matthews et al., 2011; Raley et al., 2012; Powell et al., 2017). Through the 19th and early 20th centuries, fishers decreased in abundance throughout their range and subsequent efforts to restore their populations have resulted in numerous reintroductions and augmentations (Powell, 1993; Krohn, 2012; Lewis et al., 2012; Powell et al., 2012).

Across their range, fishers maintain territories with little intrasexual overlap but the territories of males overlap those of several females (Powell, 1979b; Weir, 1995; Badry et al., 1997;

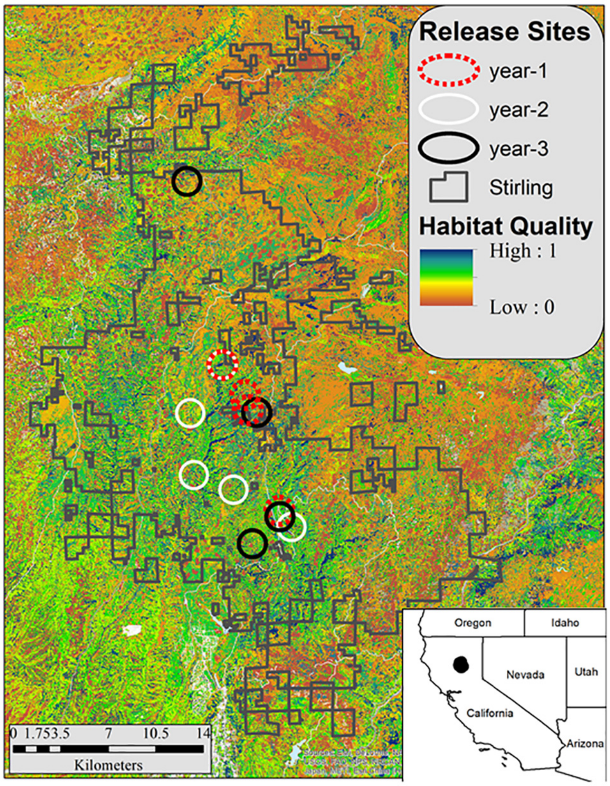

FIGURE 2 | Stirling Management Area in northern California (shown by the irregular blocks of land outlined by gray lines) and the fisher release areas by year (black circles = December 2009–February 2010, white circles = November 2010–January 2011, and red circles = October–December2011). The background shows habitat quality (blue is highest) estimated using the model of Thomasma et al. (1994).

Rennie, 2015). Fishers have large territories to fuel their high metabolic rates and they travel long distances in search of prey (McNab, 1963; Powell, 1978, 1979a; Harestad and Bunnel, 1979). Males' territories average over twice as large as those of females (Powell, 1994; Proulx et al., 1994; Badry et al., 1997) and males and females with overlapping territories avoid using the same locations simultaneously (Rennie, 2015). Fishers have diverse scent glands, including anal glands and plantar glands on their hind feet (Powell, 1993) and, presumably, communicate with other fishers *via* scent marking. Fishers apply anal gland secretions directly to objects, when fishers defecate, their anal glands leave scent and when they travel, their plantar glands leave scent. Fishers often walk along the tops of logs and jump onto stumps and big rocks, where their plantar glands leave scent that is elevated and able to disperse better (Powell, 1993).

Fishers are good subjects for testing hypotheses related to intraspecific competition, spacing patterns and movements because fisher life history and use of environments closely resemble those of most solitary carnivores (Powell et al., 2017). In addition to its goal of re-establishing a fisher population, the reintroduction in northern California was designed to test a series of hypotheses, including that fishers can maintain a viable population on a landscape managed intensively for lumber production (Callas and Figura, 2008; Facka, 2017). We hypothesized that conspecific competition affects fisher movements and establishment of territories after release for reintroduction. Specifically, we hypothesized (1) that adult female and male fishers move farther and faster when released into an existing territory compared to release into an area not occupied by another fisher. We hypothesized (2a) that newly released female fishers avoid established territories of both males and females but (2b) that male fishers are indifferent or attracted to female fishers' territories while (2c) avoiding those of established adult male fishers. We hypothesized (3) that established territories (2 months or older) from previously released fishers affect newly released fishers' movements and use of the landscape more strongly than do incipient territories, presumably because sufficient scent or visual or other cues had accumulated within established territories to indicate to new fishers that they should avoid those established territories (Gosling, 1982; Lewis and Murray, 1993; Field et al., 2005; Zhang et al., 2005; Kent and Tang-Martínez, 2014). The net result is that we tested whether fishers maintain intrasexual territories because of niche partitioning or because large males impose the territorial system onto females.

MATERIALS AND METHODS

Study Site

Fishers were reintroduced as part of cooperative effort of Sierra Pacific Industries (a forest products company), the United States Fish and Wildlife Service, the California Department of Fish and Game (now Fish and Wildlife), and researchers at North Carolina State University (Callas and Figura, 2008, United States Department of the Interior et al., 2009). Collectively, our group reintroduced fishers to the Stirling Management Area (hereafter Stirling) owned and managed by Sierra Pacific Industries in portions of Plumas, Butte and Tehama counties in northern California, United States (Stirling; Lat 39.9° Lon −121.5°; **Figure 2**) where the southern Cascade Mountains meet the northern Sierra Nevada. Stirling was 648 km^2 at elevations ranging from 425 to 2,080 m. The climate on Stirling was temperate with most (>85%) precipitation falling in late autumn and winter as snow and rain (Pandey et al., 1999). Vegetation on Stirling was typical of Sierra Nevada mixed conifer forest with ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertinia*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), douglas fir (*Pseudotsuga menziesii*), and California black oak (*Quercus kellogii*) as dominant tree species. In some locations, tanoak (*Notholithocarpus densiflorus*) and canyon live oak (*Quercus chrysolepis*) formed dense stands (Griffin and Critchfield, 1972; Beesley, 2007). We describe habitat assessment and quality on the study site later in our analysis.

Prey for fishers on Stirling included western gray squirrels (*Sciurus griseus*) and diverse small mammals (Facka, 2017; Townsend, 2019). Snowshoe hares (*Lepus americanus*) and porcupines (*Erethizon dorsatum*), major prey for fishers across most their range, were rare. Gray squirrels constituted almost

TABLE 1 | The total number of female and male fishers released by cohort, their average ages (range in parentheses), whether fishers were released within the home ranges of a female or male fisher released at least 2 months earlier, and whether released fishers encountered the established home ranges of other fishers while seeking places to establish their own home ranges.

Sex	Cohort	*N*	Mean Age (range)	Released within a female's home range	Encountered a female's home range	Released within a male's home range	Encountered a male's home range
Females	Year-1	9	2.6 (1.5)	3	3	0	0
	Year-2	7	2.4 (1.5)	5	7	6	7
	Year-3	8	2.0 (0.3)	2	2	6	8
	Females	24	2.3	10 (42%)	12 (50%)	12 (30%)	15 (63%)
Males	Year-1	6	3.0 (1.5)	5	6	0	0
	Year-2	6	3.8 (2.6)	4	6	4	6
	Year-3	4	1.8 (0.4)	1	1	3	4
	Males	16	3.0	10 (62%)	13 (81%)	7 (43%)	10 (63%)

Year-1 refers to releases in December 2009–February 2010; Year-2 to November 2010–January 2011; Year-3 to October–December 2011.

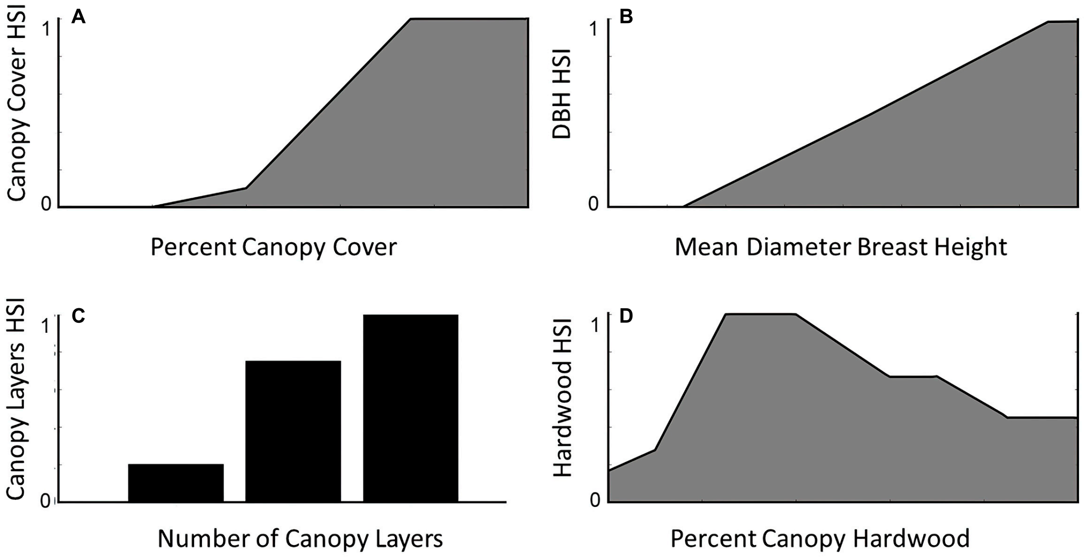

FIGURE 3 | The relationships between habitat suitability for fishers as derived from expert-opinion models and empirical assessment (model by Thomasma et al., 1994) and **(A)** percent canopy closure, **(B)** mean diameter at breast height (DBH) of overstory trees, **(C)** tree canopy diversity, and **(D)** percent of hardwoods.

40% of prey items identified in fisher scats and constituted a larger percent of the fishers' diets because, except for deer carrion, all other prey identified were small mammal or of small-mammal size (Facka, 2017).

Stirling had a history of diverse management regimes that include both even-aged and uneven-aged management. Roughly 25% of Stirling was in even-aged (clearcut) stands that were less than 30 years old during this study, whereas roughly 35% was in stands that were periodically harvested with single-tree selection approaches (Facka, 2017). Estimates of habitat quality using up-to-date data predicted that some areas on and directly adjacent to Stirling had habitat of decent quality (**Figure 2**; Facka, 2017).

Reintroduction

In late 2009, our group began moving 40 fishers (24 F; 16 M) from across the fisher range in northwestern California to Stirling (Callas and Figura, 2008). We moved fishers in three different years (**Table 1**), capturing fishers from diverse locations to minimize the impact to any one area and to infuse genetic diversity into the founding population (Callas and Figura, 2008; Facka, 2017). We transported all captured fishers to a central processing area and evaluated them for potential release onto Stirling. For females, we sought individuals that were approaching their 2nd or 3rd birthdays and would, therefore, be producing kits for the 1^{st} or 2nd times in their lives. For males, we sought individuals that we estimated to be $\geq$ 3-years old and $\geq$ 4 kg, because we surmised that big male fishers, like other carnivorans, would be the best breeders (**Table 1**; Kovach and Powell, 2003; Powell and Zielinski, 2005; Lewis et al., 2012). Actual ages were unknown at the time we selected and moved fishers but, for future analysis, we removed a 1^{st} upper pre-molar (a tiny tooth) from each fisher to estimate age by counting cementum annuli (Arthur et al., 1992; Poole et al., 1994). At least 1 field biologist and 1 wildlife veterinarian evaluated each fisher we considered for reintroduction. We immobilized fishers chemically with Tiletamine HCL and Zolazepam HCL (Telazol,

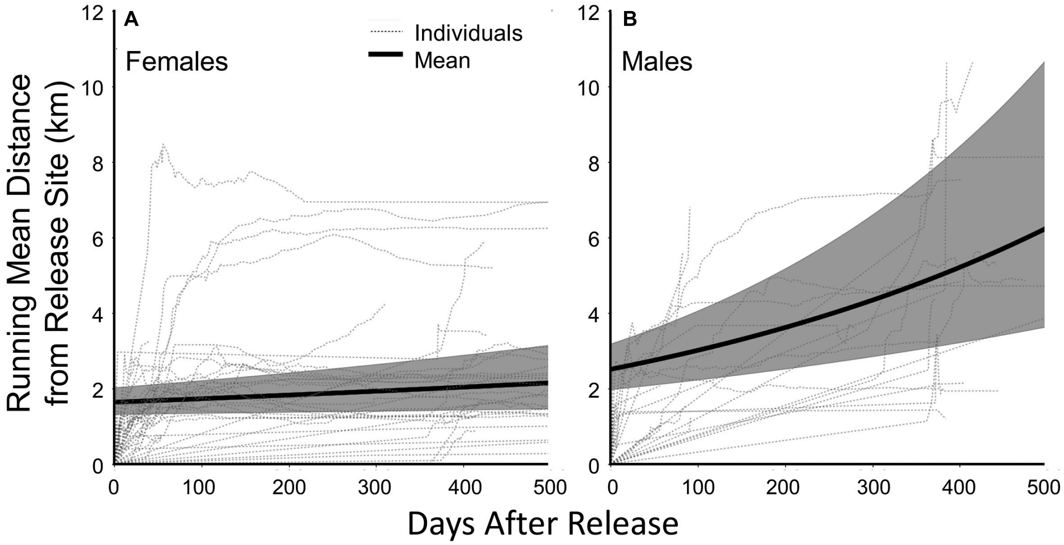

FIGURE 4 | Running mean distances from the sites of trapping and release for **(A)** female fishers and **(B)** male fishers born on the study site in northern California from 2011 through 2017 and the fitted mean curves for female and male fishers through time (solid black line; shaded areas are 95% Confidence Limits). Fitted mean line from parameter estimates from a generalized linear mixed model estimating change in distance after release.

Fort Dodge Animal Health, Fort Dodge, Iowa, United States; 7 mg/kg) to document sex, reproductive status, general condition, disease exposure, weight, and to fit transmitters. At initial capture, we collected a blood sample for genetic identification and to evaluate disease exposure, and gave each fisher a Passive Integrated Transponder (subcutaneous between the scapulae) for future identification.

No fishers had lived on the Stirling site for approximately 100 years prior to our reintroduction. Stirling was separated from the closest fisher population to the north and west by over 100 km and from the closest population to the south by over 400 km (Callas and Figura, 2008). During late autumns and early winters of 2009–2010 (year–1), 2010–2011 (year–2), and 2011–2012 (year–3), we released fishers in groups of 1–5 mostly across central Stirling (**Figure 2** and **Table 1**). After releases in year-1, we released some fishers within the established home ranges of previously released fishers and some into areas where we had not documented fishers in the year we tracked them after release (**Table 1**), alternating groups between in or out of known home ranges. We used hard releases (without site acclimation) because acclimation appears not to affect population establishment or movement patterns and is expensive (Lewis et al., 2012; Powell et al., 2012). To estimate fisher movements and survival post-release, we outfitted female fishers with either Telonics (IMP-325 or MOD-125; Mesa, Arizona) or Holohil (MI-2i, Carp, Ontario) Very High Frequency (VHF) transmitters. We fitted adult male fishers with Platform Terminal Transmitter (PTT; Argos) collars (Kiwisat 202 or 303, Sirtrack, Havelock North, New Zealand).

In autumn of 2011, we first captured fishers that had not been released and, therefore, had been born on Stirling. We followed the same capturing and handling protocols and used the same types of transmitters for Stirling-born fishers as for reintroduced fishers. We used Stirling born fishers to document how native, non-reintroduced fishers dispersed and moved within established home ranges at our study site.

Field Methods at Release Sites

We attempted to locate all fishers carrying transmitters on Stirling (reintroduced and those born on site) once per day using either VHF or PTT telemetry. We estimated fishers' locations with VHF data using three methods based on conditions, activity and the relative distances that we estimated individual fishers were from a field researcher. Most commonly, we collected azimuths in the field to triangulate fisher locations, using program Location of a Signal (LOAS, Ecological Software Solutions LLC). We collected locations of individuals throughout a 24-h diel cycle throughout the calendar year but 80% of all locations occurred during daylight hours compared to 20% at night. Less often, we located fishers from small planes or helicopter. Finally, we sometimes homed on the signal of a fisher until we saw the fisher or could identify the tree or other structure where it hid. Location estimates from PTT data were processed through the Argos system with Kalman estimation and filtering (Collecte Localisation Satellites; Ramonville-Saint-Agne, France) and delivered *via* email daily through the satellite tracking and analysis tool from the seaturtle.org web service (Coyne and Godley, 2005). Ideally, the PTT transmitters provided a minimum of one location estimate per day. Different PTT collars were active during different time blocks to allow inference to male fishers' movements throughout a 24-h cycle. We estimated VHF and PTT error by comparing locations estimated for collars and fishers to known locations. For VHF telemetry error, 25% of triangulated locations were within 50 m, 50% were within 112 m, 75% where within 300 m, and 95% were within 1,200 m of the true locations (n = 234). Triangulated locations were generally within the error radius produced by the LOAS software. The

Argos system classified locations into distinct classes based on predicted error rates (Sauder et al., 2012). The expected precision of estimates descends from those designated class-3 ($\leq$250 m), class-2 ($\leq$500 m), class-1 ($\leq$1,500 m) and class-0 ($>$1,500 m). Our estimates of error for Argos locations did not depart from these categories and were similar to results from other studies on fishers carrying Argos collars (Sauder et al., 2012). We used only Argos locations with estimated errors $\leq$ 1,500 m. Both VHF and PTT transmitters were equipped with mortality sensors to document fisher deaths, which was a key objective for the reintroduction effort (Callas and Figura, 2008; Facka, 2017).

Analyses of Field Data

Habitat

We estimated habitat quality on Stirling using Thomasma's version (Thomasma et al., 1994) of Allen's (1983) fisher habitat suitability index, which was built to index habitat for prey and habitat required for reproduction. The Thomasma model has been tested independently at our and at other study sites with diverse vegetation communities and found to predict use of habitat by fishers (Thomasma et al., 1991; Powell, 2004; Facka, 2017). This model quantifies fisher habitat quality based on four vegetative metrics: (1) percent tree canopy closure, (2) mean diameter at breast height (DBH) of overstory trees, (3) tree canopy diversity (i.e., number of canopy layers, including a ground layer if it exists), and (4) percent of overstory trees that are angiosperms (hereafter hardwoods; **Figure 3**). Proximity among habitat patches and spatial configuration (e.g., fragmentation and interspersion) do not contribute to habitat quality in Thomasma's model. We used the gradient nearest neighbor (GNN) dataset downloaded from http://lemma.forestry.oregonstate.edu/data (Ohmann et al., 2011) to create indices for each of the four vegetative metrics and then combined these into the final habitat suitability index (HSI) as:

$$\mathrm{HSI} = (\mathit{Canopy\ Closure} + \mathit{Mean\ DBH} + \mathit{Canopy\ Layers})^{\frac{1}{3}} \times \mathit{Percent\ Hardwood},$$

where all variables range from 0 to 1 (**Figure 3**; Allen, 1983; Thomasma et al., 1994).

We calculated the mean habitat value within a 1 km radius circle (3.14 km^2) around release points for all reintroduced fishers (**Figure 3**). This area was similar to the smallest reported utilization distributions for fishers (Matthews et al., 2011). To evaluate the habitat quality of home ranges of reintroduced fishers, we used all their locations (if $\geq$ 20) during a calendar year (1 January to 31 December) to estimate annual utilization distributions with a fixed kernel density estimator using Silverman's (1986) k2 for the kernel and smoothing parameter h set to 500 m (Seaman and Powell, 1996). For each utilization distribution, we calculated the mean habitat quality within the 0.50 isopleth (representing an area where we could find a fisher on 50% of occasions). Because all fishers did establish home ranges, the 50% isopleths calculated using all locations emphasized the areas where the fishers settled.

To estimate the distribution of habitat quality available on and near Stirling, we generated 80 random points and then created a 1 km radius buffer around each point. We then assigned 40 polygons randomly to serve as release sites and 40 as home range cores and estimated the mean habitat quality for those areas. One release polygon and one home range core polygon were then paired to simulate randomly released fishers that settled on the landscape randomly.

We considered that a released fisher encountered the home range of a conspecific if we released that fisher within the 95% isopleth of the utilization distribution of a known fisher or if the released fisher encountered the 95% isopleth of a known fisher within 2 weeks of being released. We noted the sex of the resident of any home range a reintroduced fisher encountered.

Fisher Movements and Analyses

We analyzed fisher movements to 500 days after release, until a fisher died or until its transmitter failed. If a fisher lost a transmitter, we gave it a new one when we next recaptured it and again tracked its movements and use of its environment. For these analyses, all locations were used excluding any that seemed erroneous. For each fisher, we calculated three metrics of movement after release: (1) the mean distance from its release location to each successive location (Distance), (2) the area of the minimum convex polygon that bounded its last 50 locations (Polygon Area) and (3) the distance between release site and the centroid of the minimum convex polygon (Centroid Distance). We used minimum convex polygons to index environmental-use through time because it is a conservative measure of the maximum area an animal used for a given period. We chose to use 50 locations for polygon estimation because that represented a trade-off between exploratory, or aberrant, movements that some fishers made and the area that fishers were using seasonally or as they settled. When we had fewer than 50 locations for a fisher, we used all available locations to create convex polygons.

For comparison to reintroduced fishers, we evaluated movements and use of the environment by fishers born on our study site. We released all captured fishers born on Stirling at their capture sites and treated those locations the same as release locations for reintroduced fishers. We calculated the same metrics of movements as we did for reintroduced fishers. We removed Stirling-born fishers with fewer than 10 locations from analyses.

Testing Hypotheses

To analyze our three metrics of movements, we used generalized linear mixed models using PROC GLIMMIX in SAS. For each metric, we tested for an appropriate distribution and found that a gamma distribution fit our data best; hence, we also used a log link function. We modeled individual fishers and time as G-side random effects with a simple diagonal covariance structure. We estimated parameters using maximum likelihood and the Laplace method. Because we had relatively few individuals, we kept the structure of our statistical models simple (Fieberg and Johnson, 2015).

Before reintroductions started, we knew that male and female fishers move and behave differently (Powell, 1979b, 1994). Furthermore, because animals' movements and use of their environments generally change through time, we included both *Sex* and *Time* as effects in all statistical modeling (our *null*

TABLE 2 | Estimates for the first move and slope parameters from generalized linear mixed models for three dependent metrics for female (F) and male (M) fishers that were born on the study site (Stirling-born) and translocated fishers that were released onto the established home ranges of other fishers (Yes) and where no home ranges existed (No). Estimates were made from 57 fishers born on the study site and 40 translocated fishers from 2009 to 2016 in northern California.

			Distance from release site to each location (km)		Release site to polygon center (km)		Polygon area (km^2)	
Sex	**Encounter**	**Sex of resident**	**Initial moves ± SE**	**Change through time**	**Initial moves ± SE**	**Change through time**	**Initial moves ± SE**	**Change through time**
F	Stirling-born	–	1.6 ± 1.1	+	1.6 ± 1.3	+	1.6 ± 1.2	+
M	Stirling-born	–	2.4 ± 1.2	+	2.7 ± 1.2	+	1.6 ± 1.1	+
F	Intruder	F	9.0 ± 1.2	-	6.6 ± 1.1	-	65.9 ± 1.2	-
	Intruder	M	8.9 ± 1.2	-	6.6 ± 1.2	-	61.8 ± 1.2	-
	Colonist	F	5.0 ± 1.2	-	4.2 ± 1.2	-	25.0 ± 1.3	-
	Colonist	M	3.1 ± 1.2	+	2.5 ± 1.2	+	17.8 ± 1.3	-
M	Intruder	F	12.2 ± 1.2	+	10.1 ± 1.2	-	17.8 ± 1.3	-
	Intruder	M	12.5 ± 1.1	+	10.4 ± 1.1	+	109.1 ± 1.3	+
	Colonist	F	17.8 ± 1.3	+	14.6 ± 1.2	-	94.4 ± 1.3	+
	Colonist	M	14.4 ± 1.3	-	11.8 ± 1.3	-	196.8 ± 1.2	-

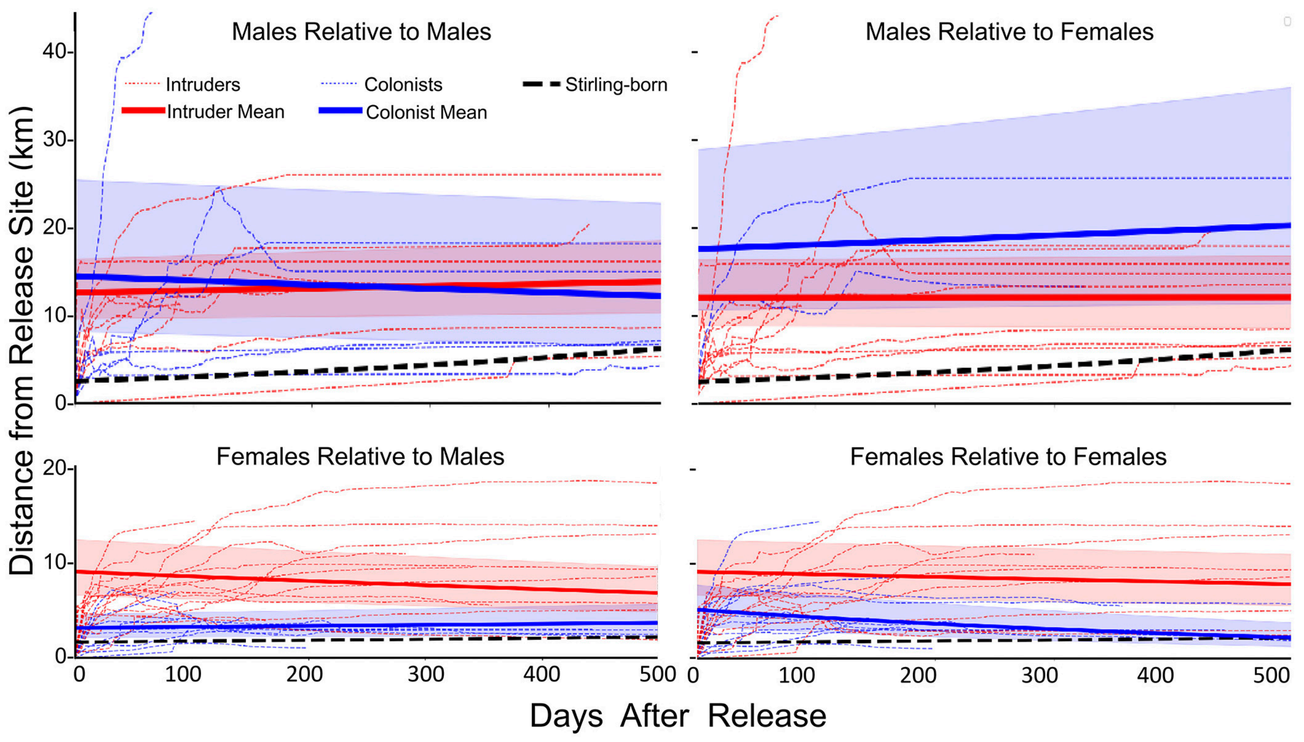

FIGURE 5 | Running mean distances (light red and blue dashed lines) from the sites of initial release following translocation for individual male **(upper panels)** and female **(lower panels)** fishers and the fitted mean distances for fishers released onto the established home ranges of previously released fishers (Intruders, red solid lines) and sites unoccupied by fishers (Colonists, blue lines) compared to fishers that were born on the study site (solid black lines). The y-intercepts represent initial movements from release sites.

model). For all fishers, we measure *Time* as the days since initial release (for reintroduced fishers) and days after capture for Stirling-born fishers. We predicted that if competition (a released fisher encountering another fisher's home range) were important to fishers of one or both sexes, then models incorporating competition should describe the data better than our null model. We predicted that a fisher of either sex could respond similarly and strongly when encountering the home ranges of only females or only males. Thus, we tested a model in which fishers of both sexes encountered males (*EncMale)* and another model where they encountered females (*EncFem)* without interactions between those groups (also including *Sex* and *Time*). Because we hypothesized that male and female fishers responded differently to competition, we tested two additional

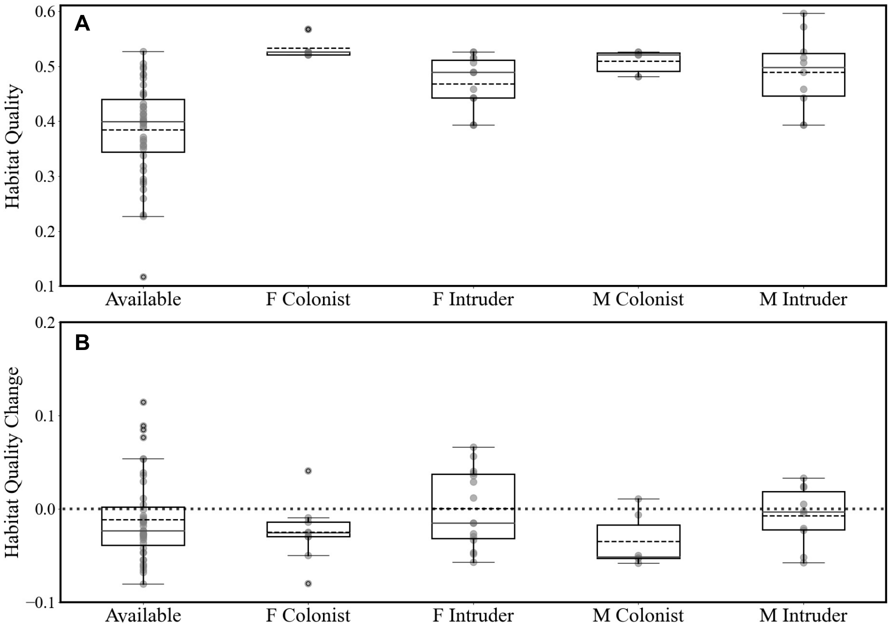

FIGURE 6 | (A) Distribution of the estimated mean habitat quality for release areas (circles with 1-km radius around release sites) and **(B)** the distribution of the difference in mean habitat quality between release sites and final home ranges of released fishers (positive values indicate that habitat quality in home ranges is higher than at release sites). We calculated habitat quality for fishers' home ranges for the area within the 50% isopleths and for available habitat.at randomly distributed circles with 1-km radius, Fishers released where no conspecifics hade established home ranges (F Colonist), Fishers released within the established home ranges of other fishers we call Intruders. Fishers released where no other fishers had established home ranges we called Colonists. Dashed black center lines are mean values and solid gray lines are medians.

models with interactions between the *Sex* term and encountering male fishers (*Sex* × *EncMale*) or female fishers (*Sex* × *EncFem*). Finally, to test whether poor habitat quality at the release sites or better habitat quality elsewhere described fishers' movements and settlement locations better than competition, we included a model with the change in habitat quality between a fisher's release area and the 50% isopleth where it settled (*HabSettle*).

We first calculated values for our three movement metrics using data from Stirling-born fishers to evaluate metric patterns over time and for subsequent comparison to data from reintroduced fishers. From preliminary plotting of the data, we recognized that a linear relationship between fisher movements and time may be insufficient. Thus, using our data for both reintroduced fishers and Stirling-born fishers, we tested three models where the effects of time on movement were linear, 3rd or 4th order polynomials. Generally, linear models performed similarly or superior to polynomial models of time. In the instances where a polynomial did fit the data better, the patterns of change through time and the y-intercepts were within the 95% confidence intervals for linear models. Consequently, in subsequent modeling we used only linear models to describe the behavior of our three metrics across time. The biological interpretations of these statistical parameters are that the y-intercepts describe fishers' movements or environmental-use 1 day after release (short initial movements yielded small intercepts while large initial movements yielded large intercepts) and the slopes describe overall trends in subsequent behavior (large movements away from release sites yielded positive slopes whereas short subsequent movements yielded negative or flat slopes).

For all models and metrics, we ranked competing hypotheses using Akaike's Information Criteria corrected for small sample size (AICc; Burnham and Anderson, 2002). Because we did not model Time as interactive to Sex or to different types of competition, we re-estimated the parameters for each group (e.g., males without competition) through time based on our top model's structure using the GLIMMIX procedure. We report and make inference based on these final estimates. In instances where we needed to make multiple comparisons or determine differences among groups, we used the Nelson-Hsu adjustment.

RESULTS

Stirling-Born Fishers

We calculated our movement metrics for the 17 male and 40 female fishers born on Stirling that we captured their first times in 2011 through 2016. (Fishers captured in 2017 did not receive collars because we removed collars that year in anticipation of research termination.) Females and males averaged 215 (95% CI = 141–289) and 271 (95% CI = 120–423) locations per individual for our analysis. Individual males and females exhibited highly varied movements and varied use of the landscape following release (**Figure 4**). On average, Stirling-born female fishers moved 1.6 ± 1.1 km and males

2.4 ± 1.3 km from their capture locations on the first day after release ($F_{1,7053}$ = 0.25, P = 0.68, **Table 2**). For all fishers, Distance (mean daily distance from release site) increased through time but males moved much farther than did females ($F_{1,7053}$ = 10.00, P = 0.0016, **Figure 4**). On average, Centroid Distance (distance from release sites to centroid of final polygon) was greater for Stirling born males than for females ($F_{1,7053}$ = 6.01, P = 0.014, **Table 2**). Polygon Area and Centroid Distances increased (low but positive slopes) over time for both female and male fishers (**Table 2**).

Reintroduced Fishers

Across all years, we estimated an average of 55 locations for female fishers and 97 locations for male fishers within the first 12 months after release. We followed 8 of 9 females released in year-1 (2009-2010) through June 2010. From June to August, three females died, and we lost contact with two others from apparent transmitter failure. We monitored five (of 6) males through the summer of 2010. We monitored all but 1 year-2 female for their entire first year (one female died in August). One male from the year-2 cohort died within 2 months of release. We had fewer estimated locations for the year-3 cohort because one female died 2 days after release and another died within 2 months. Predation was the most common source of mortality documented [7, bobcats (*Lynx rufus*), raptors], followed by accidents (5, roadkill, drowning) and disease (1); a large number of fishers who died for unknown reasons (18) carried residues of anticoagulant rodenticides.

Values for Distance ($F_{1,107}$ = 66.7, $P < 0.001$), Polygon Area ($F_{1,107}$ = 14.99, $P < 0.001$) and Centroid Distance ($F_{1,107}$ = 62.5, $P < 0.001$) were all greater for reintroduced than for Stirling-born fishers (**Table 2** and **Figure 5**). Notably, female fishers reintroduced without competition had patterns of movement and space-use most similar to Stirling-born female fishers. Reintroduced males moved larger Distances than did females ($F_{1,36}$ = 17.97, $P < 0.001$), had larger Polygon Areas ($F_{1,36}$ = 49.81, $P < 0.001$), and had larger Centroid Distances ($F_{1,36}$ = 20.48, $P < 0.001$) (**Table 2**). Both females and males developed home ranges relatively quickly. Distance reached asymptotes for most reintroduced fishers by day 100 (**Figure 5**). Similarly, Polygon Area and the Centroid Distance also plateaued or increased only slowly after 100 days. Data patterns for male fishers, however, were far more variable generally than were those for female fishers (**Figure 5**).

The estimated habitat quality at the release areas (circle with 1 km radius) was 0.50 ± 0.05 (on a scale of 0-1, n = 12; **Figures 2**, **6**). Most fishers were released into habitat that was of higher quality that would have been found at random (**Figure 6A**). Females and males settled into areas of similar habitat quality (female 0.49 ± 0.09; male 0.46 ± 0.08; $F_{1,36}$, P = 0.52) and, generally, fishers established home ranges in areas of similar quality habitat (mean = 0.48 ± 0.09; **Figure 6B**) as their release sites. Circles distributed randomly onto the landscape had a mean habitat quality of 0.38 ± 0.08, which does not differ from the means for where males or females settled (t = 0.22, df = 1, $P > 0.05$). Had we released fishers at random locations and had they established home ranges at some new random location, the average change in habitat quality would have been −0.05 ± 0.11 (**Figure 6**). Over all fishers, difference for release vs settlement habitat quality averaged −0.03 ± 0.08 (**Figure 6**).

The movements of reintroduced fishers were best described by models incorporating the presence of previously released fishers, differences (i.e., interactions between) for how males and females responded to encountering conspecifics, and included settlement habitat (**Table 3**). The highest ranked model for each of our three movement metrics had high support (Akaike's weight range 0.56–0.78) AICc for the next ranked model > 6.6 for all; **Table 3**). Models that included effects only from sex and time or changes in habitat quality from the release to settled areas of fishers had little support (weight range = 0.1–0.3). For all three metrics, model estimates indicated a negative relationship relative to settlement habitat (Distance: $\beta = -3.54 \pm 1.02$, $P < 0.005$; Polygon Area: $\beta = -4.21 \pm 0.99$, $P < 0.001$; Centroid Distance: $\beta = -3.10 \pm 0.75$, $P < 0.005$). Distance and Centroid Distance were best described by whether a fisher encountered a female fisher's home range, whereas Polygon Area was best described by encountering a female fisher's home range (**Table 3**). Female fishers that encountered the home ranges of conspecifics of either sex immediately after release moved farther and explored larger areas than did female fishers not encountering conspecifics (**Figure 5**). The effect on a female fisher of encountering another fisher's home range was apparent on all three metrics of movement (**Figure 5** and **Table 3**). Females moved similar distances if they encountered only females' or only males' home ranges (**Table 4**). Female fishers that encountered both females' and males' home ranges moved farthest. Conversely, male fishers exhibited a contrasting pattern. All male fishers encountered the home range of at least one male or female but males that failed to encounter a female fisher's home range moved farther than those that encountered only a male's home range or that encountered both (**Table 4**).

The pattern of female fishers moving farther in apparent response to conspecifics was consistent throughout the period of analysis. The patterns for all three metrics of movement for females that did not encounter another fisher's home range were more similar to the patterns for Stirling-born fishers than to the patterns for females that encountered home ranges of males or females (**Table 2**). The distances that female fishers moved (Distance) and the area used on the landscape (Polygon Area) decreased across time (**Table 2**). This pattern occurred because all females exhibited relatively high movement rates immediately after reintroduction, in contrast to non-reintroduced female fishers. The patterns for males that encountered or did not encounter home ranges of other fishers were less distinct than were those of females (**Figure 5**). All three movement metrics for reintroduced males, regardless of whether they encountered the home range of another fisher or not, increased or stabilized as time passed (**Table 2**), consistent with the patterns for Stirling-born males. For all three metrics generally, the mean values for males

TABLE 3 | Model selection criteria including the AIC_c scores, ΔAICc comparing top model to other competing models, the likelihood of each model, and the model weight (*w*) for each of six competing model from analyses of three dependent metrics of fisher movements after reintroduction.

Dependent	Model	AICc	ΔAICc	Likelihood	*w*
Mean Distance	Sex + Time + EncFem + HabSettle + Sex × EncFem	93,639.96	0.00	1.00	0.97
	Sex + Time + EncFem + Sex × EncFem	93,649.55	9.59	0.01	0.01
	Sex + Time + EncFem + HabSettle	93,649.61	9.65	0.01	0.01
	Sex + Time + EncMale + HabSettle	93,649.91	9.95	0.01	0.01
	Sex + Time + EncMale + HabSettle + Sex × EncMale	93,650.80	10.84	0.00	0.00
	Sex + Time + EncMale Sex × EncMale	93,652.10	12.14	0.00	0.00
	Sex + Time + EncMale	93,652.25	12.29	0.00	0.00
	Sex + Time + EncFem	93,653.63	13.67	0.00	0.00
	Sex + Time	93,654.32	14.36	0.00	0.00
Release Site to Polygon	Sex + Time + EncFem + HabSettle + Sex × EncFem	92,013.18	0.00	1.00	0.94
	Sex + Time + EncFem + Sex × EncFem	92,019.86	6.68	0.04	0.03
	Sex + Time + EncMale + HabSettle	92,023.58	10.40	0.01	0.01
	Sex + Time + EncMale	92,024.10	10.92	0.00	0.00
	Sex + Time + EncMale + Sex × EncMale	92,024.20	11.02	0.00	0.00
	Sex + Time + EncFem + HabSettle	92,024.34	11.16	0.00	0.00
	Sex + Time + EncMale + HabSettle Sex × EncMale	92,024.47	11.29	0.00	0.00
	Sex + Time + EncFem	92,026.06	12.88	0.00	0.00
	Sex + Time	92,026.75	13.57	0.00	0.00
	Sex + Time + HabSettle	92,028.45	15.27	0.00	0.00
Polygon Area	Sex + Time + EncFem + HabSettle + Sex × EncFem	179,384.40	0.00	1.00	0.95
	Sex + Time + EncMale + HabSettle + Sex × EncMale	179,391.40	7.00	0.03	0.03
	Sex + Time + EncMale + Sex × EncMale	179,393.90	9.50	0.01	0.01
	Sex + Time + EncFem + HabSettle	179,394.50	10.10	0.01	0.01
	Sex + Time + EncMale + HabSettle	179,395.00	10.60	0.00	0.00
	Sex + Time + EncFem + Sex × EncFem	179,397.60	13.20	0.00	0.00
	Sex + Time + EncMale	179,399.40	15.00	0.00	0.00
	Sex + Time + HabSettle	179,399.80	15.40	0.00	0.00
	Sex + Time + EncFem	179,400.90	16.50	0.00	0.00
	Sex + Time	179,402.80	18.40	0.00	0.00

The three metrics are the mean distance traveled from a fisher's release site to each successive location (Distance), the distance from release site to the center of a 100% minimum convex centroid for the last 50 locations (Release Site to Polygon Center), and the area of the minimum convex polygon bounding the last 50 locations for a fisher (Polygon Area).

TABLE 4 | The mean of the mean and maximum distances that reintroduced fishers traveled from their release sites through the first 500 days of observation.

Sex	Enc F	Enc M	N	Mean distance ± SD (km)	Average maximum ± SD (km)	Mean release habitat ± SD	Mean settle habitat ± SD
F	N	N	6	2.9 ± 1.2[b]	6.3 ± 1.4[b]	0.54 ± 0.02[c]	0.45 ± 0.08[a]
	N	Y	5	6.8 ± 4.4[a]	12.8 ± 6.8[a]	0.43 ± 0.05[a]	0.38 ± 0.12[a]
	Y	N	3	6.1 ± 3.4[a]	11.9 ± 1.5[a]	0.52 ± 0[a]	0.51 ± 0.07[a]
	Y	Y	9	9 ± 3.5[a]	15 ± 3.6[a]	0.49 ± 0.04[a]	0.49 ± 0.09[a]
M	N	N	0	–	–	–	–
	N	Y	3	23 ± 14.2[c]	48.9 ± 5.8[c]	0.49 ± 0.14[a]	0.46 ± 0.02[a]
	Y	N	6	16.4 ± 15.6[c]	30.7 ± 17.9[c]	0.51 ± 0.02[a]	0.4 ± 0.12[a]
	Y	Y	7	12.6 ± 4.5[a]	24.1 ± 12.8[c]	0.5 ± 0.04[a]	0.48 ± 0.07[a]

Some fishers encountered (Yes) or did not encounter (No) the established home ranges of female or male fishers.
Established home ranges had been occupied for at least 2 months and mostly approximately a year or longer.
[a] *Mean estimate is equal to the mean value across group based on Nelson-Hsu multiple comparison test at* $\alpha = 0.05$.
[b] *Mean estimate is lower than the mean value across group based on Nelson-Hsu multiple comparison test* $\alpha = 0.05$.
[c] *Mean estimate is higher to the mean value across group based on Nelson-Hsu multiple comparison test* $\alpha = 0.05$.

encountering or not encountering other fishers' home ranges overlapped and had high variances. Several males traveled long distances (up to > 20 km) from their release sites within the first 200 days after release, regardless of whether they encountered conspecifics, some of whom returned to the study site later (**Figure 5**).

DISCUSSION

Clearly, the movements of fishers indicate they perceive, internalize, and respond to the presence of other fishers on a landscape. Such observations are consistent with learned behaviors that modify future decisions and, potentially, fitness (Heft, 2013; Eichenbaum, 2017; Lewis et al., 2021). Consequently, the spacing of other fishers on the landscape and their potentials to affect resources are incorporated into each fisher's cognitive map and affects how each individual fisher uses that landscape. Fishers placed in, or that encountered, the existing home ranges of conspecifics did not stay long within these areas, demonstrating that they quickly learned of and responded to the presence of conspecifics. Female fishers released without competition were nearly identical in their average pattern of movement to Stirling-born fishers born on the study site. Stirling-born fishers were found in a variety of habitat qualities and, ostensibly, had created home ranges or areas that minimized competition.

The movements of female fishers are best explained best by accounting for the presence or absence of other fishers' home ranges and not exclusively by searching, and finding, areas of high habitat quality compared to where they were released. Females that did not encounter competition stayed close to their release sites and, at times, settled into marginally poorer (though still high) habitat (**Figure 6**). Were habitat their main priority these females could have moved to settle in overall higher quality habitat. In contrast, encountering the home ranges of other fishers, either male or female, caused female fishers to move farther and to explore more of the landscape before establishing their own home ranges. Female fishers discounted high quality habitat in the presence of competition and often moved to similar or worse habitat to where they were released. Our results indicate that female fishers preferred to avoid competition rather than attempt to remain in areas with already high habitat quality. Females who did not encounter other fishers' home ranges close to their release sites had movement patterns nearly identical to those of Stirling-born, non-reintroduced, fishers (**Figure 5**). Females moved less in the absence of competition regardless of habitat quality. The movements of male fishers were more varied but consistently different from females' movements. Males who encountered the home ranges of one or more females moved shorter distances both daily and until they established home ranges than did males who did not. The habitat quality where fishers established home ranges did not differ from that at the fishers' release sites nor from the habitat quality available on the landscape of our study site. Females and males established home ranges in areas with similar habitat quality (**Figure 6**).

Habitat quality was found in our top models but appeared, at least partially, as a consequence of fishers moving in response to conspecifics. Fishers that moved the furthest settled in the worst habitat relative to other fishers. Some male colonists and intruders each made long movements and settled long distances but also ended up in poorer quality habitat. Yet some males from each category moved less and settled in better habitat. Effectively, the mechanisms that seemed to cause fishers to move were their encounters with conspecifics, but the outcome was that animals that moved the most often settled into worst habitat. For males, long movements may come from both failing to find females initially or conflict with larger males. Had we more fishers to observe, we may have been better able to evaluate interactions between individual fishers and habitat choices. We do not claim that habitat is unimportant only that is appeared secondary to conspecifics interactions.

Conceivably, habitat quality could have been more influential in our study had we not chosen *a-priori* to release fishers only into areas with above average habitat quality for our study area, to maximize chances of population growth and establishment (Callas and Figura, 2008; Facka, 2017). A 4 × 4 study design with fishers released with and without competition in high- and low-quality habitat would have tested the effects of habitat better. Yet, this too may have been insufficient because fishers, like most carnivorans, can move widely and encounter other individuals incidentally—despite attempted study designs. Generally, we expect that both habitat quality and conspecifics influence movements and spacing patterns. Under other circumstances, habitat may be more important to fishers, or other animal's, movements (McNicol et al., 2020). We can state only that competition with conspecifics strongly affected the post-release movements of released fishers during this reintroduction in keeping with our initial hypotheses.

We conclude that intrasexual territoriality is a social system imposed on female fishers by males and that niche partitioning is not involved, consistent with Powell's (1994) hypothesis. Large movements by male fishers in the absence of encountering female fishers indicate that maintaining information on mating opportunities even outside of the breeding season is important to male fishers (Sandell, 1986; Holmes and Powell, 1994). The large sizes of adult male fishers prevent females from excluding males from their home ranges. Yet males and females make similar habitat choices and have similar diets (Powell, 1993; Holmes and Powell, 1994). We have established male imposition should be considered and further tested with data from other mammal populations that maintain intrasexual territories.

As with all conservation-based projects, the reintroduction forced us to make many trade-offs. We relied on Argos telemetry collars for males because of their long movements we may not have tracked with conventional VHF telemetry. Indeed, without the Argos collars, we would have missed many long-distance movements, often into unexpected areas and habitats. In the first year, telemetry collars for males did not arrive until 2 months after the first females had been released, leading males to encountered females shortly after release. In 2010, we experimented with newly produced GPS collars but found them unreliable and hence, unable to document mortality reliably (Facka, 2017). Despite these limitations, our study demonstrates how research and hypothesis testing can be designed into reintroductions.

Some male fishers that did not encounter female fishers moved long distances within the first weeks after release. Yet, some male fishers that did encounter female fishers also moved great distances. We hypothesize that such inconsistent movements depend on attributes of the male fishers that are resident or intruding. On two occasions, we released a young, relatively small male fisher whose movements became localized shortly after release. Subsequently, we introduced a large, adult male onto the small male's incipient territory and the small male moved to a new, incipient territory after wandering a long distance; the adult male settled in the small male's original incipient territory. When small male fishers are in the absence of female fishers or in the presence of large, dominant male fishers, their travel (dispersal) distances are like those observed for male fishers elsewhere (Proulx et al., 1994; Lewis et al., 2010). Unfortunately, we had insufficient data to tease apart these types of interactions. Interactions between old, experienced male fishers and young male fishers may occur relatively infrequently but probably influence structure and placement of territories on landscapes. Though males appear to have adopted a different strategy, they appeared to have learned the distributions and attributes of conspecifics quickly which were revealed in their movements.

For species with the potential for large sexual size dimorphism, the dimorphism exhibited by any cohort appears to depend on the abundance of prey during the year or years of growth for males of that cohort (Holmes, 1987; Powell and King, 1997). Thus, the extent of dimorphism is not a species trait, just the existence of the dimorphism is. Male stoats (*Mustela erminea*) growing during years of food shortage do not grow as large as those born into abundance but the small male stoats live longer, giving them more years of reproduction (Powell and King, 1997). Small males are, nonetheless, larger than females and able to impose intrasexual territoriality.

The effect of conspecific competition on use of a landscape is a critical component of assessing habitat quality for animals. Because habitat quality affects the fitness of individuals, the presence of competitors should have consequences for the fitness of the resident of a home range (Mitchell and Powell, 2003, 2004, 2007; Mosser et al., 2009). The risk of resource depression or depletion where residents had already become established caused newly released fishers to travel through and beyond areas of high habitat quality to establish home ranges elsewhere. Such complex interactions are important for understanding animals in native settings as well as for understanding how, when and where to release specific types of individuals during reintroductions.

We assessed the cost of resource depression by comparing the quality of home range-sized areas that were rejected by released fishers, the quality of areas incorporated by residents into their home ranges, and the quality of areas where newly released animal settled. For research that identifies individual animals within an established population, we propose that apparently unused areas of good habitat are actually the home ranges of animals that have not been documented. We refer to such areas with undetected residents as "ghost home ranges."

Our results provide further nuance to the consistent observation that male and female mammals use environments differently. Particularly for solitary, terrestrial carnivorans, males have larger home ranges, make longer movements, and often have home ranges that overlap with females (Powell, 1979a, 1993; Powell et al., 1997; Kovach, 1998; Stirling, 1988; Johnson et al., 2000; King and Powell, 2007; Persson et al., 2010; Sweitzer et al., 2015; Elbroch, 2017). We conclude that males effectively impose competition on females—ostensibly to monitor females for mating opportunities (Powell, 1994). Such motivations and spatial relationships are likely to be similar for many other mammals with large sexual size dimorphism, at least most solitary, terrestrial carnivorans.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Care and Use Committee of North Carolina State University.

AUTHOR CONTRIBUTIONS

Both authors contributed significantly to research design, data collection, data analyses, and writing.

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Memory and Conformity, but Not Competition, Explain Spatial Partitioning Between Two Neighboring Fruit Bat Colonies

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Spatial partitioning between neighboring colonies is considered a widespread phenomenon in colonial species, reported mainly in marine birds. Partitioning is suspected to emerge due to various processes, such as competition, diet specialization, memory, information transfer, or even "foraging cultures." Yet, empirical evidence from other taxa, and studies that tease apart the relative contribution of the processes underlying partitioning, remain scarce, mostly due to insufficiently detailed movement data. Here, we used high-resolution movement tracks (at 0.125 Hz) of 107 individuals belonging to two neighboring colonies of the Egyptian fruit bat (*Rousettus aegyptiacus*), a highly gregarious central-place forager, using the ATLAS reverse-GPS system in the Hula Valley, Israel. Based on comparisons between agent-based mechanistic models and observed spatial partitioning patterns, we found high levels of partitioning of both area and tree resources (<11% overlap) that were stable across different fruiting seasons. Importantly, partitioning could not have emerged if the bats' movement was only limited by food availability and travel distances, as most commonly hypothesized. Rather than density-dependent or between-colony competition, memory, and, to a lesser extent, conformity in tree-use explain how partitioning develops. Elucidating the mechanisms that shape spatial partitioning among neighboring colonies in the wild under variable resource conditions is important for understanding the ecology and evolution of inter-group coexistence, space use patterns and sociality.

Keywords: partitioning, memory, conformity, competition, *Rousettus aegyptiacus*, animal movement, coloniality

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INTRODUCTION

Foragers that congregate at a central place in large numbers (e.g., in roosts) face several conflicting demands. On the one hand, as the colony grows, direct and indirect competition forces individuals to spend energy exploring resources farther away from the colony (Ashmole, 1963; Gaston et al., 2007; Hinsch and Komdeur, 2010). On the other hand, congregations in roosts and around food patches offer ample opportunities to gather and transfer information about the location and status of unfamiliar resources (Dall et al., 2005; Van Moorter et al., 2009; Evans et al., 2016; Trapanese et al., 2019).

The tension between the risk of competition and information gain is even more acute when individuals from several conspecific colonies forage within the same landscape. In such cases, colonies often divide their territories to minimize conflict while sustaining intra-colony information flow (Adler and Gordon, 2003; Bolton et al., 2019). When resources and roosts are abundant, colonies are typically located far from each other, passively creating minimal resource mixing and competition risk (Wakefield et al., 2013; Aarts et al., 2021), a division termed the Hinterland Model (Cairns, 1989). Yet, accumulating evidence shows that spatial partitioning also occurs between neighboring colonies separated by a distance smaller than the individuals' typical foraging distance. For example, Wakefield et al. (2013) showed that 12 colonies of northern gannets (*Morus bassanus)*, distributed around the British shoreline, forage in mutually exclusive areas, including six colonies located very close to each other. Other studies reported spatial partitioning between neighboring colonies in a wide range of systems, most commonly in breeding colonies of marine birds (Ainley et al., 2004; Ceia et al., 2015; Corman et al., 2016; Mott et al., 2016; Sánchez et al., 2018; Bolton et al., 2019; Ito et al., 2020; Jessopp et al., 2020), but also in other birds (Cecere et al., 2018), ants (Gordon and Kulig, 1996; Adler and Gordon, 2003; Richardson et al., 2017) and a few other taxa (Ellis et al., 2009; Papastamatiou et al., 2018).

Although this line of evidence implies that spatial partitioning between neighboring colonies is widespread, three key elements are missing for understanding how and by which cognitive and social mechanisms partitioning is sustained. First, studies are biased toward marine birds while breeding, which cannot be readily generalized to other species that live within the same home range year-round or have different types of diet, such as non-mobile food (Bolton et al., 2019; Riotte-Lambert and Matthiopoulos, 2020). The degree of resource unpredictability, in particular, has been suggested as the key evolutionary driver of animal congregations, increasing information transfer and therefore reducing resource uncertainty (Ward and Zahavi, 1973; Egert-Berg et al., 2018; Gager, 2019; Riotte-Lambert and Matthiopoulos, 2020). Yet, most studies focus on a single season or average spatial partitioning across seasons and resource conditions, thereby neglecting the dynamic nature of resource availability (Grémillet et al., 2004; Aarts et al., 2021). Second, spatial partitioning is often reported based on the observation that colonies maintain minimal overlap between their foraging areas. However, to confirm that partitioning does not emerge through a random process or is the consequence of travel distance limitations alone, the observed overlap must be compared against those emerging from appropriate reference models that can isolate effects associated with these processes (Cecere et al., 2018; Bolton et al., 2019; Ito et al., 2020). Third, most studies did not systematically examine the mechanisms contributing to partitioning, namely competition, memory of resources, and information transfer within the colony (Grémillet et al., 2004; Corman et al., 2016; Bolton et al., 2019; Aarts et al., 2021). Furthermore, studies that investigated these mechanisms used population or agent-based simulations that were only partially derived from observed movement distributions, without comparing the results to the observed between-colony overlap (e.g., Barta and Szép, 1995; Adler and Gordon, 2003; Wakefield et al., 2013; Dallas et al., 2019; Aarts et al., 2021). Therefore, it remains unknown which mechanism, if any, explains observed spatial partitioning patterns under natural conditions. A major limitation in making these inferences has been the lack of movement data at a temporal resolution high enough to measure (and model) local spatial overlap. The emergence of new technologies, namely high-throughput reverse-GPS systems such as ATLAS (Toledo et al., 2020) and some acoustic telemetry systems (Baktoft et al., 2015), can now collect long-term, high-resolution movement data that can bridge these gaps.

The most hypothesized driver of spatial partitioning between neighboring colonies is density-dependent competition and its tradeoff with travel costs (Grémillet et al., 2004; Wakefield et al., 2013; Corman et al., 2016; Sheppard et al., 2018). According to this idea, coined the Density Dependent Hinterland Model by Wakefield et al. (2013), individuals of one colony expand their home range into areas overlapping an adjacent colony's patches following local food depletion. As the number of individuals within the overlapping area increases, both colonies are pushed back to exploit more available resources in non-overlapping areas until an equilibrium is reached and the two colonies hold mutually exclusive ranges. However, this hypothesis assumes that density-dependent competition exists, despite little and very system-specific evidence (Lewis et al., 2001). Another possibility that has been given less attention is that individuals compete only with members of the other colony, that is, a *between-colony* competitive response that might affect spatial partitioning more directly than density-dependent competition. Yet, this idea assumes that conspecifics can differentiate between foreign and self-colony members and attribute the level of perceived competition accordingly. Some taxonomic groups, especially eusocial insect such as ants and bees, and highly social mammals such as mongoose, are known to recognize individuals from a rival group by processing chemical "signature mixtures." Yet, chemical or similar recognition mechanisms are less likely to emerge in other groups, such as birds and less social mammals (Wyatt, 2005, 2010).

Information about resources may operate on top (or independent) of competition to sustain spatial partitioning between colonies (Wakefield et al., 2013; Riotte-Lambert and Matthiopoulos, 2019). Different levels of home-range familiarity and the ability to memorize previous visits to resource patches have been shown to drive home-range formation for many species (Moorcroft, 2012; Fagan et al., 2013; Merkle et al., 2014; Bartumeus et al., 2016). In fact, memory on its own was shown to create non-overlapping individual home ranges in simulated free-ranging foragers, even when resources deplete relatively fast due to intense competition (Riotte-Lambert et al., 2015). At the colony level, theoretical simulations incorporating individual memory without competition were sufficient to form spatial partitioning in central-place gregarious foragers that show high fidelity to their colony roosts (Aarts et al., 2021). A practical challenge in modeling the effect of memory on resource and spatial partitioning is evaluating the true, or realistic, memory coefficient, such as the mean probability of the return to previously visited sites (Aarts et al., 2021). This is because metrics of revisits are highly dependent on the tracking and resource data resolution (Bracis et al., 2018). For example, low temporal resolution may cause short area-restricted-search events to be overlooked and therefore revisits to these areas might be underestimated. From a spatial perspective, low resolution may attribute false revisits if the selected grid size of the study area is too large, compared to the real size of foraging patches (Fagan et al., 2013).

When resources are temporally predictable (e.g., mobile prey, carcasses, or fruits of different plant species), group-living animals often share information to reduce uncertainty about resources (Ward and Zahavi, 1973; Kerth et al., 2001; Weimerskirch et al., 2010; Evans et al., 2016; Harel et al., 2017). One potential outcome of repeated exposure to information within a group, whether gained intentionally or inadvertently, is that individuals may conform to the same behavior (Herbert-Read et al., 2013; Somveille et al., 2018). Accumulating evidence shows that some species conform to the most abundant behavior, even without personal experience, regarding food preferences (Van De Waal et al., 2013), strategies for problem-solving (Dindo et al., 2009; Aplin et al., 2015), and group movement speeds and habitat use (Herbert-Read et al., 2013; Wilson et al., 2019). Although theoretical models show that information sharing minimizes overlap between neighboring colonies (most evidently in Wakefield et al., 2013), this mechanism has not yet been explicitly examined using empirical data (Aarts et al., 2021).

In this study, we used high-resolution movement data (collected at 0.125 Hz) of 107 Egyptian fruit bats (*Rousettus aegyptiacus*; hereafter abbreviated as EFB) from two large neighboring colonies in the Hula Valley, north Israel, along with a complete dataset of all fruit trees they visited within the study area. Preliminary exploration of these data revealed considerable spatial partitioning between bats from two large colonies, which motivated the investigation of three main hypotheses on the mechanisms that might be responsible for the observed resource and spatial partitioning between neighboring colonies. We first hypothesized that such partitioning could not have emerged due to travel distance limitation only, nor by chance. Second, we hypothesized that partitioning could have emerged due to one or more of three mechanisms commonly suggested in the literature, namely density-dependent competition, memory of resources, and information sharing within each colony. Third, we hypothesized that the observed partitioning could have occurred at some theoretical memory or conformity coefficients, which do not necessarily match the observed ones. To examine the first two hypotheses, we built competitive agent-based models derived from real bat tracks to simulate the tree-use patterns formed when using each of the abovementioned mechanisms, separately and in conjunction. We then compared the simulated partitioning indices of each model—representing the overlap of trees and home ranges between colonies—against the observed ones. Due to the ambiguity about how competition operates between colonies, we examined the empirical evidence for density-dependent and between-colony competition separately before including competition in our models. To address the third hypothesis, we repeated the same simulation models but replaced the observed memory and conformity coefficients with theoretical values and examined the thresholds above which partitioning develops.

MATERIALS AND METHODS

Study Species and Area

The Egyptian fruit bat (*Rousettus aegyptiacus*) is a long-lived, widely distributed Old World fruit bat (Pteropodidae, Kwiecinski and Griffith, 1999). In Israel, EFBs are generalist foragers consuming a wide variety of fruits, most of which have a predictable seasonal fruiting phenology (Tsoar et al., 2011). However, some fruit trees, especially of the non-native *Ficus* genus (Moraceae), fruit in unpredictable cycles, ranging from 1 to 8 cycles a year (e.g., Galil et al., 1977). The study area in the Hula Valley, north Israel (**Figure 1**), covers a 19,000-ha area and is an agriculturally dominated landscape inhabited by ∼2,500 EFB fruit bats that roost mainly in two large caves—Gershom with ∼1,400 and Zemer with ∼500 individuals. Three other caves are occasionally inhabited for varying periods, from days to months (pers. obs.). The two main cave-roosts are located 3.5 km apart, a distance much shorter than the average 10.3 km an EFB covers a night, based on our long-term (4 years) tracking data. Two lines of evidence and observations guided our reasoning in testing the effect of memory and conformity on resource-use patterns in this species. First, similar to other fruit bats, individual EFBs tend to feed on a small subset of available trees and repeatedly revisit them for weeks and even months (Egert-Berg et al., 2018; Toledo et al., 2020), which affirms that EFBs rely heavily on individual memory. Additionally, we have recently shown that EFBs obtain a "cognitive map," which encompasses information about a large number of tree locations, suggesting that memory expands beyond the trees used at a given time (Toledo et al., 2020). Second, EFBs are highly gregarious central place foragers, found in the hundreds in cave-roosts and dozens around fruit trees during foraging. High roost fidelity (**Figure 1**), together with repeated visits to the same trees, creates opportunities to exchange information on fruit locality and status, driving individuals to conform to the use of the same resources.

Captures and Tracking

EFBs were captured using mist nets, either around trees or at cave-exits. Bats were tracked by ATLAS (Advanced Tracking and Localization of Animals in real-life Systems), a reverse-GPS system that utilizes extremely lightweight, low-cost tags at a high temporal frequency with a 5 m mean localization error (Toledo et al., 2016; Weiser et al., 2016). ATLAS tags were either mounted using a shrink-coated cable-tie collar to allow tracking for up to 9 months or glued on their upper-backs with surgical cement (Perma- Type, Plainville, CT, United States) for bats that had not yet reached full adult size. Tag units weigh 7.4 g (5.2% of mean adult body mass) for collars or 3 g without. Captures and tagging procedures have been approved by the Ethics Committee of the Hebrew University (permit NS-15-14-14660-2) and the Israeli Nature & Parks Authority (permit NS-2020/42577).

This study analyzed data of 107 bats that regularly roosted in one of the two main caves during 2018–2020. Bats were tracked

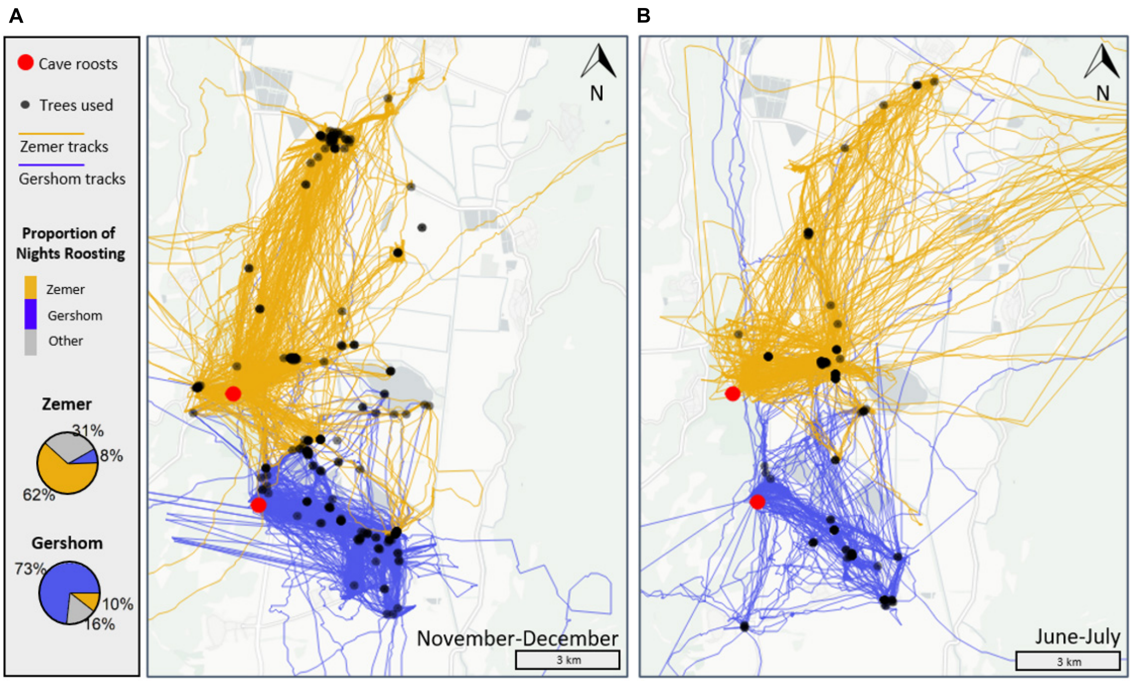

FIGURE 1 | Tracks of Egyptian fruit bats of two neighboring colonies, Zemer in yellow and Gershom in purple, showing resource (trees) and spatial (area) partitioning of foraging areas within the Hula Valley, Israel. Bats of both colonies show high fidelity to their cave-roosts (red spheres), expressed by the proportion of nights individual bats roosted in each focal cave (pie-charts per colony on the left panel). Gray portions of the pie-chart are the percent of cave switching nights from the focal cave to other caves. Black spheres are individual fruit trees visited by bats. Each map shows foraging movements within the **(A)** lean-fruit months of November-December (147 bat-nights of Gershom and 155 from Zemer, left map), and **(B)** during peaks of fleshy fruits in June-July (82 bat-nights Gershom and 108 Zemer, right map), accumulated across 2018–2020.

at a 0.125 Hz sampling rate for an average tracking period of 23.7 nights and up to 131 nights. We also mapped nearly all fruit trees in the study area (14,314 trees and 18,111 orchard trees), which enabled us to identify specific tree visits.

Observed Metrics of Resource and Spatial Partitioning

To estimate resource and spatial partitioning between colonies, we first filtered raw EFB tracks for localization errors based on the covariance matrices attributed to each ATLAS fix (Gupte et al., 2021) and localization that exceeded the highest realistic speed threshold for this species of 20 m/s. Then, we defined visits to trees (location, tree ID, and duration) based on track segmentation utilizing the first-passage algorithm to determine the center of a "cloud of fixes" where the animal has spent a specified number of observations within a certain radius (source code and details at https://github.com/ATLAS-HUJI/R/tree/master/AdpFixedPoint). We then related the median coordinates of each cloud to the closest tree in the dataset. Colony membership was assigned based on the cave-roost a bat exited from each night. For this analysis, we took out foraging nights that followed cave switching events between the two main colonies because we could not choose the colony membership for those particular cases and since they were relatively rare (< 11% of bat-nights, **Figure 1**). Resource partitioning was measured as the percent of tree overlap (shared trees/all trees used, **Table 1**). Spatial partitioning was estimated by drawing the 75% Kernel utility density (KUD) contours for all bats of each colony and calculating the percent of area overlap (overlapping KUDs area/total area used, **Table 1**). We chose KUDs with the most common "href" bandwidth and selected the 75% contours to represent a compromise between falsely enlarging the area due to single events of longer bouts and underestimating the area due to the exclusion of short, but sometimes repetitive, visits to trees. For simplicity, we did not consider variation in tree quality when calculating overlap, for instance, by using the duration in time spent on a tree as a proxy of tree value. Both types of overlap are expected to vary according to fruit availability. For instance, some periods are characterized by a dense concentration of fruits around the line of equidistance between caves (e.g., *Morus nigra* and *Ficus carica* trees in May–July), while in other periods, bats rely on the emergence of less predictable fruits, e.g., invasive species of the *Ficus* genus (family Moraceae) in November-December. We, therefore, corrected for changes in fruit availability by estimating trees and area overlap for each month separately, including only months that contained at least five bats from each cave (range 20–33 total bats), aggregated across 2018–2020. Finally, the overlap estimation between tracked bats is more accurate for months in which we had more data. Hence, we weighted the percentage of overlap by the number of bat-nights in each month to create the weighted

TABLE 1 | Observed movement parameters used in the agent-based models and indices of observed resource (trees) and spatial (areas) partitioning, for two neighboring Egyptian fruit bats colonies during 2018–2020.

	Feb	Mar	Jun	Jul	Nov	Dec	
Movement parameter							
Number of foraging nights per tracked bat	1018,15]	6 [6,6]	6 [3,10]	6 [3,10]	9 [6,12]	14 [3,24]	
Total Number of tracked bats (Gershom/Zemer)	13/10	15/5	18/18	12/10	18/15	14/16	
Number of trees visited per bat-night	9 [5,18]	12 [7,23]	14 [11,21]	16 [9,22]	25 [14,42]	26 [15,47]	
Roost-to-first-tree travel distance (m)	2400 [2200,4300]	3500 [2200,5200]	2600 [2300,3900]	2900 [2400,3900]	2900 [1900,4000]	3700 [2200,4000]	
Tree-to-tree travel distance (m)	51 [27,109]	52 [30,101]	64 [25,205]	67 [32,409]	65 [32,209]	79 [38,262]	
Memory coefficients (μ)-							
The probability of an individual to return to the same tree on	0.87 [0.8, 1]	0.85 [0.7,1]	0.75 [0.7,0.9]	0.95 [0.8,1]	0.8 [0.7,0.8]	0.8 [0.75, 0.85]	
Consecutive nights (proportion of trees already-used each night)							
Conformity coefficients (β)-							
The probability to visit trees used by other members of the same colony (maximal proportion of shared trees for Gershom/Zemer)	0.2/0.4	0.2/0.6	0.1/0.2	0.2/0.2	0.2/0.2	0.2/0.4	
Partitioning indices							
Tree Overlap (%):							
The percent of trees shared between colonies	10	2	6	7	2	5	**WTO = 5.4%**
Area Overlap (%):							
The percent of the 75% KUD home-ranges' overlap between colonies	3	7	10	15	14	14	**WAO = 10%**

All parameters are summarized per month to account for differences in resource conditions. For movement parameters, medians are presented [25–75% interquartile range] unless stated otherwise. Partitioning indices represent the proportions of overlap per month, and the derived weighted tree overlap (WTO), and weighted area overlap (WAO), both weighted by the proportion of bats tracked each month.

mean tree overlap (WTO) and the weighted mean area overlap (WAO) indices (**Table 1**).

Agent-Based Simulations

The purpose of the agent-based models was to tease apart the contribution of memory, conformity, and competition on the observed resource and spatial partitioning patterns. To this end, we simulated the movement of bats with and without these different mechanisms and compared the emergent simulated partitioning indices against the ones observed in real EFBs (WTO and WAO, see section "Observed Metrics of Resource and Spatial Partitioning"). The first set of models uses movement data derived from observed bat tracks to identify the mechanism contributing to partitioning in our system. The second builds upon the same structure but uses theoretical values for memory and conformity to identify the value beyond which partitioning can (theoretically) develop. Here, we begin by detailing the empirical parameters used in the simulations (see **Table 1** for a summary), and then we outline the principle simulation workflow (**Figure 2**). See supporting information for a more detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2020).

Observed Parameters

Observed movement parameters were based on the tree-visit patterns from real bat tracks, the trees they visited, and the location of each colonys' roost (**Table 1**). Movement parameters and the available tree dataset were collected separately for each month to account for seasonality (for reasoning, see section "Observed Metrics of Resource and Spatial Partitioning"). Movement parameters can be divided into three categories: (1) variables used to simulate the number of bats, nights tracked, and trees used per bat-night (steps). (2) Parameters to account for distance constraints—the distributions of flight distances undertaken by bats between the cave-roost and the first tree, as well as between consecutive trees (i.e., tree-to-tree distance). (3) Memory and conformity coefficients. Memory coefficients are the probabilities of visiting a tree used in previous nights (number of already-used trees/total trees, per bat-night). Since simulations have a time interval of 1 month, we assume that bats can remember all trees they used during this period, following our previous finding that EFBs memorize trees for at least 158 nights

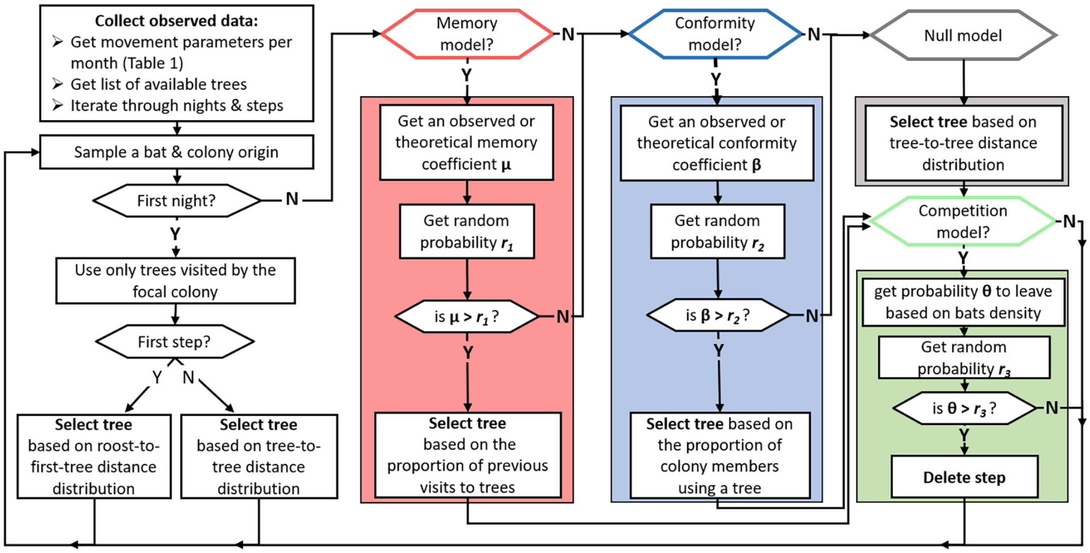

FIGURE 2 | Flowchart showing the decision-making process of a simulated bat at each step (tree visit) of the agent-based models. A step begins by sampling a bat-agent and ends with a tree selection. Colored frames represent the null model (gray) or the implementation of the different mechanisms that are hypothesized to affect resource and spatial partitioning—memory (red), conformity (blue) and competition (green). At the end of the simulation, each colony is attributed a set of trees from which the between-colony partitioning indices (WTO and WAO) are calculated.

(Toledo et al., 2020). Conformity coefficients are the maximum proportion of shared trees among colony members (maximum number of shared trees/total trees, per colony). Conformity reflects information transfer indirectly because it assumes that if the information is shared (unrelated to *how* it is shared), it will push bats to conform and use the same trees. We used the maximum value of shared trees because the real proportion of trees shared (including non-tracked bats) is likely higher since EFBs almost always congregate around fruit trees (Kwiecinski and Griffith, 1999). Before incorporating competition into the model, we evaluated whether there is evidence for it in our data. Two types of competition were tested—density-dependent (bats are negatively affected by the presence of other bats on trees) and between-colony competition (bats are negatively affected by bats *from the other colony*). For density-dependent competition, we first estimated if the density of tracked bats increases around trees used by both colonies (i.e., "shared") against trees used by a single colony. Then, we measured the probability to visit and the duration of time spent on trees that hosted increasing numbers of tracked bats to see if individuals changed their behavior in response to higher densities. Similarly, whether between-colony competition occurs was estimated based on the same dependent variables, but as a function of the number of bats from the other colony only. According to the competition results (**Supplementary Figures 2–5**), we implemented a simple and weak competition rule without considering different competition strengths in our models.

Simulations Workflow

All simulations (illustrated in **Figure 2**) followed the same temporal hierarchy: First, the list of trees and the observed movement parameters were collected for each month (section "Observed Parameters" and **Table 1**). Then, the maximal number of observed tracked nights was sampled, and tree visits were simulated for each night separately. Since any of the studied mechanisms probably affected bats before our tracking began, we forced agents to select only trees originally attributed to their colony on the first night. Lastly, we derived the number of steps for each month and night to be twice the number of tracked bats and all the trees they visited (2 × n bats × n trees) as a compromise between sample size and computational load.

Each step began by randomly sampling a bat and ended with a tree visit (**Figure 2**). Bats were randomly sampled so that they could simultaneously forage and affect each other's tree choices. The first time a bat was sampled, it was given a colony ID based on the observed probability of belonging to each colony (proportions of tracked bats from each roost). We assumed bats do not switch between colonies, owing to the high levels of roost-fidelity we observed (**Figure 1**). Additionally, although colony size changes seasonally (pers. obs.), there is no data to date on the duration, or even existence, of group cohesion of any size in this species. The selection of trees for the first night was initialized the same way in all models: for the first tree, a distance was randomly sampled from the observed distances from the roosts to the first tree that real bats visited (**Table 1**). Then the tree that was positioned the closest to that distance (± 100 m) was selected. The rest of the trees in the first night were selected in the same way, only based on a distance sampled from the observed tree-to-tree travel distance distribution (**Table 1**). The above first-night initiation resulted in a baseline of trees that bats of the given colony originally visited.

In the null model, bat-agents could choose among all seasonally available trees (of both colonies) and selected a tree based only on the tree-to-tree travel distances, as in the initiation phase (**Figure 2**). Simulating memory and conformity from observed coefficients (**Table 1**) followed the same decision sequence. For the memory model, a memory coefficient μ was randomly sampled from the probability distribution of visiting already-used trees. We then randomly sampled a probability r_1, taken from a uniform distribution [0,1]. If $\mu > r_1$, the bat proceeded to select among known trees, i.e., made a memory step. The specific (known) tree was selected based on the relative proportion of the focal individual's previous visits to each tree (a linear tendency to select highly used trees). For the conformity model, bats would select among unknown (new) trees that they did not memorize. Then, a conformity coefficient β was selected for each colony (a single value, see section "Observed Parameters"). We sampled another random number r_2, and a conformity step was made if $\beta > r_2$. The specific tree was then selected based on its "attractiveness," i.e., the proportion of the same-colony members that used a tree. When neither the memory nor conformity models were applied, or when $\mu < r_1$ and $\beta < r_2$, a tree was selected based on the tree-to-tree travel distance distribution, as in the null model. Competition in the simulation operated in retrospect after a tree was selected. When applied, a step was deleted if a probability θ that grows logarithmically with the density of simulated bats that used that tree was higher than a randomly sampled number r_3 (**Figure 2**). Because removing visits results in an overall smaller number of steps, corresponding to a mean of 7 ($\pm$ 3) percent of steps lost, we added 10% more steps when running the competition models.

In addition to the observed movement parameters (**Table 1**), the procedure above was repeated using theoretical and constant memory and conformity coefficients (range 0.2–0.97) to identify thresholds above which resource and spatial partitioning emerge. These resulted in one set of agent-based models derived from observed memory and conformity coefficients and additional sets for each theoretical memory and conformity coefficient, with and without their interaction with competition.

All models executed 100 iterations per month. Then WTO and WAO were calculated based on the trees and area overlap and the total number of simulated bat-nights per month (as for the observed indices, see section "Observed Metrics of Resource and Spatial Partitioning"). All models were constructed in R version 4.0.4 (R Core Team, 2021), with the *rgeos* package (Bivand and Rundel, 2020) for spatial object manipulations and *amt* package (Signer and Fieberg, 2019) for home range estimations and area overlap. Code will be made available upon request. *p*-values for testing the difference between each model against the observed tree or area overlap (WTO and WAO, respectively) were determined as the proportion of 100 simulated indices smaller than the observed index.

RESULTS

Colonies Characteristics and Observed Partitioning

We analyzed 107 bats that were tracked for a total of 1,271 foraging nights. Out of which, 764 bat-nights originated from Gershom roost and 507 from Zemer. Bats visited < 10% of fruit trees in the study area (1,874 trees overall, mean per bat-night = 7.1). The data includes only tracks of months for which we had a sufficient number of bats from each roost simultaneously (>5 bats, 6 months in total), pooled across 2018–2020, and representing varying levels of fruit availability (see section "Observed Metrics of Resource and Spatial Partitioning"). The age and sex structures of tracked bats from each colony were similar: from Gershom, 51% were adults and 66% from Zemer, with the remaining individuals being < 1-year-old juveniles. Sex structure was also similar between colonies, with 62% males in Gershom and 54% in Zemer. The movement parameters of individual bats per colony were statistically the same (e.g., maximal distance, time spent foraging, mean duration foraging on a tree, $p > 0.05$, ArtAnova, Wobbrock et al., 2011) but differed in the total area covered, showing varying differences between colonies depending on the month (**Table 1**), and slightly in the number of trees used per bat (mean trees difference = 6 trees per bat-month, **Table 1**). Regardless of the relative fruit tree distribution, bats of both colonies showed markedly different foraging ranges, with very little overlap between them (**Figure 1**). As represented by the WTO index, resource partitioning was substantial, with only 5.4% of trees used by both colonies (ranging from 2 to 10% between months, **Table 1**). Similarly, spatial partitioning, represented by the WAO index, showed that 10% of the total area was shared between colonies (ranging from 3 to 19%), which is 11.8 km^2. High levels of colony fidelity further reinforce observed partitioning as bats of both caves continued to roost in the same cave between 62 and 73% of foraging nights. For the remainder of the nights, bats mostly switched to temporary and smaller caves, spending only 8–10% of the nights at the other main cave (**Figure 1**).

Testing Mechanisms That Explain Resource and Spatial Partitioning

We found support for the first hypothesis postulating that partitioning between EFB colonies is not the outcome of distance limitations nor chance, based on significantly lower observed WTO and WAO relative to the null model (null models indices = 48 and 25%, respectively, $p < 0.01$, **Figure 3**). Among the three drivers of partitioning in EFB, outlined in our second hypothesis, the memory model created the strongest effect with WTO < 20% and WAO < 5% (**Figure 3**). The observed conformity model had a smaller effect, with WTO < 35% and WAO < 15% and the competition model did not result in WTO or WAO distributions that were meaningfully different than those of the null model (**Figure 3**). Additionally, the combined effect of memory with conformity and competition did not reduce WTO or WAO substantially more than each mechanism in isolation (**Figure 3**). These results are directly linked to the observed memory and conformity coefficients (**Table 1**): memory was high, with > 83% of trees already visited in previous nights. The mean of the maximal conformity coefficient for each month was 25% (range 10–60%, **Table 1**), suggesting that only a small proportion of trees are shared between same colony members. We did

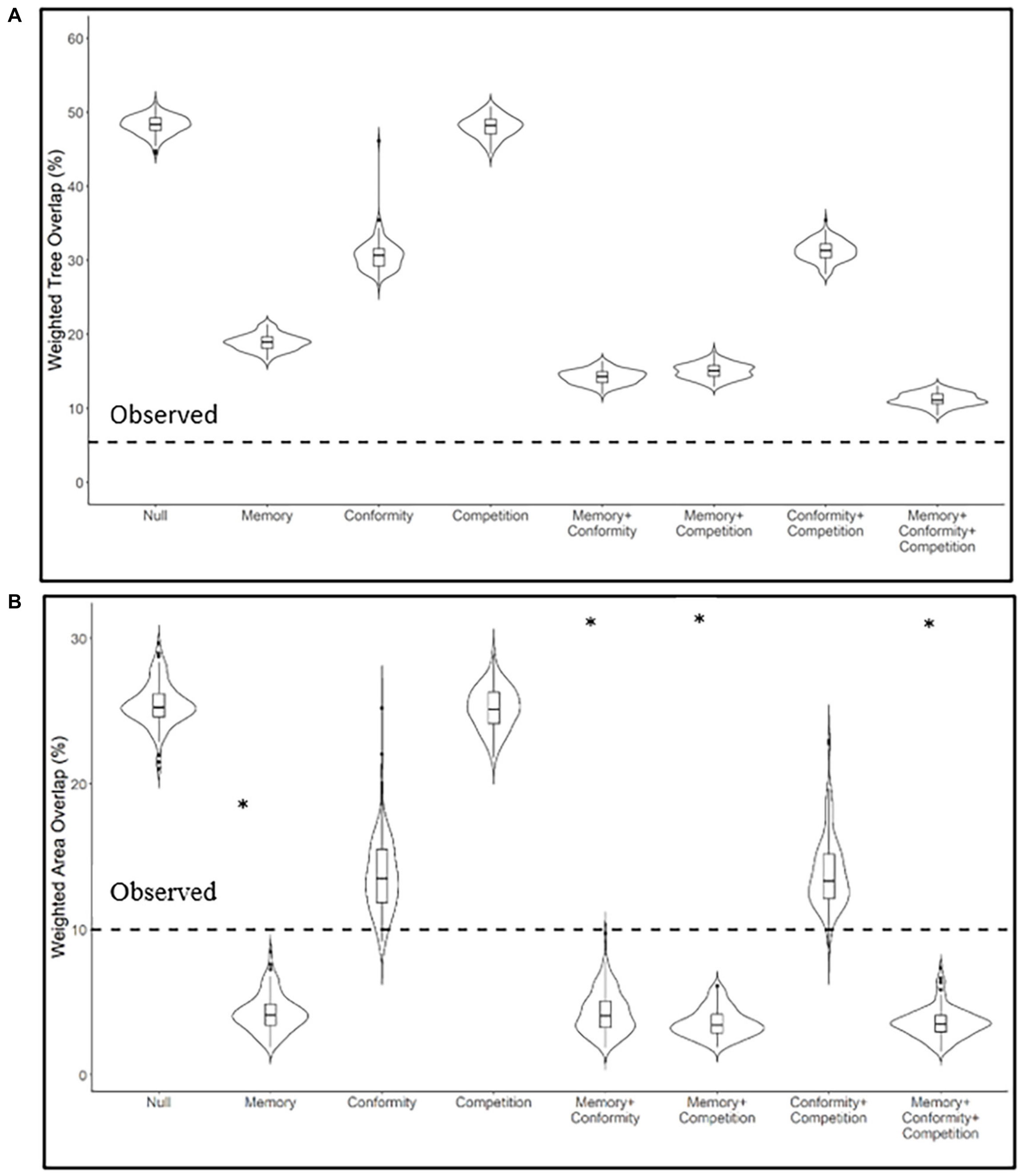

FIGURE 3 | Resource and spatial partitioning between two neighboring Egyptian fruit bat colonies. Violin plots represent the frequency distribution of **(A)** the weighted tree overlap (WTO, range: 9–51%) and **(B)** weighted area overlap (WAO, 75% KUDs, range: 0–31%) after 100 iterations of agent-based models for observed coefficients of memory and conformity, density-dependent competition, and their interactions. The dashed line represents the observed values of tree and area overlap. *p-value $\geq$ 0.05 comparing simulated and observed.

not find evidence for competition because higher densities did not affect the duration bats spent on trees nor their revisit probabilities. This held both in the case of density-dependent competition (i.e., when considering total bat density, **Supplementary Figures 2**, **3**) and between-colony competition (i.e., when considering only the densities of bats from the other colony, **Supplementary Figures 4**, **5**). In the simulations, we nevertheless included competition, using only the density-dependent form, since it is more commonly considered the main driver of partitioning in the literature, to reference the effects of the two other tested mechanisms and all possible interactions between them. The effect of memory and conformity was stronger for WAO than WTO (**Figure 3**). Importantly, none of the models for resource partitioning derived from real tracks, and none of their interactions, significantly reached the observed level of WTO (**Figure 3A**). For area partitioning, however, all models incorporating memory (alone or associated interactions) showed a lower level of WAO compared to the observed ones, while those incorporating conformity (alone or with competition) nearly matched the observed level (**Figure 3B**).

To address the third hypothesis and identify the thresholds above which resource and area partitioning can theoretically be reached, we used controlled and constant coefficients of memory, conformity, and the interaction between them and with density-dependent competition (**Figure 4**). We found that relatively high values of memory (= 0.97) and conformity (= 0.8), without any interactions, result in the observed WTO.

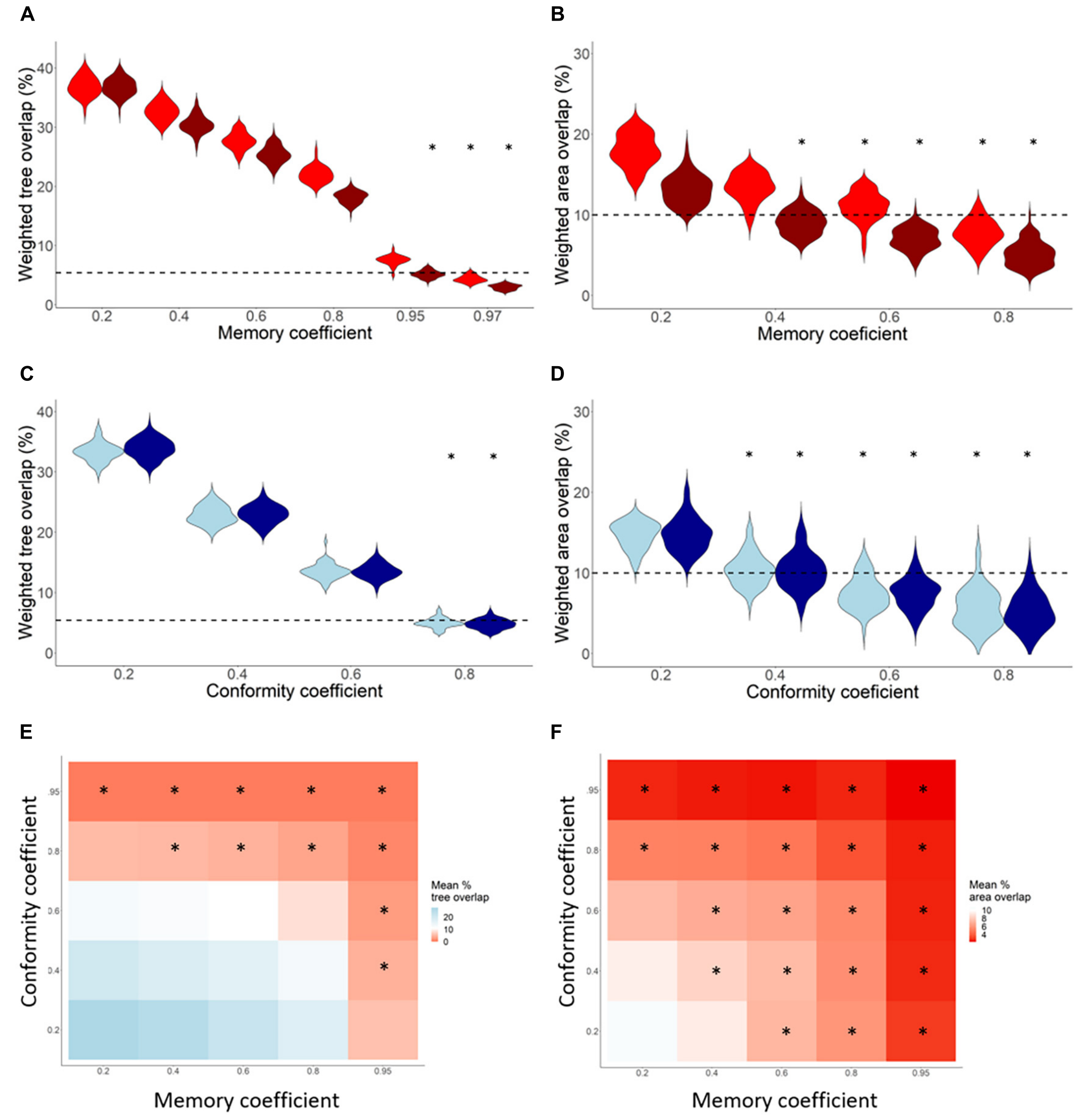

FIGURE 4 | Resource and spatial partitioning between two neighboring Egyptian fruit bat colonies. Each violin plot **(A–D)** represents the frequency distribution of the weighted tree overlap (WTO, **A,C**) and weighted area (75% KUDs) overlap (WAO, **B,D**) after 100 iterations of the agent-based models. **(A–B)** represent increasing values of theoretical memory coefficients on the x-axis in red (range 3–42% for WTO and 2–23% for WAO), and memory with competition in dark red (range 3–42% for WTO and 2–23% for WAO). **(C,D)** Represent increasing values of theoretical conformity coefficients on the x-axis in blue (range 3–39% for WTO and 0–19% for WAO), and conformity with competition in dark blue (range 3–40% for WTO and 0–23% for WAO). All dashed lines represent the observed WTO or WAO. Heatmaps **(E,F)** show the combined effect conformity and memory coefficients on the WTO **(E)** and WAO **(F)** indices, with darker red colors indicating smaller overlap. **p*-value ≥ 0.05 comparing simulated and observed.

These results suggest that if memory is the only mechanism and more than 97% of trees are repeatedly visited night after night, the observed resource partitioning is achieved. Similarly, the WTO is reached for conformity when 80% of the trees are shared among colony-members. Unlike partitioning of trees, the observed WAO was achieved at smaller coefficients (memory = 0.6, conformity = 0.4). Furthermore, the threshold values did not change meaningfully for both resource and area overlaps when each mechanism interacts with density-dependent competition. Surprisingly, the combined effect of conformity with memory at lower values (< 0.6 for WTO and < 0.4 for WAO) did not reach partitioning (heatmaps on **Figure 4**). A lack of interaction effects highlights that partitioning of both types is achieved by one of these mechanisms (at relatively high values), suggesting they act in a non-additive, independent manner.

DISCUSSION

Spatial partitioning between neighboring colonies is considered a widespread phenomenon in colonial species, especially marine birds (Bolton et al., 2019). Although several plausible mechanisms have been proposed to explain what drives wild populations to segregate, they have rarely been systematically examined using competing models. Comparisons based on real movement data collected under varying resource availabilities are even more scarce (but see Wakefield et al., 2013; Cecere et al., 2018; Ito et al., 2020). Here, we analyzed high-throughput movement tracks from two neighboring colonies of Egyptian fruit bats, tracked during different fruit seasons. We found that the partitioning of both resources and areas was high, with $< 11\%$ of fruit trees and area being shared between colonies (**Figures 3**, **4**). Importantly, these values could not have emerged if colonies' foraging ranges were limited strictly by food availability and travel distances, as represented in our null-model (**Figure 3**) and hypothesized by the Hinterland model (Cairns, 1989). As such, this forms the first account of strong within-species spatial partitioning in a terrestrial mammal. We also found that memory was the strongest and most significant driver of resource and spatial partitioning (**Figure 3**). The role of memory suggests that individually acquired information, with or without information-sharing and competition, most likely sustains segregation between the two neighboring EFB colonies. This result is consistent with the high memory probabilities observed in this study (**Table 1**) and with known tendencies of these bats revisiting and thus memorizing the state of particular trees (Tsoar et al., 2011; Toledo et al., 2020).

However, when replacing the observed memory and conformity coefficients with theoretical ones, both memory and conformity resulted in the observed partitioning in isolation, at relatively high values (**Figure 4**). It is thus evident that information sharing can also drive resource and spatial partitioning (as suggested by, e.g., Wakefield et al., 2013; Corman et al., 2016). But conformity was less important in our study system characterized by animals that are highly familiar with their home-range and use mostly spatially predictable food resources (Gager, 2019; Harten et al., 2020; Toledo et al., 2020). Although the mechanisms that we tested explain the observed partitioning of colony areas, the weighted overlap of trees was statistically smaller than the one that emerged from all the models (**Figures 3**, **4**). This may be due to tree characteristics, other than the fruiting season, which may have biased the bats' tree selection more than we considered, resulting in fewer trees revisited overall and less of them shared between colonies.

The Roles of Competition and Information in Shaping Partitioning

Competition

The most commonly proposed mechanism for explaining inter-colony spatial partitioning is density-dependent competition (Grémillet et al., 2004; Wakefield et al., 2013; Bolton et al., 2019). However, competition is typically inferred based solely on the indirect measure of a positive relationship between colony size and foraging distances (Ashmole, 1963; Corman et al., 2016; Lamb et al., 2017). Here, we measured competition directly by examining changes to bat behavior as the local density on a tree increases. Based on this analysis, we did not find evidence for density-dependent competition (**Supplementary Figures 2**, **3**) nor between-colony competition (**Supplementary Figures 4**, **5**). Congruently, competition had no apparent effect on partitioning (**Figure 4**).

However, we cannot fully dismiss density effects, given that the number of tracked bats might not represent the true bat densities. Importantly, we assume that the relationship between the number of tracked and true bat densities is the same for both colonies. To resolve the ambiguity about the role of competition in spatial and resource partitioning, we hypothesize that density dependence might have driven foraging site selection strongly, following the Density Dependent Hinterland model (see section "Introduction" and Wakefield et al., 2013), but only during the initial stages of the colonies' establishment. After the colonies formed, memory maintained partitioning by channeling individuals to use the same (non-overlapping) resources, and competition was reduced to act only as a "ceiling effect" by negatively influencing the experience of individuals that seldom invaded the neighboring colony's range. In addition to memory, information transfer between same-colony members reinforce partitioning further because newly detected resources are more likely to be discovered within the colonys' range, making exploration into the neighboring colonys' territory less profitable unless the colony reached its carrying capacity (Grémillet et al., 2004; Wakefield et al., 2013). Because our models did not simulate the long-term dynamics of colony establishment across generations, this hypothesis could not be tested. Future studies aiming to untangle the links between density-dependence and inter-group partitioning could benefit from incorporating data on *in situ* aggressive interactions, for instance, recording social calls to estimate the intensity of agonistic interactions at sites with different densities (Prat et al., 2016).

Memory

The tendency of individuals to repeatedly visit the same locations is typical in many species and was given many synonyms, e.g., foraging site fidelity, recursive movement, memory-based, and reinforcement-learning movements (Grémillet et al., 2004; Fagan et al., 2013; Merkle et al., 2014; Berger-Tal and Bar-David, 2015; Wakefield et al., 2015; Bracis et al., 2018; Riotte-Lambert and Matthiopoulos, 2019; Goldshtein et al., 2020). While environmental cues could potentially trigger these behaviors, two characteristics of EFB movement imply that their recurrent visits to trees are driven by individual memory, following Fagan et al. (2013)'s classification. First, EFBs revisit specific trees, not patches with multiple foraging options, which must be beyond the individual's perceptual range. Second, EFBs fly in very straight routes without using landmarks or beacons (Harten et al., 2020; Toledo et al., 2020), suggesting prior knowledge of their target location.

Several studies, mostly based on data-inspired simulations, point to the possibility that memory-based movement drives individual spatial and resource partitioning (Van Moorter et al., 2009; Merkle et al., 2014; Riotte-Lambert et al., 2015). For example, Goldshtein et al. (2020) tracked the movements of lactating females of the lesser long-nosed bat (*Leptonycteris yerbabuenae*), which travel immense distances to forage on isolated patches of flowering cacti each night. Once at the location, individuals partition into consistent foraging "cores," with little overlap between them. Based on competitive agent-based models, the authors found that the best explanation for this division into cores was reinforcement-learning, a similar algorithm to the one used in our memory model. Recently, Aarts et al. (2021) showed that similar memory-based rules that create partitioning between individuals also drive between-colony segregation of central-place foragers. In their simulations, inspired by tracked movements of harbor seals *(Phoca vitulina)*, they show that for species with spatial cognitive abilities and high levels of colony fidelity, memorizing a sub-set of available resources is sufficient to minimize overlap and conflict. Our results lend empirical support to these findings, showing that spatial partitioning in wild bats' is primarily maintained by high memory levels (**Figure 3** and **Table 1**).

Information Transfer

Whether, how, and where information is shared in congregating species is species-specific and a matter of continuous debate (Barta and Giraldeau, 2001; Danchin et al., 2004; Evans et al., 2016; Jones et al., 2017). However, it appears plausible that fruit bats, which roost and forage in groups, use social information, irrespective of whether it was gained inadvertently or intentionally. For example, controlled captive experiments on Peter's tent-making bats (*Uroderma bilobatum*) show that individuals prefer to interact with an unknown conspecific carrying a novel and palatable food item over an interaction with a familiar roost-mate carrying no food (Ramakers et al., 2016). Moreover, interactions were stronger if the odor originated from the information givers' mouth than if it was only present on the surface of its fur, suggesting that bats also evaluate the quality of social information (O'Mara et al., 2014). Specifically for EFBs, it has been shown that roost-mates form long-lasting bonds, fitting to the producer-scrounger game where a sub-set of individuals actively collect food while others scrounge for it from their mouths (Harten et al., 2018).

However, the specific way information on food resources is used remains unknown in this species. For example, EFBs were not observed foraging in pairs or groups (Harten et al., 2020; Toledo et al., 2020), rendering following behavior—a prerequisite for the information center hypothesis—highly unlikely (Barta and Giraldeau, 2001; Harel et al., 2017; Egert-Berg et al., 2018). Some bat species, mainly echolocating insectivores, gather local information by foraging in groups and eavesdropping on each other's feeding buzzes (Fenton, 2003). Yet this pathway of local enhancement is less likely for EFBs (and fruit bats in general) because they rarely use echolocation or are found foraging in groups, and other types of local enhancement were not yet verified (Prat et al., 2016; Gager, 2019). Given this level of inquiry, we did not attempt to model complex information pathways. Rather, we used the term "conformity" and assumed that if information about fruit trees is shared and used by colony members, it will result in individuals conforming to use similar trees. We found that the observed conformity level of this EFB population was low (**Table 1**). Yet, conformity could, on its own, reach the observed resource and area partitioning at high (theoretical) coefficient values (**Figure 4**). The discrepancy between observed and theoretical conformity values (**Figure 3** vs. **Figure 4**), as well as the independent effects of memory and conformity (**Figure 4**), point to a potential trade-off between the use of personal and social information, which is likely affected by the level of resource predictability, as elaborated in the next section.

The Effect of Resource Predictability and Resolution

The level of resource predictability in space and time determines whether individuals rely more on self-acquired (memory) or socially transferred information (Janmaat et al., 2016; Egert-Berg et al., 2018; Riotte-Lambert and Matthiopoulos, 2020). For example, when resources are spatially predictable, as are fruit trees, personal memory would be advantageous, as knowledge about the location of trees is not expected to vary. However, some introduced tree species, mainly of tropical origin, are temporally unpredictable in their fruiting phenology, producing abrupt and large fruit crops that are especially important in times of fruit scarcity (Galil et al., 1977; Marshall, 1983; Bleher et al., 2003; Fahr et al., 2015; Crestani et al., 2019). Accordingly, foragers highly familiar with their home range may adjust the frequency of using memory or information transfer based on the reliability of the information. At the group-level, one would expect an advantage of confining information transfer to the limits of a single colony. This is because separation into smaller units ensures naïve individuals are more rapidly exposed to the resources (e.g., in the roost). Moreover, density-dependent competition over the newly discovered resources is guaranteed to be limited to a single colony, at least until exploratory individuals of the other colony discover the same site.

While information affects movement decisions, individual space use patterns themselves alter resource predictability (Spiegel and Crofoot, 2016). For example, memory affects partitioning, which minimizes competition, reduces uncertainty about the accessibility to food resources, and feeds back to promote even higher reliance on memory (Lee et al., 2016; Riotte-Lambert and Matthiopoulos, 2020). More research is needed to understand how animals maneuver between using personal and social information under different predictability scenarios and how their behaviors affect the same considerations of conspecifics. Such endeavors might be achieved by field experiments that manipulate resource predictability, such as preventing access to highly used (memorized) resources or creating completely novel feeding opportunities in conjunction with long-term movement data.

Our simulations revealed differences in the level of partitioning depending on the resolution of the resources examined. Specifically, the simulations based on observed coefficients of memory and, to a lesser extent, conformity, were able to reconstruct the observed values for partitioning of areas (colony range) but not of the finer-grained level of trees (**Figure 3**). Technically, this discrepancy is unavoidable as multiple areas can be estimated between the same set of visited trees, similar to the "clique problem" for the distribution of suitable resources (Donovan et al., 2012). Thus, whereas estimating overlap among trees visited by members of each colony is straightforward and has a single solution, estimating area overlap requires subjective decisions on how to measure area coverage (e.g., choosing different kernel bandwidths or home range calculation methods) and has multiple solutions, implying a higher level of uncertainty. Furthermore, careful step-by-step observations of how tree and area overlap measures changed when simulated bats visited more trees revealed that the vast majority of newly visited trees were placed within the colony area at some relatively high number of steps. This finding implies that sufficiently long simulations lead to a higher level of tree overlap without increasing area overlap. Therefore, area and tree overlap estimates are likely to be under- and over-estimated, respectively, as reflected in our results.

Conceptually, this discrepancy raises the question of whether partitioning should be estimated at the finest grain of a single discrete resource, the larger grain of a resource patch, or perhaps the whole foraging range. In the case of EFBs, mounting evidence suggests high familiarity and fidelity to specific fruit trees (Tsoar et al., 2011; Harten et al., 2020; Toledo et al., 2020), indicating that a single tree is an appropriate resolution for this species. However, resources available to seabirds and probably many other animal species are unlikely to be fine-tuned to particular point locations. The relevant resolution is presumably at least as large as the typical size of a foraging patch (Vilk et al., 2021). Looking forward, the expansion of high-throughput tracking systems provide the means to examine further if, how, and why patterns of partitioning vary across spatial resolutions.

CONCLUSION

This study assessed the role of different mechanisms which underly resource and spatial portioning, one of the most fundamental processes enabling inter-colony coexistence. Methodologically, our study highlights the merits of high-throughput tracking systems like ATLAS that generate large high-resolution movement datasets. These datasets provide the means to reliably estimate the observed patterns and construct highly realistic models to unravel alternative underlying mechanisms, namely memory, information sharing, and competition, in free-ranging animals under various environmental conditions. Major questions for further research highlighted in this study are the lack of support for the role of the density-dependent competition in sustaining partitioning patterns continuously, the possibility for independent roles of personal memory or socially transferred information, and their potential association with variation in resource predictability.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Ethics Committee of the Hebrew University (permit NS-15-14-14660-2) and the Israeli Nature and Parks Authority (permit NS-2020/42577).

AUTHOR CONTRIBUTIONS

EL and RN conceived the study. RN conceived. ST developed the ATLAS system. EL carried out fieldwork and analyzed the data together with IS. EL and RN wrote the manuscript with input from all other co-authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.732514/full#supplementary-material

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Spatial Memory Drives Foraging Strategies of Wolves, but in Highly Individual Ways

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The ability of wild animals to navigate and survive in complex and dynamic environments depends on their ability to store relevant information and place it in a spatial context. Despite the centrality of spatial memory, and given our increasing ability to observe animal movements in the wild, it is perhaps surprising how difficult it is to demonstrate spatial memory empirically. We present a cognitive analysis of movements of several wolves (*Canis lupus*) in Finland during a summer period of intensive hunting and den-centered pup-rearing. We tracked several wolves in the field by visiting nearly all GPS locations outside the den, allowing us to identify the species, location and timing of nearly all prey killed. We then developed a model that assigns a spatially explicit value based on memory of predation success and territorial marking. The framework allows for estimation of multiple cognitive parameters, including temporal and spatial scales of memory. For most wolves, fitted memory-based models outperformed null models by 20 to 50% at predicting locations where wolves chose to forage. However, there was a high amount of individual variability among wolves in strength and even direction of responses to experiences. Some wolves tended to return to locations with recent predation success—following a strategy of foraging site fidelity—while others appeared to prefer a site switching strategy. These differences are possibly explained by variability in pack sizes, numbers of pups, and features of the territories. Our analysis points toward concrete strategies for incorporating spatial memory in the study of animal movements while providing nuanced insights into the behavioral strategies of individual predators.

Keywords: discrete choice modeling, wolf, movement, predation, boundary patrolling, central place foraging, foraging site fidelity, foraging site switching

1. INTRODUCTION

Spatial memory is fundamental to successful navigation of complex, dynamic environments (Fagan et al., 2013). Theoretical and simulation studies have shown that memory can be essential in structuring movements and space use (Mueller and Fagan, 2008; Barraquand et al., 2009; Van Moorter et al., 2009; Avgar et al., 2013; Watkins and Rose, 2013; Schlägel and Lewis, 2014; Bracis et al., 2015; Riotte-Lambert et al., 2017), and can help optimize resource acquisition in dynamic environments (Bracis et al., 2015, 2018). In parallel, movement data is rapidly accumulating. A central task of movement analysis is to infer behavioral mechanisms that underlie decision making processes (Nathan et al., 2008). Much effort has been devoted to inferring unobservable behavioral states from movement data (Morales et al., 2004; Forester et al., 2007; McClintock et al., 2012; Gurarie et al., 2016), while step and resource selection functions quantify animal movement responses to heterogeneous environments (Boyce and McDonald, 1999; Hebblewhite et al., 2005; Thurfjell et al., 2014). However, the underlying models almost always assume a straightforward, tactical response to immediate environmental cues, e.g., a fully informed preference for a particular habitat, or a probabilistic rule for switching behaviors under certain environmental conditions without accounting for memory driven responses. In fact, it has been demonstrated that *not* accounting for simple memory-based behavior can lead to misleading inferences in a step-selection framework (Van Moorter et al., 2013).

Despite the centrality of spatial memory and the abundance of movement data collected on animals in the wild, demonstrating that animals are using spatial memory is a surprisingly steep challenge. Many relevant studies have focused on terrestrial herbivores, which have the advantage of being relatively easy to study. Thus, bison (*Bison bison*) keep track of meadow patch locations and quality (Merkle et al., 2014, 2016), thereby constraining their space use in a way reminiscent of simulation-based predictions (Van Moorter et al., 2009). Migratory zebras (*Equus zebra*) demonstrate a memory-based anticipation of seasonal resource flushes (Bracis and Mueller, 2017), as do blue whales (*Balaenoptera musculus*) (Abrahms et al., 2019). Boreal woodland caribou (*Rangifer tarandus caribou*) movements can be modeled with respect to a stored estimates of forage quality and predation risk according to a nuanced cognitive model (Avgar et al., 2015). Recently used locations were among the most significant predictors of wild boar (*Sus scrofa*) movements and habitat use (Oliveira-Santos et al., 2016).

The herbivorous examples above feed primarily on stationary resources. In contrast, large carnivores feed on mobile and cryptic prey, which are themselves capable of spatial mapping and event-based memory when making movement decisions. This adds a non-trivial level of complexity to applying a foraging strategy. It is unclear, for example, whether predators should prefer or avoid locations where they were most recently successful. Re-use of those locations, referred to as "foraging site fidelity" is a suitable strategy if locations of recent success correlate with locations of future success. This hypothesis explains the large scale selection of foraging sites for several avian central-place predators (Davoren et al., 2003; Carroll et al., 2018). On the other hand, foraging site switching can occur if prey avoid an area where they have witnessed or are aware of the death of a conspecific. In this case, predators are best off changing the location where they predate, as had been demonstrated for lions (*Panthera leo*) in savannas (Valeix et al., 2011). Whether an immediate decision by a predator follows one strategy or another likely depends on the spatial scale of prey patches and foraging ranges, and on the temporal scale of prey patch persistence and depletion-recovery dynamics relative to the temporal scale of a predator foraging bout.

Wolves (*Canis lupus*) are highly adaptable, generalist, social predators of large prey. Their reproductive, hunting, territorial, seasonal, and dispersive behavior has been observed and described in great detail (Mech and Boitani, 2003), mainly in descriptive terms based on extensive field observations. Wolves are routinely described as having high cognitive abilities and complex information retention and communication skills. For example, Peters and Mech (1975) write that "*Wolves appear to have well-organized memories for routes, points, junctions, and their juxtaposition*," and propose that the spatial distribution of wolf markings were a physical manifestation of their "cognitive maps."

Despite this, compelling quantitative or model-based inference on the cognitive processes of wolf behavior in the wild has been elusive, in part because of the layered behavioral complexity of predator-prey interactions. In a recent study (Schlägel et al., 2017) winter wolf movements were modeled as a function of local prey density and boundary visitations, relating these to the time of return for each location as a indication of use of spatial memory. The results provide compelling evidence that wolves do track space and time. However, the modeling framework was constrained to a temporal scale fixed by the arbitrary sampling frequency of the GPS locations and a spatial scale of landscape rasterization fixed by computational limitations. The structure of the model thereby precluded an exploration of the temporal and spatial scales at which memory was operating.

Here, we develop, parameterize, fit, and explore a predictive, memory-driven model of spatial decision-making by wolves, focusing on the summer, den-centered, pup-rearing period. In this period, reproductive adult wolves must balance several important prerogatives: (1) they must hunt successfully, not just to feed themselves but to provide energetic surplus to pups, (2) they must regularly revisit the den to feed pups via regurgitation, and (3) they must periodically visit the edges of their territories to mark and patrol. The data we analyze were obtained from an intensive summer predation study contrasting established and dispersed packs of wolves in Finland, where wolves have reestablished themselves at relatively low densities via a process of natural dispersal from Russia (Kojola et al., 2006; Barry et al., 2020). During these predation studies, we obtained a detailed, behaviorally annotated time-series by visiting nearly all non-den GPS locations over a two-month period. Importantly, we identified carcasses, allowing us to infer the location, composition and timing of most kills (Gurarie et al., 2011), as well as boundary visits.

Our first goal was to demonstrate that wolves do use spatial memory by developing a cognitive model that outperforms a non-cognitive null model for predicting wolf foraging decisions. An important goal in developing the model was to have a heuristic that would allow us to estimate or approximate the temporal and spatial scales at which wolves weigh and act upon their recent predation success and boundary visitation. Once fitted, we anticipated that this model would provide insights into the fundamental decision-making strategies used by wolves to forage and maintain their territories.

Based on our knowledge of wolf behavior, we had several predictions: (1) that the valuing of predation might depend on the size of prey (e.g., an adult moose *Alces alces* being many magnitudes larger than a beaver *Castor castor*) and on the effort, in terms of time spent hunting, required to make a kill; and (2) that wolves would be inclined to return to territorial boundaries that had not been visited with some time lag to ensure they were marked, at a time lag approximately equal to the duration of a scent marking persistence. We also anticipated (3) that wolves would be more inclined to head toward (or value more highly) areas where they have had more recent predation success. We considered this more likely than site switching as the limited viewshed in forested environments may make it more difficult for prey to be aware of conspecific kills.

2. MATERIALS AND METHODS

2.1. Study Area

The study focused on eight summer-tracking studies of seven wolves in five unique territories in eastern Finland near the border with Russia (**Figure 1**). These territories are in the sparsely populated "core range" where wolves first recolonized Finland from Russia in the 1970's (Kojola et al., 2006), with primarily coniferous boreal forest dominated by Scotch pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula pendula* and *B. pubescens*). As a result of extensive logging, clear cuts and young successional mixed forests are common. The landscape is further dotted with lakes and peat bogs, about half of which have been drained. Moose (*Alces alces*) and reindeer (*Rangifer tarandus L.*) are the two resident ungulate species in the study area (Kojola et al., 2004). Reindeer include the wild forest subspecies (*R. t. fennicus*) and the free-ranging semi-domesticated reindeer (*R. t. tarandus*). The distribution of wild forest reindeer is limited to the north by the area of semi-domesticated reindeer management, separated physically by a fence extending across Finland at roughly 65° N. North of this border, wolves have no legal protection and are commonly killed by local hunters (Kojola et al., 2006).

2.2. Wolf Capture and Handling

Wolves were captured and collared in late winter or early spring (between February and April) (Kojola et al., 2006). Individuals were captured using snowmobiles when the snow was soft and at least 80 cm. Snowmobiles were driven alongside wolves, which were looped using a neck-hold noose attached to a pole. The wolves were placed in a wooden box that had been strengthened with a metal grating around the outside and had doors at both ends. Wolves were kept in the box for at least 30 min before being injected with a mixture of medetodimine and ketamine with a dose ratio of 1:20 (Jalanka and Roeken, 1990). The wolves were equipped with collars that contained global positioning system receivers (GPS Plus 2, Vectronic Aerospace GmbH, Berlin, Germany) and Very High Frequency (VHF) radio beacon transmitters (Televilt, Lindesberg, Sweden). The collars weighed approximately 760 g and had expanding, adjustable collars. Capture, handling, and anesthetizing of the wolves met the guidelines issued by the Animal Care and Use Committee at the University of Oulu and permits provided by the provincial government of Oulu (OLH-01951/Ym-23).

2.3. Field Tracking

We analyzed data from seven intensively field tracked wolves. Each wolf was followed intensively for 60 days from the beginning of June to the end of July for one summer each from 2006 to 2013, with the exception of one wolf (Hessu) that was followed for two summers (2011 and 2013). All of the collared wolves represented breeding individuals, and we did not have more than one wolf collared in any particular pack.

GPS locations were obtained for all the wolves at half hour intervals via the GSM (Global System for Mobile) network, which covered the entirety of all wolves' territories. In seven of the eight studies, every location was visited in the field after a minimum five day time lag, excluding locations near or around the den. The lag was maintained to minimize disturbance, and the locations visited on a given day were as far as possible from the location of the focal wolf on that day. The overall median lag was 8 days (inter-quartile range 5 to 11 days). A minimum radius of 25 m around each location was surveyed with the help of trained tracking dogs, who were able to efficiently identify signs of wolf presence, such as carcasses, caches, bedding sites, and scats. For the remaining study, only those locations that were clustered, corresponding to likely kill, bedding and cache sites, were visited. Cervid prey carcasses and age status (adult or calf) were identified by the bones and antlers. Several were not identifiable in the field, and were recorded as "unknown ungulate." Other prey items, including hare (*Lepus europaeus*), beaver (*Castor castor*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and one each of raccoon dog (*Nyctereutes procyonoides*), and Northern goshawk (*Accipiter gentilis*) were identified by pelage and plumage and classified as "minor" prey, with no further subdivision into age categories. For additional details on the field methodology, see (Gurarie et al., 2011), which provides a close analysis of the summer habitat preferences of two of the wolves. The simplified outcome of the intensive field tracking was a movement track annotated with behaviors, and location and identity of most prey consumed over the period of the studies. Separately, howling surveys (Fuller and Sampson, 1988) and winter tracking after each of the summer periods were used to estimate the number of adults, juveniles, and pups in each pack.

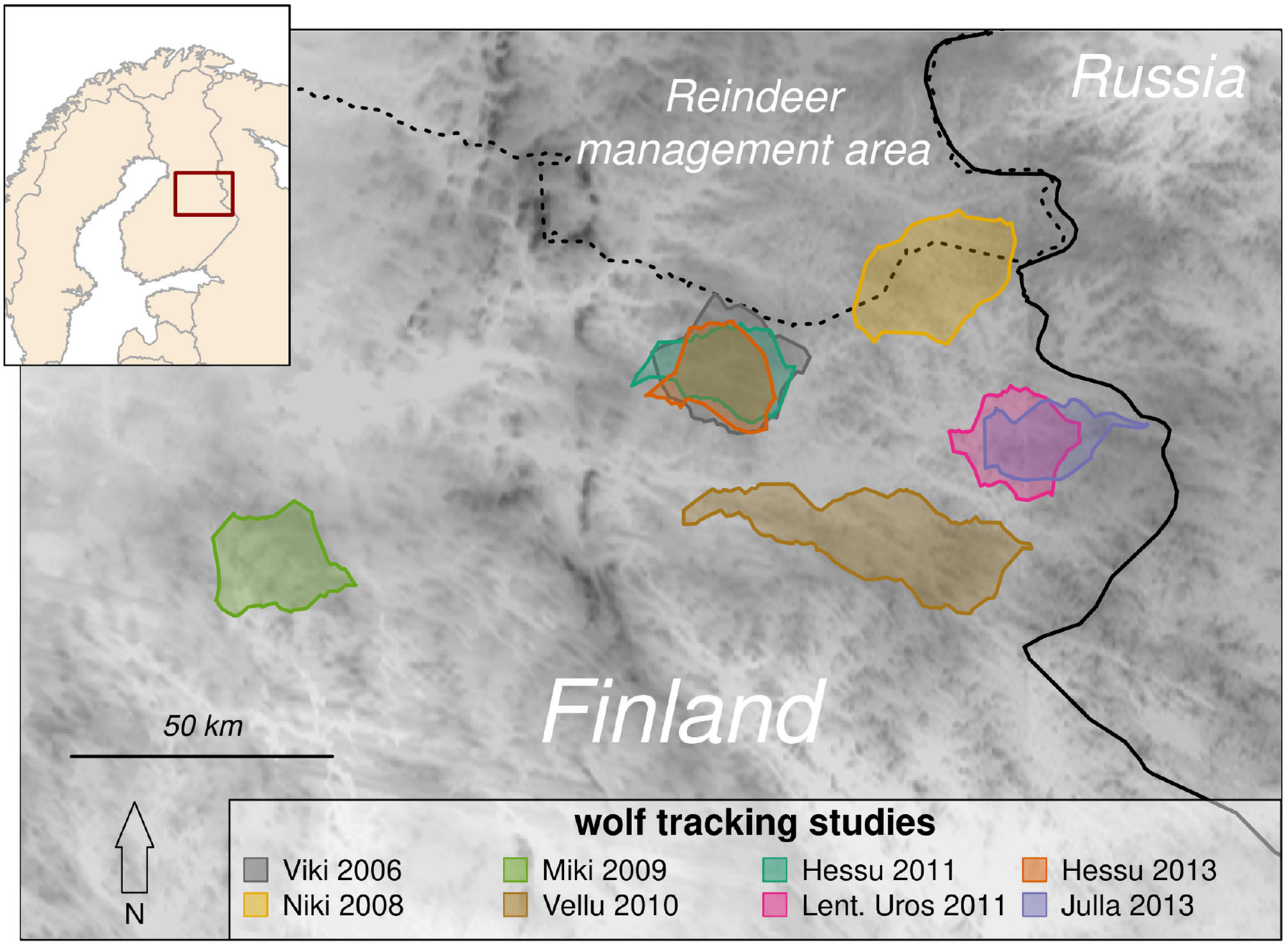

FIGURE 1 | Map indicating the boundary polygons of eight wolf tracking studies in Finland (inset map). Several of the studies occurred in overlapping territories: Lentuan Uros's (magenta) territory in 2011 was inherited by Julla in 2013 (blue), and Viki's territory in 2006 was inherited by Hessu, who was tracked in 2011 and 2013 (gray, green, and orange). Darker colors on the map reflect higher elevations (maximum 340 m). These territories are in the core of the Finnish wolf range, near the border with Russia, whence the population naturally dispersed, but south of the reindeer management area (dashed line) which is separated from southern Finland by a fence north of which wolves are unprotected.

2.4. Cognitive Model

Our overarching goal was to specify and estimate a model that predicts the movement behavior of a wolf during the summer den-centered pup-rearing period. In summer, wolves expend considerable effort and energy on obtaining enough nutrition to feed and rear pups, leaving and returning to the den on a near daily basis (Jędrzejewski et al., 2001; Alfredéen, 2006; Gurarie et al., 2011). A secondary important goal of wolf movements is to patrol the territorial boundary, a task that is particularly important when other wolves inhabit adjacent territories (Peters and Mech, 1975).

In order to demonstrate the utility of memory, we needed to isolate a behavioral variable that could be explained by the prior experience of the wolves. Wolves are highly mobile and free to hunt and visit any location in their territories. In Finland, there are few topographical constraints to available habitat, only larger water bodies are truly inaccessible in the summer. However, the movements of wolves in summer are den-centered, allowing us to specify and enumerate *trips*, defined as the set of GPS locations framed on either end by departure from and return to the known den site. One dependent variable which reflects an apparently free (i.e., unconstrained and uncoerced) choice is the *direction* chosen by the wolf, i.e., the portion of the territory toward which the wolf headed when leaving the den to initiate a trip.

In order to enumerate or quantify this choice, we discretized the entire territory into some number of *zones* ranging between 3 and 8 (see example in upper panels of **Figure 4**). We used a range of zone numbers as we have no idea how the wolf organizes its mental map of the territory, but the range of zones allowed us to roughly explore the spatial scale at which the wolves' decision making process might occur. In order to make the spatial classification unsupervised and algorithmic, we used a nearest neighbor clustering on the location data sets, with the slight modification that the square root was taken of the distance of each location to the den (i.e., $||\mathbf{x}_i^T|| = \sqrt{||\mathbf{x}_i - \mathbf{x}_{den}||}$, where x^T refers to the transformed location). This transformation had

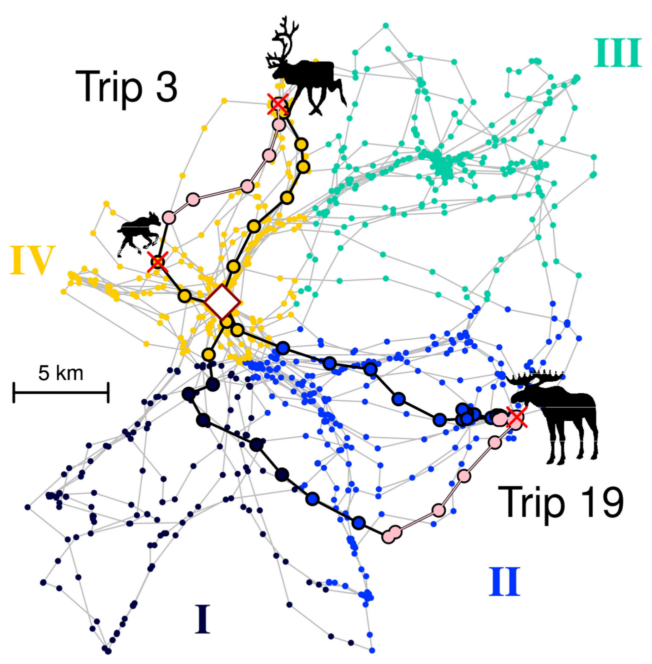

FIGURE 2 | Illustration of two trips (#3 and #19) for wolf Niki superimposed on a four zone classification. Colored dots represent all locations collected for Niki over the two month period of the study. The four colors represent Zones I to IV as labeled along the exterior. In Trip 3, the wolf departed within Zone IV, killed a reindeer calf, moved along its boundary (pink colors), killed an adult reindeer, and returned to the den, entirely within Zone IV. In Trip 19, the wolf departed within Zone II, killed an adult moose at the boundary, moved along the boundary and returned *via* Zone I. Regardless of the return Zone, this trip is classified as a Zone II trip, since that is the direction chosen by the wolf at departure. The rhombus in the middle indicates the den site.

the effect of generating zones that were more likely to be radially arranged around the hub of the den site. After performing the clustering on the transformed locations, a polygon was drawn around a Dirichlet tessellation of each set of original points, thereby breaking the entire set of original locations into the specified number of zones. The tesselation was performed using the `dirichlet` function in the `spatstat` R package (Baddeley et al., 2015). Each trip was classified as heading out into a particular zone by taking the set of points from the beginning of the trip to that trip's furthest location from the den or first kill—whichever came first—and finding the mode of the visited zones (e.g., if the set of zones were 3,3,2,3,3, the *selected zone* would be 3) (see **Figure 2** for an illustration of the zone classification process).

Whatever the eventual outcome of the trip (i.e., which zones the wolf visited, whether, where and how many prey are killed, etc.) the selected zone is a free and unconstrained choice that the wolf makes when it departs. The central assumption of our memory-based model is that choice of zone is driven, in part, by prior experiences—specifically, predation success and boundary visits—that are specific to each zone.

2.4.1. Discrete Choice Model

We model the selected zone for each trip (denoted Z_t where $t \in 1, 2, ...n_t$) using a discrete choice modeling framework fitted with multinomial conditional logistic regression (Chapman and Staelin, 1982; Croissant, 2013). Discrete choice models are behavioral models designed to forecast the behavior of individuals facing a choice with unknown or unobservable estimates of utility of respective choices. They have been widely applied mainly to model human behavior, e.g., in behavioral economics (Louviere et al., 2000; McFadden, 2001; Dubé et al., 2002), including modeling transportation (Antonini et al., 2006) and food (Gracia and de Magistris, 2008; Czine et al., 2020) choices. In wildlife ecology, discrete choice models have been applied in the context of habitat selection, including in hierarchical frameworks across multiple individuals (Cooper and Millspaugh, 1999; McDonald et al., 2006; Thomas et al., 2006).

Discrete choice modeling allows for the statistical estimation of a ranking of choices where each choice can have a dynamic set of covariates. The model assumes that the wolf maintains a preference (or "desirability" or "priority") score (U_{it}) for the ith zone at the time of trip t, and always chooses to head in the direction with the highest score. The preference score is separated into a systematic component (V_{it}) and unobserved component (ϵ_{it}):

$$U_{it} = V_{it} + \epsilon_{it} \tag{1}$$

It is important to note that the actual choice U_{it} may in fact be deterministic from the wolf's perspective, and neither the systematic nor the random component can be directly observed, as they represent the decision making process. But the partitioning allows us to analyze the process statistically. The deterministic portion is further decomposed into trip-specific and zone-specific component:

$$V_{it} = \beta_i + \sum_v \gamma_v X_{itv} \tag{2}$$

The coefficients β_i are the zone-specific intercepts, reflecting the time-independent quality or preference of the particular zone. The trip-dependent set of variables X_{it} captures the dynamic scoring of the zones and the set of coefficients γ_v reflects the overall intrinsic response to each of the variables (indexed by v).

In our most complex model, we include three variables in X_{it}: a predation quality score ($X_{it1} = P_{it}$), which tracks the zone-specific hunting success based on the wolf's experience, a boundary coverage score ($X_{it2} = B_{it}$), which tracks whether a zone's boundary has been visited and, presumably, marked, and a repetition score ($X_{it3} = R_{it}$) which tracks simply whether an animal went to a particular zone on the previous trip. The impact of these variables are driven by the wolf's memory and depend on several parameters as explained in detail below. The coefficients β and γ capture the relative contribution of each of environmental and experiential (cognitive) covariates. In total there are $k + 2$ parameters in the most complex fitted model, one each for predation memory, boundary memory and repetition, and $k - 1$ intercept parameters for each zone, minus one degree of freedom as the sum of the probabilities is always fixed to 1.

2.4.2. Scoring Zones

We assume the wolf tracks a zone-specific *predation score*, which is higher in areas with greater and more recent predation success, and a *boundary score*, which is higher in zones with more recent boundary visits. It is important to note that these scores (which are all positive) only quantify predation success and boundary visits, without making any claims as to whether higher values make directed departures more or less likely. Whether higher or lower scored areas are preferred is indicated by the strength and sign of the coefficient estimates of discrete choice model detailed in the next section. In fact, given the complexity of wolf and prey behavior, it is difficult to know *a priori* whether areas with a higher or lower number of kills would be preferred or avoided. Large prey items (e.g., adult moose or reindeer) are often cached, i.e., unconsumed portions are buried in the ground and returned to later (Peterson and Ciucci, 2003), which can make a recent kill site attractive. Similarly, the general suitability of a particular area for certain prey species can make areas of high predation success sequentially attractive. Prey behavior can further complicate these responses, as prey may also avoid areas with recent kills generating a "landscape of fear" (Laundré et al., 2010), and it may be more strategic to temporarily avoid a recently successful site.

Each kill contributes individually to the predation score corresponding to the zone of the kill. We assume that the score is higher the greater the mass of the kill, the shorter the time to the kill (i.e., the less the effort), and the more recent the kill. An expression that combines all of these assumptions is:

$$P_{it} = \sum_{j=prey_{i,t}} \left(\frac{M_j^{\alpha}}{E_j} \right) \exp\left(- \left(\frac{\Delta p_j}{\tau_p} \right)^{\kappa} \right) \tag{3}$$

where the sum is performed over all of the prey items captured in zone i up to trip t ($prey_{i,t}$); M is the approximate mass of the prey item; $\alpha \in [0, 1]$ is a mass-scaling parameter (details below); the effort E_j is the time spent moving before each kill either after leaving the den, or events that "pause" the hunting behavior, including cache revisits, or bedding; Δp_j is the time since the predation event; τ_p is a memory time scale which captures how long the wolf considers previous successes valid or actionable; and κ is a memory discounting coefficient. Estimates for adult mass and estimated linear growth rates for the calves of the main ungulate prey (moose, forest, and semi-domesticated reindeer) were obtained from the literature as well as approximate mass of smaller mammals and birds (**Table 1**). Growth rates were, in particular, important to capture the growth of reindeer and moose calves, which are many times larger in late July than in the beginning of June.

The form of this predation score reflects several strong structural assumptions, which we tested to a limited extent. For example, we set κ to be either 1 for exponential memory decay, or 2 for Gaussian decay. We also fitted models where the predation score did not include the discounting for effort, i.e., where E_j was always set equal to 1. This allowed us to test, in a narrow way, whether effort was also tracked. In both cases, fitted discrete choice models with the two different values of κ and with and without the effort term were compared using likelihood ratios.

TABLE 1 | Prey species, numbers killed, and growth models or estimated used to approximate mass obtained from each prey item in the predation module of the cognition model.

Species	n. killed			Mass and growth				Source
ungulates	*adult*	*calf*	*unk.*	*b. date*	*b. mass*	*growth*	*max. kg*	
moose	37	81	3	01-Jun	13	1.123	200	S
semi-domesticated reindeer	2	12		26-May	10	0.75	100	F&P
wild forest reindeer	9	34		26-May	10	0.75	100	F&P
small mammals	*total*			*estimated mass*				
hare	13			4				S,M
beaver	2			18				S
racoon dog	1			6				
birds								
capercaillie	2			3				
black grouse	2			1				
goshawk	1			2				

The growth rate is in kg/day; for animals killed before the mean birth date, the birth weight was used. The cited sources are: S—(Sand et al., 2008); M—(Markgren, 1969), F&P—(Finstad and Prichard, 2000).

The two free parameters for the predation memory module are the prey mass parameter α and the predation memory time scale τ_p. If $\alpha = 0$, any prey item (whether a hare or an adult moose) contributes equally to the score. If $\alpha = 1$, the contribution is proportional to mass. The memory coefficient τ_p captures the time scale at which memory is retained: if $\tau_p = \infty$, all predation experience accumulates with no discounting for time.

The *boundary memory* attempts to track whether the wolf has patrolled and marked its boundary, an important behavioral goal. To algorithmically classify locations as boundary locations, we developed a concave hull algorithm that works as follows: (1) select the convex hull (i.e., vertices of the minimum convex polygon) Z_{mcp}, (2) compute the angle θ_{inner} between all of the inner points Z_{inner} and the respective pair of closest convex hull points, (3) retain the subset Z^*_{inner} where $\theta_{inner} < \theta^*$, where θ^* is a threshold of concavity, (4) repeat these steps using the combined set of Z_{mcp} and Z^*_{inner} as an input, (5) stop the iteration when the new set is identical to the input set. We used a threshold angle of $\theta^* = \pi/2$ (90°). This algorithm generated territorial boundary sets that were consistent with field determined boundary locations (see Figure A.1 for an example of the algorithm and Figure A.2 for all boundaries in **Appendix A**).

The boundary memory, denoted $B_{i,t}$ is a binary (0, 1) variable that tracks whether the wolf has visited at least two locations on the boundary of zone i in a fixed time period λ preceding each trip. The λ parameter captures the interval of time that the wolf feels it is necessary to re-mark the territory and, therefore, related to the time a scent-marking fades. We anticipated that the choice regression coefficient for the boundary would be negative, indicating that a zone with a recently visited boundary will be scored lower.

Finally, we added a *repetition* variable $R_{i,t}$, which is simply 1 if the selected zone at trip $t - 1$ was also i and 0 otherwise. This variable is included in the model to account for any serial auto-correlation (or anti-correlation) in the wolf's zone choice, which could be confounded with either of the predation or boundary variables.

2.4.3. Model Fitting and Selection

Under the generic assumptions of independent and identical Gumbel distributions for the unobserved terms ε_{it} in Equation (1), the probabilities $\Pr_{it} = \Pr[U_{it} = \max(U_t)]$ can be written in terms of the logit probability function:

$$\Pr_{it} = \frac{\exp(V_{it})}{\sum_{j=1}^{k} \exp(V_{jt})}, \qquad (4)$$

and the coefficients can be estimated by full-information maximum likelihood estimation, as implemented in the `mlogit` package in R (Croissant, 2013).

The likelihood procedure provides estimates of the regression-like choice coefficients β (zone-specific estimates) and γ (contribution of predation, boundary memory, and repetition). However, the memory parameters (τ_p, λ, memory type κ) and the structural parameters (number of zones k) have to be assessed separately. Likelihood based criteria are useful for comparing models with different values of the memory coefficients; however, because the number of zones fundamentally alters the underlying data, likelihoods cannot be used to compare different fitted models across different numbers of zones. We, therefore, introduce an intuitive measure of predictive power of the models to use a basis of comparisons: the *relative predictive improvement* index (RPI) defined as the ratio of the mean of the predicted probabilities over the mean of the null probabilities, i.e.:

$$RPI = \sum_{t=1}^{n_t} \widetilde{\Pr(z_t)} / \sum_{i=1}^{n_t} \Pr_0(z_t)$$

where the sums are across all trips $t \in 1, 2, ..., n_t$, and the null probabilities are the proportion of trips for each zone (note, since both sums are over the same number of trips, the ratio of the sums is equal to the ratio of the respective means). As an example, if an entire dataset consisted of one visit to each of 4 zones: $\mathbf{z} = (1, 2, 3, 4)$, and the model predictions for choosing each of those trips were $\mathbf{Pr}_t = (0.75, 0.5, 0.25, 0.5)$, then $\widetilde{\overline{Pr(z_t)}} = 0.5$. The mean of the null probabilities is $\overline{P_0(z_t)} = 0.25$ and the ratio of the two is RPI = 2, which can be interpreted as a doubling of the predictive power of the model. Note that model log-likelihoods and RPI are monotonically related: the former is the sum of the log of probabilities, while the latter is proportional to the sum of the probabilities. Thus a "maximum RPI" point estimate is equivalent to a maximum likelihood point estimate, though without the convenience of asymptotic theory for estimating confidence intervals on coefficients. However, a randomization test of the null hypothesis (that the model provides no improvement, i.e., RPI = 1) can be conducted by resampling the order of the trips some large number of times from the null set of probabilities, recalculating the RPI, and comparing the observed RPI to the resulting null distribution. Similarly, a resampling confidence interval can be obtained by sampling sequences of trip zones from the predicted probabilities of the model, and comparing to a sampling of zone sequences from the null model. By computing the RPI of these resamplings and repeating the process some large number of times (e.g., 1,000), a confidence interval can be obtained around the RPI. The RPI thus provides an intuitive, interpretable tool for assessing discrete choice models where the number of choices itself is variable, as well as a statistical mechanism for hypothesis testing and inference.

We fitted the discretized trip-choice data across a range of 3 to 8 zones, with predation time scales τ_p ranging from 0.5 to 4 (interval 0.25), boundary marking lags λ from 0.5 to 12 days (interval 0.5), for each of $\kappa = 1$ (exponential memory) and $\kappa = 2$ (Gaussian memory), for each of 8 summer movement data sets. We computed the RPI, and selected the combination of these parameters for which the RPI was maximized. The theoretical total number of fitted models was 45,360, but in many cases—usually those with a high number of zones of which some are never selected—the fits did not converge. In other cases, there are no evident maxima in the RPI. Nonetheless, from this set of models, we can pick out the best combination of selected parameters (k, τ_p and λ) for each wolf. Once those were determined, we compared eight models with every combination of explanatory variables (predation memory P, boundary memory B, or repetition R; i.e., P+B+R, P+B, P+R, B+R, P, B, R, Null) using AIC as a model selection criterion. From the final selected model, we report the estimates, confidence intervals and p-values of the retained coefficients.

As an added analysis, we compared estimates of the boundary and predation coefficients across respective memory time-scales to see if a particular response shifted across scales. A transition from, e.g., a positive to a negative response across time-scales would indirectly suggests that the memory driven response to a particular zone operates in different ways at different time-scales. In performing this analysis, we selected the best model and combination of structural parameters, i.e., number of zones and combination of covariates.

All symbols and definitions for the modeling, data preparation, and model assessment are presented in **Table 2**.

3. RESULTS

Pack size varied considerably, which in turn meant the number and composition of prey killed varied by pack (**Figure 3**). The overwhelming majority of prey consumed was cervids (176 of 206 identified carcasses: 85%): 80 (39%) moose calves and 46 (22%) were reindeer calves, another 36 (17%) were adult moose and 11 (5%) were adult reindeer. The remaining prey items were all minor, mainly hare. The two largest, most

TABLE 2 | Definitions and symbols for modeling, data preparation and model assessment.

Cognitive wolf foraging model		
	Z_t	Selected zone for each trip *t*
	U_{it}	Preference score for *i*th zone for trip *t*
	V_{it}	Systematic component of preference score
	ϵ_{it}	Unobserved component of preference score
	P_{it}	Predation quality score
	B_{it}	Boundary coverage score
	R_{it}	Repetition score
	X_{it}	Vector of covariate values: $\{P_{it}, B_{it}, R_{it}\}$
Predation scoring		
	M	Approximate mass of prey item
	E_j	Effort preceding kill (hours)
	Δp_j	Time since predation event
Boundary identification		
	Z_{mcp}	Minimum convex polygon (convex hull) of all locations
	θ^*	Threshold of concavity
	Z^*_{inner}	Subset of points in convex hill where $\theta_{inner} < \theta^*$
	θ_{inner}	Angle between inner points Z_{inner} and respective pair of closest convex hull points
Estimated parameters		
	β_i	Zone specific intercept of preference for *i*th zone
	γ	Coefficients on covariates
	τ_p	Time scale of predation memory
	α	Mass-scaling coefficient (set to 0.5)
	λ	Time scale of boundary memory
Metrics		
	AIC	Akaike Information Criterion
	RPI	Relative predictive improvement

established packs, on which we reported on in previous work (Gurarie et al., 2011), consumed by far the most prey (over 45 items each, compared to 22 for the next highest, **Figure 3**), which can partially be explained by their consumption of larger prey which was easier to locate in the field. Over the respective 60 day periods of field tracking, the number of trips greater than 2 h varied between 34 and 67 (mean 53, s.d. 12).

3.1. Parameters of Non-focal Interest

While there are many structural parameters in the full cognitive model, the main ones of interest were those related to time scales of memory for predation and boundary visits, and spatial scales as reflected in the number of zones. We did, however, have to make decisions regarding several other parameters.

Thus, we initially explored two values of the memory decay shape parameter [κ in Equation (3)]: $\kappa = 1$ corresponding to an exponential memory decay, and $\kappa = 2$ corresponding to a Gaussian memory decay. We also explored two values of the mass scaling parameter α: $\alpha = 0.5$—i.e., a square root scaling, and $\alpha = 1$, a linear scaling. We fitted the complete (predation + boundary visit + repetition) discrete choice model over a range of scaling parameter values and each of the four combinations of α and κ and compared the likelihoods of fitted models. Results are summarized and presented in **Appendix B**.

There was high variability among individual animals when these models were fitted (see results in **Appendix B**). Some (e.g., Viki 2006) had a much higher likelihood with Gaussian decay and square root scaling, while for others (e.g., Niki 2008), the exact inverse was the case. The absolute differences in the log-likelihoods were not—typically—much larger than one, suggesting that the process was not sensitive to either of these parameters. We, therefore, chose to fix the "Viki" pattern (Gaussian decay and square root scaling) for all subsequent results, noting that those discrepancies may be worth further investigation. Subsequent analyses focused on the time scales of predation and boundary memory, and the spatial scales as defined by number of zones.

Similarly, we assessed the structural assumption that the effort component [E_j in Equation (3)] contributed significantly to the predation score as a predictor by comparing likelihoods of fits with and without the effort component across a range of parameter values. Again, there was considerable variability among individuals (see **Appendix C**), but for those four studies for which the effort model was a better model (Viki 2006, Niki 2008, Lentuan Uros 2011 and Julla 2013), the difference was rather large (most ΔAIC values < -2). These four wolves are also the four wolves for which predation was retained in the final discrete choice model (see below and **Table 4**). A broad preliminary conclusion is that hunting effort is indeed tracked by the wolf, and the "predation score" is tempered by longer effort times. We retained the effort term for all subsequent analyses.

3.2. Cognitive Model: Example Analysis

We illustrate fits of the complete (P+B+R) cognitive model for one wolf, Lentuan Uros (LU 2011), across a range of zone breakdowns (**Figure 4**, upper panels) and values of boundary time lag λ and predation memory time scale τ_p (**Figure 4**, lower panels). We obtained over a 50% improvement on null predictions for this wolf (the highest of any of the other wolves), with RPI maxima ranging between 1.51 and 1.54 for spatial break-up into 5 to 8 zones. The RPI profile across boundary time scales is fairly consistent across number of zones, around 4.5 days, with the most prominent peak at 5 and 6 zones. The RPI profile against predation memory time scale peaks consistently between 1.25–1.75 days, though differences across time scales were less dramatic. Interestingly—the RPI-predation profile was sharper at the higher breakdown of zones (7 and 8) where the profile for boundary memory was flatter.

At the highest RPI set of parameters (5 zones, $\tau_p = 1.75$, $\lambda = 4.0$), a model comparison against all linear combinations of P, B, and R models show that there is essentially no difference between the P+B+R and B+R model, but that both of these are much better than any of the other models (ΔAIC > 4), and the null model performs much worse than any of the others (**Table 3**). The coefficients for boundary and repetition were both highly significant and positive, suggesting that the wolf tended to repeat its previous behavior, and, unexpectedly, that visits to boundary locations were further reinforced by recent

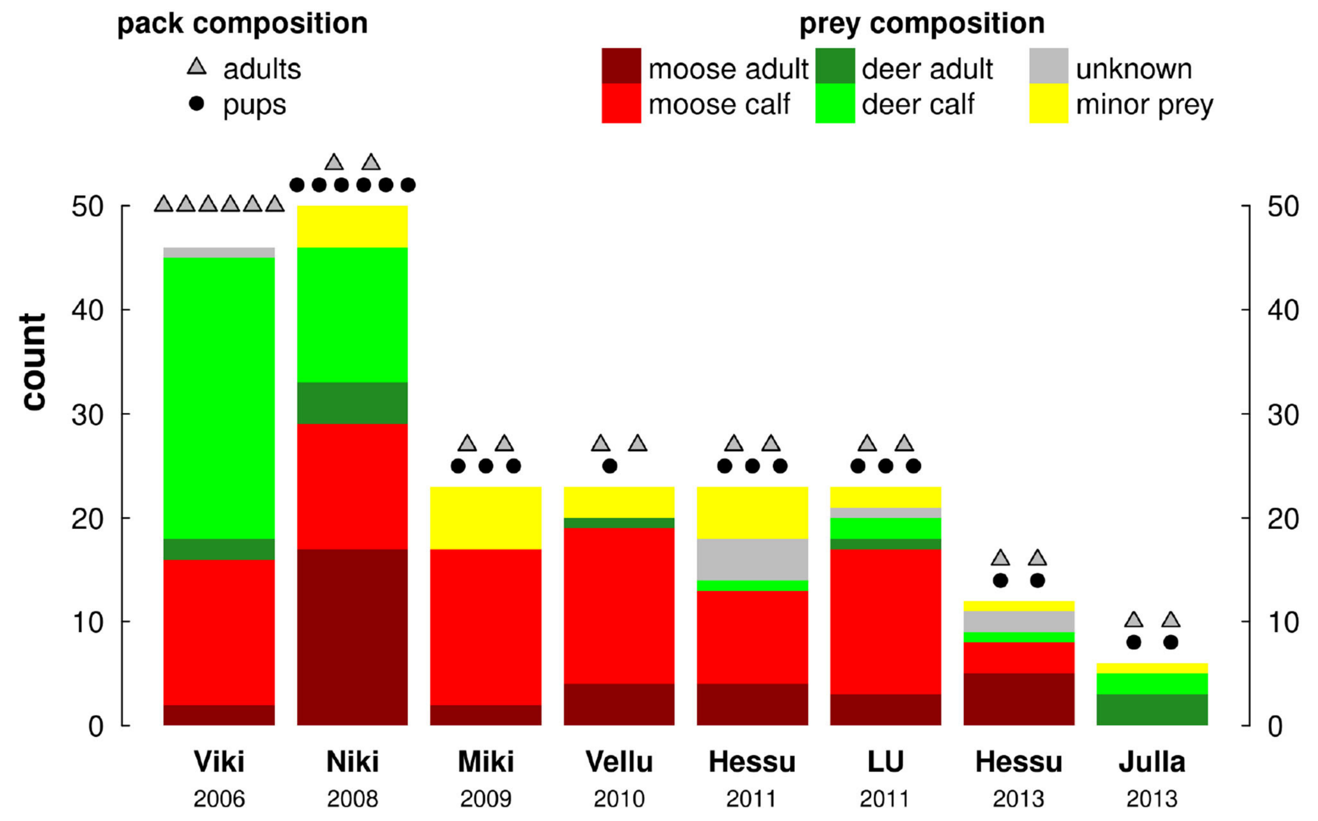

FIGURE 3 | Pack and prey composition of all 8 pack-year studies, arranged chronologically by year. Colors indicate prey composition as per the legend, dots and triangles above the bars indicate the number of adults and pups in each pack, respectively.

TABLE 3 | ΔAIC table for comparison of fitted cognitive choice models for wolf LU 2011 with 5 zones, $\tau_p = 1.75$, $\lambda = 4.0$, sorted by decreasing AIC, with d.f. representing the degrees of freedom (number of parameters).

Main effects				**Estimated coefficients**			
Models	**d.f**	**AIC**	**ΔAIC**	**RPI (95% C.I.)**	***P***	**B**	**R**
B + R	6	120.38	0	1.51 (1.34-1.68)		**1.483**	**0.85**
P + B + R	7	120.79	0.41	1.54 (1.41-1.68)	*0.22*	**1.372**	**0.784**
P + B	6	125.05	4.68	1.38 (1.21-1.54)	*0.29*	**1.579**	
B	5	126.21	5.83	1.31 (1.14-1.47)		**1.76**	
P + R	6	128.51	8.13	1.40 (1.27-1.54)	*0.34*		**1.03**
R	5	130.24	9.86	1.34 (1.21-1.47)			**1.152**
P	5	138.02	17.64	1.17 (1.07-1.34)	**0.456**		
null	4	144.07	23.69	1.00 (0.87-1.14)			

Bold faced coefficient values are significant at the $\alpha = 0.01$ level; italicized coefficients are significant at $\alpha = 0.1$. The top two models have almost identical AIC values. P, B, and R refer to predation score, boundary score, and repetition predictors, respectively. Note that the "null" model here is an intercept-only model, in which each zone has a constant preference unaffected by the covariates.

visits, rather than recent visits obviating the need to return to a boundary.

3.3. Cognitive Model: All Wolves

A cognitive model improved significantly on the null RPI for six of the eight wolf studies at the best (or near best) combination of parameters (**Table 4**). We refer to these six studies as "cognitive wolves." There was, however, considerable variability in the values of the RPI-maximizing parameters and in the signs of the fitted coefficients.

The repetition effect was positive and significant in all but one of the cognitive wolves, suggesting that wolves have some straightforward auto-correlation in their choice of departure direction. For three of the four cognitive wolves for whom the

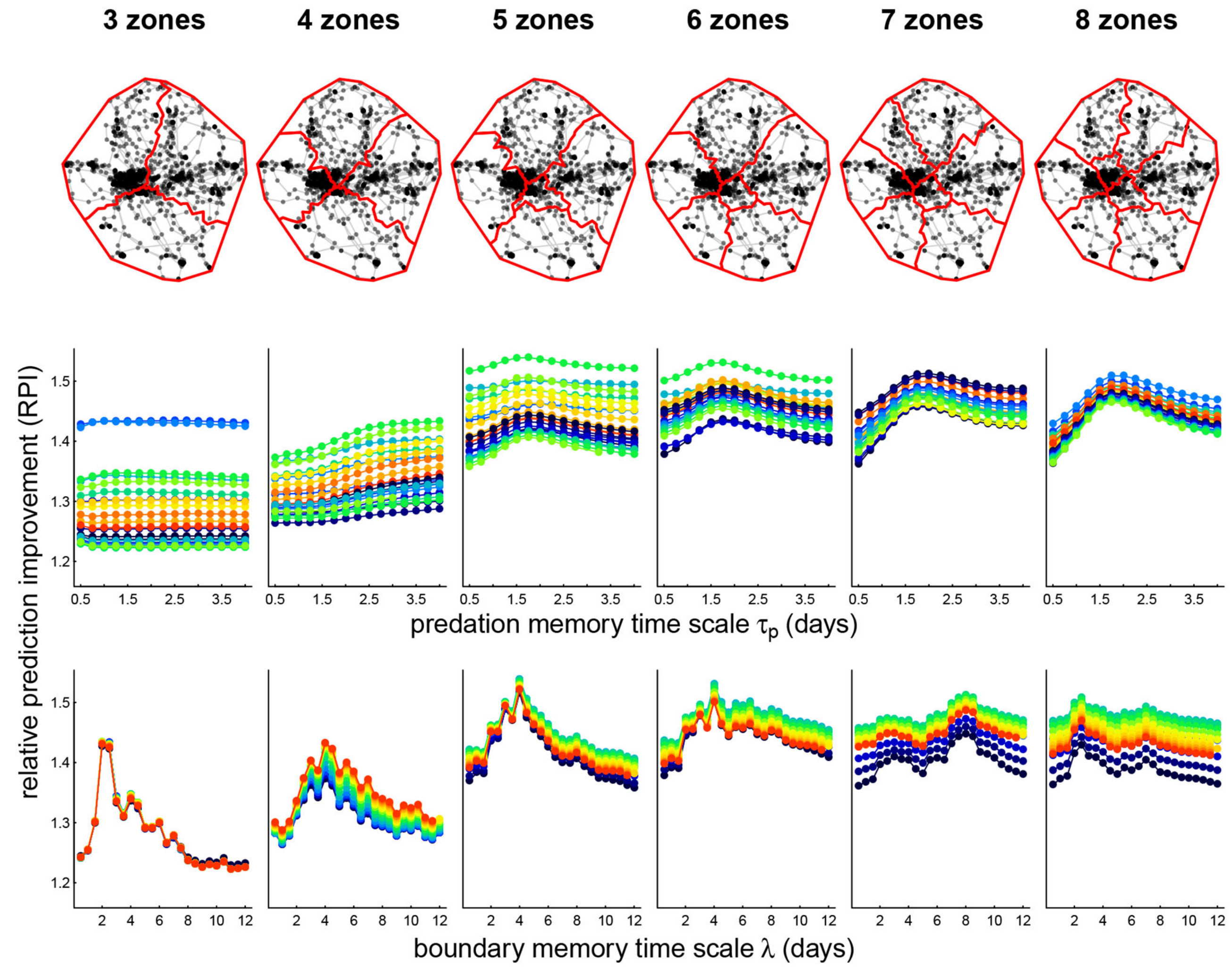

FIGURE 4 | Zone breakdown (upper panels) and parameter sweep of memory models (lower panels) for wolf Lentuan Uros (LU). Upper panels illustrate the roughly axial separation that the zone clustering algorithm generated. Lower panels illustrate the computed prediction improvement (RPI) for predation and boundary fitted models across various values of predation memory time scale τ_p (middle panels) and boundary visit lags λ (lower panels). The color spectra correspond to the other time scale in each plot. Thus, for example, the maximum RPI (1.54) is attained at 5 zones, τ_p = 1.75 days and λ = 4 days.

predation coefficient was retained, the effect was significant and positive—consistent with our *a priori* hypothesis that there would be a preference for zones with higher predation scores, consistent with the foraging site fidelity hypothesis. The exception was Viki 2006, who showed a negative response to predation at a memory time scale of 0.75 days. Similarly, the boundary effect was retained for five studies, of which three showed positive responses, while two showed negative responses. Vellu 2010, the only cognitive wolf for which repetition was non-significant, had a strongly negative boundary coefficient (at a lag of 8.5 days), indicating that boundary patrolling was a significant driver for this wolf, which also had the most elongated of all the territories (**Figure 1**). The only wolf that conformed with both of our hypothesized predictions was Julla 2013, with both a positive response to predation and a negative response to boundary visits.

3.4. Coefficients Across Time Lags

We explored how the estimated effect sizes and signs changed across time scales of memory for boundary visits (λ from 1 to 20 days) and predation scores (τ_p from 0.5 to 5 days) for those wolves for which both were significant predictors of departure directions. **Figure 5** illustrates three such examples.

Generally, for both predation and boundary visits, at the longest time scales, the less important is the memory for predicting intrisic values of areas, or at least at predicting the direction of foraging. However, unique patterns do emerge for each individual. Thus, Julla 2013 had a fairly consistent positive predation response (mean effect size 0.58), and negative boundary response (mean -0.72), more or less consistently across all time scales. For wolf LU, the positive boundary response peaks in magnitude around the value corresponding to the highest likelihood, around 4 days (**Table 4**), and then steadily decays

TABLE 4 | Summary of model results for best (or near-best) model for each study, with selected parameter values, selected model, and coefficient estimates.

ID	year	trips	model	zones	τ_p	λ	RPI	Predation		Boundary			Repeat		
Significant improvement over null															
	LU	2011	53	P + B + R	5	1.75	4	1.54	0.22		**1.37**	**		**0.78**	**
Hessu	2011	72	B + R	7		0.5	1.53			**0.92**	–		**1.25**	**	
Niki	2008	61	P + R	8	0.75		1.35	**0.75**	*				**0.85**	**	
Viki	2006	52	P + B + R	8	1.25	3	1.32	*-0.56*	–	**1.26**	**		**0.79**	*	
Vellu	2010	39	B	5		8.5	1.25			*-1.60*	**				
Julla	2013	88	P + B + R	6	4	3	1.21	**0.53**	**	*-0.76*	*		**0.5**	–	
No significant improvement over null															
Hessu	2013	40	P + R	9	1.25		1.37	**0.18**	*				0.73	–	
Miki	2009	73	B + R	8		3	1.07			*-1.13*	–		-0.71	–	

*Significance indicators **, *, and – indicate p-values less than 0.01, 0.05, and 0.1, respectively. For coefficients that were significant at the 0.1 level, bold facing and italics indicate positive and negative coefficients. The overall improvement over null was determined by the lower 95% confidence interval of the RPI being entirely greater than 1.0.*

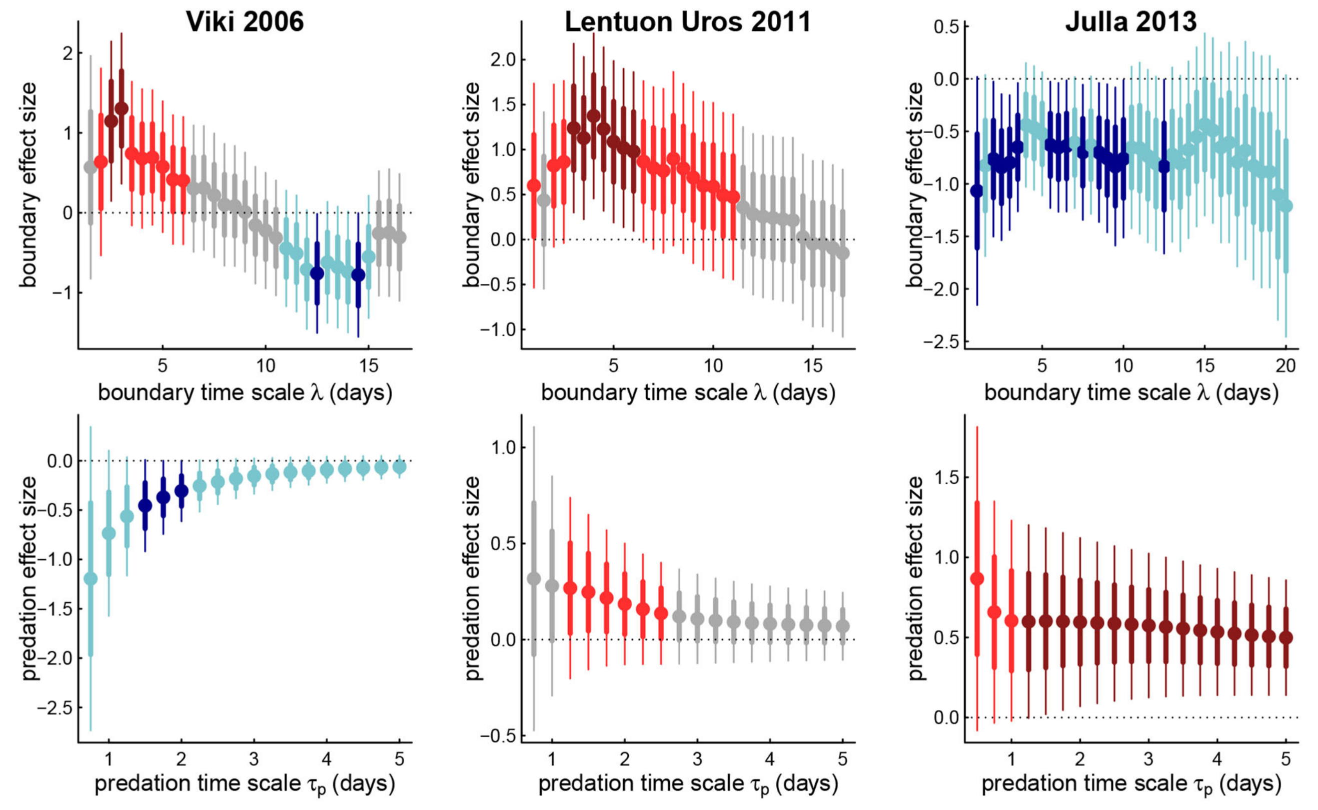

FIGURE 5 | Estimated coefficients for boundary effects against boundary memory time scales (upper panels) and predation effect against predation memory timescale (lower panels) for three example wolves. Thick and thin bars represent 1 and 2 standard errors around respective point estimates, blue are negative, red are positive, light and dark colors represent 1 and 2 standard errors away from 0. Note that the boundary coefficient for Viki (left panels) switches signs across memory time scales.

until it ceases to be significant after about a value of $\lambda = 10$ d. The predation response decays steadily with greater time scale, becoming statistically insignificant after about 3 days.

Most strikingly, wolf Viki 2006 undergoes a switch in the sign of the boundary coefficient between short time lags (≈ 3 days) and longer time lags (≈ 12 days). This suggests that the wolf is more likely to revisit (or highly value) an area of recent visitation, but if the score considers whether there have been visits over a two week period, that area is less likely to be selected. This result is somewhat consistent with the short and long time-scaled memory, often referred to as "working" and "reference" which has been both experimentally measured (Green and Stanton, 1989; Becker and Morris, 1999) and modeled (Bracis et al., 2015, 2018). Recent visits to portions of a boundary may require more visits for good marking. But if a boundary has been marked over a larger time scale, while others have not been, then the need to go to unmarked areas increases. The strength of the predation response for Viki 2006 is significantly negative at a 1.5–2 day time scale, indicating that more or less immediate returns to areas with successful kills are unlikely. However, as that predation memory time scale increases, recent predation success becomes less significant as a predictor of future movements.

4. DISCUSSION

Cognitive processes cannot be directly observed for animals in the wild; even in controlled experiments memory can only be inferred. Studying cognition, therefore, requires developing a cognitive model to make inferences on those behavioral observations, like movements and predation events, that are the observable outcomes of cognitive processes. In order to demonstrate that central-place foraging wolves are using memory to make movement decisions, we needed several specific ingredients: (1) a discrete, observable set of choices made by wolves in the wild, (2) significant events (kills and boundary visits) that could reasonably have influenced the valuing of those choices, (3) a statistical framework that allowed for a rapid exploration of various temporal and spatial scales at which memory might operate, combined with a model selection framework to narrow down significant explanatory variables, and (4) a metric by which we could demonstrate that our model outperforms a non-cognitive model. For most wolves, fitted and parameterized cognitive models were 20 to 50% better at predicting choices than non-cognitive null models (**Table 4**).

In order to develop and fit such models, we relied on an extraordinarily detailed dataset which contained reliable information on objects and locations that are known to be of importance to wolves during the breeding season: the precise location of the den, of kill sites with identification of prey species, and—with slightly more guesswork—the contours of the territorial boundary. We therefore constructed our model around the behavioral imperatives of predation and territorial marking, anchored around fairly regular, central-placed trips that began and ended at the den site. The model assumed a spatially-explicit scoring that emerges directly from prior experiences for both priorities. These are generic assumptions that are consistent with well-known aspects of wolf behavior (Mech and Boitani, 2003).

Nonetheless—and most intriguingly—the results we obtained in many cases contradicted our expectations and were highly individual and idiosyncratic. We comment here on the design and structure of our modeling framework, discuss the cognitive spatial ecology of the wolves in our study, and conclude with some broad ideas on the ingredients needed to make cognitive inferences on animals in the wild.

4.1. Discrete Choices

We chose a discrete choice framework with a design that focused on the apparently unconstrained choice of direction taken by the wolf when leaving the den. The discrete choice approach is a natural one for exploring cognition for several reasons. First, experimental studies of memory and learning in animals almost always reduce to discrete choice frameworks (Thorpe et al., 2004), including such classic experimental designs as the turns a rat chooses to navigate a maze (Tolman and Honzik, 1930) or key-pecking by pigeons (Wilkie and Willson, 1992). More relevant to wolves, experiments on domestic dogs *Canis familiaris* that have shown explicit episodic and working memory have been designed around hiding food rewards in discrete boxes (Fiset et al., 2003; Fujita et al., 2012). Second, the statistical analysis of observational data on discrete choices is a well-developed field, in particular as related to human economic choices (Louviere et al., 2000; McFadden, 2001; Dubé et al., 2002). Fitting discrete choice models is, therefore, fast and technically straightforward, and provides easily interpretable effect sizes for any number of statistically supported covariates that might independently influence choices. Finally, a discrete choice framework provides a straightforward measure of the predictive success of models by comparing probabilistic predictions to randomized observations.

Despite the natural fit of the discrete choice framework to studying cognition, this study is the only example we are aware of as applied to a free-ranging wild animal. The key ingredient is the discrete choice itself. We focused on a very specific kind of movement: namely the early stage of departure from a den. Given the high motility of wolves and the relatively unstructured Finnish mixed woodland landscape, any destination was more or less equally available. Furthermore, it seemed a safe assumption that each departure from the den had similar essential purposes: first to obtain food by hunting or visiting existing caches, with the goal of returning with enough nourishment to feed pups in the den, and to patrol territories. By reducing our movement variable in this way, we greatly simplified the general problem of "modeling movements." This is in contrast to a thematically similar study, in which a memory-based model of winter (i.e., non den-centric) wolf movements with boundary visits and prey habitat used as covariates (Schlägel et al., 2017). In their compelling analysis, every movement step was modeled and the spatial map was fixed to a computationally feasible grid. Thus, the spatial and temporal units of analysis were set not by biological or behavioral considerations but by the battery power trade-off of collar transmission, and by computational constraints of spatial grid processing. The intensive computation of fitting a single model (several days, Schlägel, *pers. comm.*) limited the ability to explore different parameterizations, model structures or covariates. Furthermore, the nature of movements can vary considerably depending on the motivation or behavioral imperative. For example, previous work on several of the wolves in this study showed that movements are faster and more directed when returning to a den post-kill than while hunting (Gurarie et al., 2011), a distinction that is lost when all movements are assumed to be driven by the same process.

By focusing on a limited set of discrete trip departures and a coarsely discretized spatial structure, we were able to compare thousands of models in a short amount of time, sweeping across multiple temporal and spatial scales and combinations of structural parameter values. The obvious trade-off is that we had relatively few departures to model, no more than 1 per day per wolf, which limited the inferential power of more complex models.

4.2. Scales of Space and Time

Among the many structural assumptions underlying our framework, perhaps the most tenuous was the discretization of the wolf territories into a countable number of zones. There is no objective way to know how similar a wolf's mental map might be to our clustering-based zonal partitioning. However, we were able to test a range of numbers of zones, from 3—too few to provide interesting insights—to 8—at the limit of discrete choices given the number of trips that we analyze per wolf. By comparing these different spatial structures, we were able to obtain a coarse idea of a spatial scale at which wolves might be conceptualizing their territory. The number of zones that best separated the discrete choice making of the wolves was between 5 and 8, i.e., in the upper half of the range. Noting that the mean area of the wolf territory was around 670 km^2 (s.d. 275), this would suggest that a relevant cognitive spatial scale for valuing areas would be on the order of 80–130 km^2. Note that this sweeping of structural parameters is made tractable, even trivial, by the discrete choice model framework.

For the animals for which predation memory was significant, three were between 0.75 and 1.75 days (**Table 4**), which might be considered an indication of the time frame over which the spatial location of a predation success is relevant to a wolf. Larger prey items were often torn into smaller pieces and cached, i.e., buried shallowly, by the wolves. Those caches are often revisited within some relatively short period after the kill before any useful meat is too spoiled, and the 1–2 day time scale might reflect that specific cache-revisit behavior. For those wolves for which boundary visits were a significant factor, time-scales were nearly all much longer: from 3 to 8.5 days (**Table 4**).

The shift in the magnitude of the coefficient responses (**Figure 5**) adds nuance to this discussion of time scales. Most notably, the shift in the sign of the boundary response against time scales for wolf Viki is somewhat consistent with the paradigm of "working" (short-term) and "reference" (long-term) memories that often operate in different ways (with opposite signs) at different time-scales. Similarly, while we discretized space into relatively few large zones, in **Figure 4** it appears that the RPI peak against predation time-scale is narrower at a larger number of zones (8), i.e., at a finer spatial scale, while RPI against boundary memory is more sharply optimized at fewer zones (5). This may indicate that the spatial scale at which predation success is remembered is finer than the spatial scale of boundary patrolling. This is consistent with the fact that predation occurs unpredictably in very specific locations, whereas the boundary is a known, fixed entity which is most efficiently marked by making larger territorial movements. Including multiple temporal and spatial scales in a model like this, however, stretches the power of limited observations for making inferences.

4.3. Wolf Foraging Strategies: Patch Depletion or Site Fidelity?

While the fitting, parameterization and predictive assessment of the cognitive model was largely successful, many of the estimated effects contradicted our original expectations and point to nuanced and context-dependent strategies of foraging. In particular, we anticipated that the predation memory effect would be positive, corresponding to a strategy of foraging-site fidelity, and that the boundary visit effect would be negative, as recently visited boundaries would not need to be revisited immediately.

In fact, only one wolf (Julla) has a significant positive predation memory at a time scale of 4 days (by far the longest time scale) combined with a significant negative boundary memory (time scale 3 days). Julla was a wolf in a small pack (2 adults) which apparently only killed 5 reindeer (of which three were adults) that were identified by field workers over the study period. With so few animals, caching and memory takes on an additionally important role, and likely contributed to the higher scoring of recent predation kill sites. Apparent foraging site fidelity in this context is possibly more closely related to cache returns than persistent prey density.

Julla can be contrasted to another wolf (Viki) that had a weak (0.1 > p-value > 0.5) negative coefficient on the predation memory (time scale of 1.25 days). Viki apparently did not value locations of recent predation success as highly as moving to other areas of its territory. Viki was a reproductive member of the largest, most established pack in our data set in the core Finnish wolf area, and had among the largest number of kills, 44 reindeer and moose, mainly calves, in total (**Figure 3**). It is possible that the high success rate of predation throughout the range, together with the higher need to patrol boundaries, and reinforcing territorial marking, deemphasizes the need for foraging site fidelity. Furthermore, it is possible that local prey depletion can occur, analogous to the "patch-disturbance" hypothesis that leads lions to regularly change the location they predate after successful hunts due to prey species avoiding environments that are demonstrably risky (Valeix et al., 2011). While the viewshed and corresponding cross-prey species communication of successful hunts is much more limited in the boreal forest than in the savanna, many of the prey ungulates have much smaller ranges than the smallest of the wolf zones. For example, summer home ranges of female moose in Fennoscandia range from 1000 to 2000 ha (Cederlund and Okarma, 1988; Eriksen et al., 2011). Moose are, furthermore, solitary and somewhat territorial, with minimal range overlap (Eriksen et al., 2011). A single adult kill may, therefore, significantly deplete the availability of prey on a hyper-local level, while a calf kill—which a mother moose is likely to be aware of—may also result in a shift in the female's range.

In contrast to both Viki and Julla, Niki had a strong positive predation coefficient (at time lag 0.75), and no boundary model selected whatsoever, despite having the greatest number of kills. This may be explained by the fact that Niki's territory was largely structured by several major roads and an extended fence separating the reindeer management area (RMA, **Figure 1**). In fact, Niki was the only wolf whose territory overlapped with the RMA and the only wolf to have killed several semi-domesticated reindeer (Gurarie et al., 2011). All of these highly structuring features are consistent with certain areas being consistently better for predation, making foraging site fidelity a more viable strategy for this wolf.

While accounting for the wide variability in cognitive strategies among these wolves is impossible, we can broadly conclude that wolves may engage in either major foraging strategy, or—indeed—can move with no particular attention to prey distribution at all. It bears noting that the territories in this study were all very similar, many neighboring or overlapping across years (**Figure 1**). The main differences among wolves were related to pack composition and density and distribution of primary roads and houses, which can significantly impact wolf behavior and space use in general (Gurarie et al., 2011; Barry et al., 2020). Thus, when it comes to using and responding to spatial memory, wolves appear to be highly idiosyncratic and individual, much as the social and ecological context of individual wolves can be very specific, even within the same territory across years (see also **Appendix B**). Even as it can be demonstrated *statistically* that some decisions are influenced by prior experience, there are few overarching generalities that can be made about the spatial or temporal scales and relative importance of various cues on wolf cognition.

4.4. Inferring Cognition From Movement Data

It is—in short—a surprisingly steep challenge to infer the use of memory for animals moving in the wild, mainly because of the large number of variables that cannot be controlled and the complexity of animal behavior. Nonetheless, cognitive inferences can be made when certain criterion are met. We propose here a checklist building on the somewhat qualified success of fitting our own cognitive model on the wolf data set.

1. Identification and isolation of a **distinct quantifiable behavior** that might hypothetically be driven by prior experiences and otherwise be minimally confounded by unknown behavioral imperatives; e.g., den departures to specific spatial zones.
2. Identification of key **events or cues** that might determine the movement behavior to be modeled; in our example, predation events and boundary visits. Generally, food resources are the most important trigger, echoing experimental setups where food rewards are routinely used. As a rule, movement data alone without a context will almost never be sufficient to unambiguously identify a cognitive signal.
3. A **plausible cognitive mechanism** for a movement response to those events; i.e., the memory-based movement model itself. Ideally, this model can be developed in a hierarchical way, such that increasingly complex models can be compared to test specific hypotheses.
4. A **statistical framework** to estimate the properties of that mechanism from movement data; e.g., the discrete choice modeling framework and parameter sweeps for maximum likelihood exploration of parameter values.
5. A reliable **metric** to demonstrate the relative performance of the cognitive model against simpler, non-cognitive models; e.g., the relative prediction improvement score.

This checklist may be useful in pointing toward general principles for the development of cognitive analysis of movement data.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

This research adheres to the ASAB/ABS Guidelines for the use of animals in research. The capture protocol of wolves in 2008–2013 followed conditions in permits approved by the Animal Experimental Board–ELLA, Southern Finland State Administrative Agency (licence numbers ESLH-2008-01012/Ym-23, ESLH-2008-10222/Ym-23, ESAVI-0000184/041003/2011, and ESAVI/3893/04.10.03/2011), to which the use of the permit is reported annually. The capture of wolves in 2006–2007 met the guidelines issued by the Animal Care and Use Committee at the University of Oulu (OYEKT-6–99), under permits provided by the provincial government of Oulu (OLH-01951/Ym-23). All protocols adhered to directives 86/609/EEC (2006–2012) and 2010/63/EU (2013–2017).

AUTHOR CONTRIBUTIONS

EG, OO, and IK formulated the original concept. IK and JS coordinated and collected wolf data (with some help from EG). EG, WF, and CB contributed to conceptual model development. AB and SP contributed to data processing and coding. SP contributed to supplementary figures. EG conducted the analyses and wrote the initial manuscript draft. All authors contributed to manuscript revisions and have read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.768478/full#supplementary-material

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Predicting near-term, out-of-sample fish passage, guidance, and movement across diverse river environments by cognitively relating momentary behavioral decisions to multiscale memories of past hydrodynamic experiences

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Predicting the behavior of individuals acting under their own motivation is a challenge shared across multiple scientific fields, from economic to ecological systems. In rivers, fish frequently change their orientation even when stimuli are unchanged, which makes understanding and predicting their movement in time-varying environments near built infrastructure particularly challenging. Cognition is central to fish movement, and our lack of understanding is costly in terms of time and resources needed to design and manage water operations infrastructure that is able to meet the multiple needs of human society while preserving valuable living resources. An open question is how best to cognitively account for the multi-modal, -attribute, -alternative, and context-dependent decision-making of fish near infrastructure. Here, we leverage agent- and individual-based modeling techniques to encode a cognitive approach to mechanistic fish movement behavior that operates at the scale in which water operations river infrastructure is engineered and managed. Our cognitive approach to mechanistic behavior modeling uses a Eulerian-Lagrangian-agent method (ELAM) to interpret and quantitatively predict fish movement and passage/entrainment near infrastructure across different and time-varying river conditions. A goal of our methodology is to leverage theory and equations that can provide an interpretable version of animal movement behavior in complex environments that requires a minimal number of parameters in order to facilitate the application to new data in real-world engineering and management design projects. We first describe concepts, theory, and mathematics applicable to animals across aquatic, terrestrial, avian, and subterranean domains. Then, we detail our application to juvenile Pacific salmonids in the Bay-Delta of California. We reproduce observations of salmon movement and passage/entrainment with one field season of measurements, year 2009, using five simulated behavior responses to 3-D hydrodynamics. Then, using the ELAM model calibrated from year 2009 data, we predict the movement and passage/entrainment of salmon for a later field season, year 2014, which included a novel engineered fish guidance boom not present in 2009. Central to the fish behavior model's performance is the notion that individuals are attuned to more than one hydrodynamic signal and more than one timescale. We find that multi-timescale perception can disentangle multiplex hydrodynamic signals and inform the context-based behavioral choice of a fish. Simulated fish make movement decisions within a rapidly changing environment without global information, knowledge of which direction is downriver/upriver, or path integration. The key hydrodynamic stimuli are water speed, the spatial gradient in water speed, water acceleration, and fish swim bladder pressure. We find that selective tidal stream transport in the Bay-Delta is a superset of the fish-hydrodynamic behavior repertoire that reproduces salmon movement and passage in dam reservoir environments. From a cognitive movement ecology perspective, we describe how a behavior can emerge from a repertoire of multiple fish-hydrodynamic responses that are each tailored to suit the animal's recent past experience (localized environmental context). From a movement behavior perspective, we describe how different fish swim paths can emerge from the same local hydrodynamic stimuli. Our findings demonstrate that a cognitive approach to mechanistic fish movement behavior modeling does not always require the maximum possible spatiotemporal resolution for representing the river environmental stimuli although there are concomitant tradeoffs in resolving features at different scales. From a water operations perspective, we show that a decision-support tool can successfully operate outside the calibration conditions, which is a necessary attribute for tools informing future engineering design and management actions in a world that will invariably look different than the past.

KEYWORDS

ecohydraulics, ethohydraulics, multi-timescale perception, perceptual decision-making, multiplex signal disentanglement, psychophysics, habituation, fish behavior model

1. Introduction

Fish in rivers are important ecologically, culturally, recreationally, commercially, and as a key food resource (Murray et al., 2020; Su et al., 2021). Inland waters make up less than 0.01% of Earth's water yet simultaneously support both 40% of the world's fish production and more than 40% of the global human population (Stiassny, 1996; Helfman et al., 2009; Kummu et al., 2011; Lynch et al., 2016). Rivers are a portion of inland waters and particularly vital, making up just 0.0002% of the water supply (Shiklomanov, 1993; Vince, 2012). Water operations provide human society with irrigation, navigation, power, and flood protection and include built infrastructure such as dams, levees, and water diversions. More than 2.8 million dams have been built globally, and 500,000 km of waterways are regulated in some form (Grill et al., 2019; Belletti et al., 2020; Yang et al., 2022). In the U.S. alone, there are more than 90,000 dams (U.S. Army Corps of Engineers, 2018) and 40,000+ km of levees with 45,500+ built structures associated with 17 million people and $2 trillion in property (U.S. Army Corps of Engineers, 2020). More than 60% of the US inland navigation steel structures have reached or exceeded their design life. As infrastructure is designed, re-designed, and/or re-imagined, the ability to predict near-term fish movement during the engineering design phase has the potential to save time and money as well as living resources. The success of structures and management actions designed to facilitate the safe travel of aquatic species past built infrastructure is frequently dictated by the volitional decision-making of freely-moving fish.

Managing fish near water diversions and dams often involves some form of separating individuals from the bulk flow of water and guiding them to specific safe transit locations within the river channel. In other species management scenarios, in-river structures may be used to facilitate the capture or limit the spread of invasive species (Zielinski et al., 2020). Both species management goals are a daunting engineering challenge.

More than a half-century of field and laboratory research has yielded a substantial amount of work and literature in which there are many, and sometimes contradictory, findings for how fish respond to natural and manageable environmental stimuli (**Table 1**). Fish respond to multiple factors that can be managed in a river including hydrodynamics, electrical fields, carbon dioxide, and insonified bubble curtains with light stimuli. In some settings, water temperature, salinity, dissolved oxygen, and stratification are factors that influence fish movement in rivers.

TABLE 1 Fish stimuli-response factors, cognition, behavior modeling, and general cognitive characteristics across many different kinds of organisms.

Area of scientific inquiry	Abbreviated synopsis of historical and more recent works
Fish stimuli-response factors, cognition, and behavior modeling	
Multiple factors	Chamberlain, 1907; Chidester, 1924; Collins, 1952; Brett and Alderdice, 1958; Hocutt et al., 1980; Anderson, 1988; Feist and Anderson, 1991; Coutant and Whitney, 2000; Schilt, 2007; Sweeney et al., 2007; Katopodis and Williams, 2012; Noatch and Suski, 2012; Jones et al., 2021; Cooke et al., 2022; NMFS, 2022
Hydrodynamics	Gray, 1933a,b; McLeod and Neményi, 1941; MacKinnon and Hoar, 1953; Jones, 1956; Sutterlin and Waddy, 1975; Kalmijn, 1988; Webb, 1989; Drucker and Lauder, 2003; Lauder and Tytell, 2004; Liao, 2007; Windsor et al., 2010a,b; Lacey et al., 2012; Coutant, 2023
Temperature, salinity, dissolved oxygen	Gurley, 1902; Chamberlain, 1907; Shelford and Allee, 1913; Galtsoff, 1924; Gutsell, 1929; Creaser, 1930; Brett, 1952; Collins, 1952; Erichsen Jones, 1952; Sullivan and Fisher, 1953; Brett, 1956; Ferguson, 1958; Garside and Tait, 1958; Whitmore et al., 1960; Moss and Scott, 1961; Javaid and Anderson, 1967; Coutant, 1975; McCauley and Huggins, 1979; Reed and Balchen, 1982; Coutant, 1985; Kramer, 1987; Thomson et al., 1992; Goodwin, 2000; Humston et al., 2000; Nestler et al., 2002; Humston et al., 2004; Carter, 2005; Prchalová et al., 2006; Booker et al., 2008; Mork et al., 2012; Chittenden et al., 2013; Burke et al., 2014; Byron et al., 2014; Moriarty et al., 2016; Clancey et al., 2017; LaBone et al., 2021; Quinn et al., 2022; García-Vega et al., 2023
Electrical fields	Baker, 1928; Applegate et al., 1952; Brett and Alderdice, 1958; Johnson et al., 2014; Miller et al., 2021; Kowalski et al., 2022; Miller et al., 2022
Carbon dioxide	Shelford and Allee, 1913; Wells, 1913; Gutsell, 1929; Creaser, 1930; Powers and Clark, 1943; Collins, 1952; Donaldson et al., 2016; Cupp et al., 2017; Treanor et al., 2017; Hasler et al., 2019; Cupp et al., 2021
Acoustic, light, bubbles	Parker, 1912; Reeves, 1919; von Frisch, 1938; Lowe, 1952; Brett and MacKinnon, 1953; Fields et al., 1956; Brett and Alderdice, 1958; Patrick et al., 1985; Sager et al., 1987; Kalmijn, 1988; Nestler et al., 1992; Popper and Carlson, 1998; Bullen and Carlson, 2003; Johnson, 2003; Prchalová et al., 2006; Kock et al., 2009; California Department of Water Resources, 2012, 2013; Flammang et al., 2014; Mussen et al., 2014; Perry et al., 2014; Zielinski et al., 2014a,b; Febrina et al., 2015; Zielinski and Sorensen, 2015, 2016, 2017; Miehls et al., 2017; Dennis et al., 2019; Hansen et al., 2019; Jesus et al., 2019; Mickle et al., 2019; Piper et al., 2019; Dennis and Sorensen, 2020; Popper et al., 2020; Flores Martin et al., 2021; Jesus et al., 2021; Leander et al., 2021; Pratt et al., 2021
Cognition; orientation to environmental cues	Gurley, 1902; Churchill, 1916; Fraenkel and Gunn, 1940; Thorpe, 1956; Royce et al., 1968; Gleitman and Rozin, 1971; Quinn, 1991; Dukas, 1998; Shettleworth, 1998, 2001; Brown et al., 2011; Eliassen et al., 2016; Salena et al., 2021; Hein, 2022; Rodriguez-Santiago et al., 2022; Fahimipour et al., 2023
Cognition, orientation in natural world for conservation	Galtsoff, 1924; Dodson, 1988; Kieffer and Colgan, 1992; Odling-Smee and Braithwaite, 2003; Greggor et al., 2020
Behavior, movement modeling	DeAngelis, 1978; Balchen, 1979; Neill, 1979; Reed and Balchen, 1982; Anderson, 1988; Bartsch et al., 1989; Foreman et al., 1992; Lough et al., 1994; Reyes et al., 1994; Tyler and Rose, 1994; Zabel, 1994; Davidson and Deyoung, 1995; Tregenza, 1995; Giske et al., 1998; Heath et al., 1998; Goodwin, 2000; Humston et al., 2000; Humston, 2001; Bracis, 2010; Byron and Burke, 2014; Jager and DeAngelis, 2018; DeAngelis and Diaz, 2019; Lilly et al., 2022
Agent-, particle-, individual-based movement behavior model with 2-D/3-D hydrodynamics, water quality, and/or other stimuli	Walsh et al., 1981; Thomson et al., 1992; Werner et al., 1993; Thomson et al., 1994; Hermann et al., 1996; Hinckley et al., 1996; Werner et al., 1996; Rand et al., 1997; Walter et al., 1997; Ault et al., 1999; Quinlan et al., 1999; Goodwin, 2000; Friedland, 2001; Guensch et al., 2001; Werner et al., 2001; Nestler et al., 2002; Scheibe and Richmond, 2002; Giske et al., 2003; Blumberg et al., 2004; Booker et al., 2004; Goodwin, 2004; Humston et al., 2004; Goodwin et al., 2006; Werner et al., 2007; Booker et al., 2008; Willis, 2011; Bracis and Anderson, 2012; Fossette et al., 2012; Mork et al., 2012; Abdelaziz et al., 2013; Chittenden et al., 2013; Burke, 2014; Burke et al., 2014; Byron et al., 2014; Goodwin et al., 2014; Arenas et al., 2015; Febrina et al., 2015; Moriarty et al., 2016; Putman et al., 2016; Railsback et al., 2016; Naisbett-Jones et al., 2017; Putman, 2018; Zielinski et al., 2018; Gilmanov et al., 2019; Snyder et al., 2019; Brosnan and Welch, 2020; Morrice et al., 2020; Ounsley et al., 2020; Padgett et al., 2020; Rossington and Benson, 2020; Benson et al., 2021; Bjørnås et al., 2021; Gross et al., 2021a,b; Kulić et al., 2021; LaBone et al., 2021; McIlvenny et al., 2021; Newton et al., 2021; Olivetti et al., 2021; Szabo-Meszaros et al., 2021; Zhu L. et al., 2021; Gisen et al., 2022; Holleman et al., 2022; Lai, 2022; Powalla et al., 2022; Quinn et al., 2022; Tan et al., 2022; Whitty et al., 2022; Zeng, 2022; Hajiesmaeili et al., 2023; Kerr et al., 2023; Mawer et al., 2023; Sridharan et al., 2023
General cognitive characteristics across many different kinds of organisms	
Role of time in behavior	Dodson, 1988; Kieffer and Colgan, 1992; Odling-Smee and Braithwaite, 2003; Park et al., 2016; Dabiri, 2017; Oteiza et al., 2017; Bi and Zhou, 2020; Auger-Méthé et al., 2021; Chen et al., 2021; Fagan et al., 2023
Behavioral choice/decision via evidence accumulation	Stone, 1960; Laming, 1968; Vickers, 1970; Ratcliff, 1978; Dodson, 1988; Kieffer and Colgan, 1992; Giske et al., 1998; Usher and McClelland, 2001; Odling-Smee and Braithwaite, 2003; Bogacz et al., 2006; Bogacz et al., 2007; Ossmy et al., 2013; Dabiri, 2017; Oteiza et al., 2017; Dragomir et al., 2020; Chen et al., 2021; Salena et al., 2021
Multiple timescales	Gleitman and Rozin, 1971; Giske et al., 1998
Related to temporal features of the environment	Harris, 1943; Thompson and Spencer, 1966; Anderson, 2002; Steele-Feldman, 2006; Bromberg-Martin et al., 2010; Nassar et al., 2010; Kato et al., 2014; Murray et al., 2014; Piet et al., 2018
Tracking of time-varying information in behavioral analysis	Anderson, 2002; Steele-Feldman, 2006; Van Moorter et al., 2009; Anderson et al., 2010; Bernacchia et al., 2011; Fagan et al., 2013; Kacelnik et al., 2013; Wilson et al., 2013; Murray et al., 2014; Bracis et al., 2015; Wilson et al., 2018; Iigaya et al., 2019; Lin et al., 2021; Ranc et al., 2022
Short- and long-term categorizations	Sharpless and Jasper, 1956; Gleitman and Rozin, 1971; Harley, 1981; Giske et al., 1998; Rose and Rankin, 2001; McNamara et al., 2008; Wilson and Linster, 2008; Thompson, 2009; Bernacchia et al., 2011; Das et al., 2011; Murray et al., 2014; Iigaya et al., 2019; Bi and Zhou, 2020; Shen et al., 2020; Spitmaan et al., 2020; Lin et al., 2021; Meister, 2022; Wang and Salmaniw, 2023

Here, we limit our focus to hydrodynamic stimuli. The study of fish and water flow has a rich history dating back about a century. Also dating back about a century yet somewhat separate from the hydrodynamic investigations is the study of fish cognition and how they orient to environmental cues, which have long been applied to understand their behavior in the natural world for conservation purposes (**Table 1**).

Ecological decision-making for conservation is inherently a forecasting problem (Werner et al., 2007; Dietze et al., 2018), and numerical modeling makes precise our underlying hypotheses (Dietze et al., 2018). Numerical fish behavior and movement modeling has been a powerful tool in conservation for more than 40 years (**Table 1**). Near-term ecological forecasting, specifically, focuses on meeting the needs of daily to decadal environmental decision-making under high uncertainty and adaptive management. Iterative near-term ecological forecasting involves rapidly testing hypotheses through comparison of quantitative predictions to new observational data under different scenarios, one of the strongest tests of scientific theory (Dietze et al., 2018). However, there is no such thing as a perfect forecast (Werner et al., 2007; Dietze et al., 2018). Key challenges remain.

The number of fish behaviors that need to be factored in order to reproduce movement and passage/entrainment patterns at river infrastructure increases concomitantly with environmental complexity (Goodwin et al., 2014). An important question for water operations management, therefore, is how different fish behaviors emerge, one at a time, from a multi-response repertoire to meet the momentary challenges of an individual. In other words, how does a specific fish-hydrodynamic response suited for a given environmental context emerge from an evolved repertoire of multiple behaviors that, together, facilitate the animal's navigation through diverse, time-varying conditions such as flood and ebb tides (Dodson, 1988). We pursue three main lines of scientific inquiry in our study:

- what might the evolved repertoire of fish-hydrodynamic responses be for downstream-migrating fish in rivers;
- what degree of mathematical complexity is needed to reproduce and predict fish swim path patterns and observed passage/entrainment at infrastructure; and
- what level of numerical sophistication is required of river hydrodynamic modeling to inform a computationally-tractable management decision-support tool?

We cannot measure all internal and external factors in the natural world that may influence how a fish moves through an open river. However, sensory processing and cognitive decision-making is evident even in simple laboratory settings where an individual fish changes its behavior response over time to a stimulus that itself does not change (Haro et al., 1998; Enders et al., 2009a). In rivers, the same phenomena is observed near infrastructure (Goodwin et al., 2006, 2014). We piece together concepts, theory, and mathematics across multiple scientific fields as well as findings dating back in some cases nearly a century ago within the areas of organism sensory perception and cognitive decision-making, fish environmental and hydrodynamic response, and numerical behavior and environmental modeling (**Table 1**).

We start by, first, describing some general characteristics of cognition that apply to many organisms, not just fish. Then, second, we describe our tidal study system and data involving juvenile Pacific salmonids (hereafter salmon). Third, we tailor the general characteristics of animal cognition that we introduce in the next section to salmon navigating a tidal river junction in the context of water operations to understand and predict their movement and passage/entrainment.

2. Methods: general characteristics of animal cognition

The present era is one of rapidly developing knowledge about animal cognition (Greggor et al., 2020; Salena et al., 2021; Bialek, 2022; Hein, 2022; Petrucco et al., 2022; Triki et al., 2022; Wang and Salmaniw, 2023). At a fundamental level, we lack understanding of the complexities and context dependencies that underlie behavior changes in multisensory conditions (Bak-Coleman et al., 2013; Coombs et al., 2020). A critical part of interpreting changes in behavior is understanding the role of time (**Table 1**). One reason for our existing knowledge gaps is that invaluable laboratory experiments are also limited in the available degrees of freedom compared to the natural world (Salena et al., 2021), the latter of which involves continuous decisions with ever-changing options influenced by recent responses (Yoo et al., 2021). Fish may exhibit different behaviors in the field environment than in simpler settings (Dennis and Sorensen, 2020).

Note that for the purposes of our work herein that terminology can differ among scientific fields and, here, we take an expansive and inclusive view of the terms *cognition* and *cognitive*. By the terms *cognition* and *cognitive* we are referring generally to perception, attention, memory, learning, and the processes of perceptual decision-making that we can predict at the scale of a river. Also, we use the terms *behavioral choice* and *decision* interchangeably. We recognize that in our attempt to make our nomenclature understandable across a broad audience that we may deviate from more stringent terminology definitions in some of the scientific fields that we leverage in this work.

Our cognitive approach to mechanistic animal movement behavior modeling is not a study of brain architecture. We necessarily relegate many cognitive phenomena to parameterization that summarily represents subresolution dynamics that may seem crude if viewing our work from the perspective of other scientific fields that investigate neuroscience, neurobiology, and cognition at a finer scale. Here, we must encode cognitive phenomena more simply than what happens inside an animal's brain in order for a model of movement behavior to operate at the scale of landscape and waterscape infrastructure in the open world for natural resources management.

2.1. Sensory experience influences stimulus perception and behavioral choice

The sensory experience of an individual strongly influences the perception of a stimulus (Akrami et al., 2018) and resulting behavioral choice (**Table 1**). Momentary stimuli are noisy, so animals constantly integrate sensory evidence over time and space to infer the state of their environment (Bahl and Engert, 2020; Dragomir et al., 2020). A relative difference between momentary and previously experienced stimuli influences the movement of even primitive organisms (Ikeda et al., 2020). In next section, we describe the first step in our modeling process for encoding how sensory experience influences the perception of a stimulus and resulting behavioral choice.

2.1.1. Stimulus: physical vs. perceived intensity

We first convert a stimulus physical (measured/modeled) value into a perceived intensity, I_φ, by applying a treatment analogous to the decibel scale for any stimuli variables whose quantities, φ, span orders of magnitude, such as gradients and other derivative values:

$$I_\varphi(t) = \log_{10}\left(\frac{\varphi(t)}{\varphi_o}\right) \qquad (1)$$

where φ_o is an arbitrary reference or baseline. The logarithm of a physical quantity, I_φ, at momentary time t often better represents an animal's perception of intensity for a stimulus whose measured/modeled quantities span orders of magnitude (Fechner, 1860), e.g., sound. In our approach, physical stimulus quantities that do not span orders of magnitude remain unmodified from their measured/model value.

After this step, we refer to each stimulus i whose measured/modeled quantity is φ as its *perceived* intensity, I_i. Also, note that in limited places we use the terms *quantity* and *intensity* interchangeably in order to convey a few concepts herein.

A common feature of perception across taxa is the sensory system's translation of a physical stimulus magnitude to a perceived quantity using proportional differencing (Akre and Johnsen, 2014). While our first step accounts for some psychophysical characteristics of perception, it does not account for an animal's continuous sampling of the environment. In next section, we describe our approach for how continuous sensory sampling and experience over time influences an individual's perception of a stimulus.

2.1.2. Stimulus: perceived change in intensity

Continuous sampling of a stimulus over time impacts how its perceived quantity may be registered by an animal. Each animal has its own unique sequence of preceding experiences, or history, so the momentary perception of a stimulus can be registered differently by separate individuals. Detecting the change in a stimulus using a proportional difference between two magnitudes allows an animal's sensory system to cope with the enormous diversity of intensities experienced in the environment (Akre and Johnsen, 2014).

Note that in the first step, we converted stimuli to perceived intensities, yet the perceived change in intensity is also a perceptual characteristic. To keep our steps clear and nomenclature simple, hereafter, we refer to *perceived intensity* simply as *intensity*, I_i, so we can refer to the notion of a *perceived change in perceived intensity* more simply as the *perceived change in intensity*.

Our second step for encoding how sensory experience influences stimulus perception is to describe the perceived *change* in intensity, E_i, following an analogy to the *just noticeable difference* (*jnd*) concept of the Weber-Fechner law (Weber, 1846; Fechner, 1860). We compute E_i by comparing the momentary intensity, I_i, to recent past sensory experience in the form of a habituated (or acclimatized) level, I_{a_i}, at time t as:

$$E_i(t) = \frac{I_i(t) - I_{a_i}(t)}{I_{a_i}(t)} \qquad (2)$$

Habituation is the foundation of selective attention that perceptually desensitizes an animal over time to static, common, irrelevant, or inconsequential stimuli. Habituation allows the individual to focus on the most salient signals in their environment at a given moment even amid high background noise (Rose and Rankin, 2001; McNamara et al., 2008; Rankin et al., 2009; Blumstein, 2016; Shen et al., 2020; Tafreshiha et al., 2021). Habituation is a form of plasticity, more specifically, a simple memory and learning process that is found across sensory systems and taxa, including fish (Dennis and Sorensen, 2020). Habituation is a building block of animal cognition and behavior (Harris, 1943; Konorski, 1948; Sharpless and Jasper, 1956; Thompson and Spencer, 1966; Peeke and Peeke, 1973; Rose and Rankin, 2001; McNamara et al., 2008; Das et al., 2011).

The *jnd* does not universally capture perceptual performance in every kind of task (Carriot et al., 2021). Our treatment of signal-to-background, or signal-to-noise *jnd*, $E_i(t)$, is perhaps better described instead as a *notable streaming differential* (*nsd*) because animals update the ratio in Equation 2 perpetually, not just at a single decision moment in time that is often the basis for *jnd* evaluation. We use an exponentially weighted moving average (EWMA) to encode habituation although more sophisticated algorithms exist. Using an EWMA, the habituated intensity, I_{a_i}, updates as follows:

$$I_{a_i}(t) = \left(1 - m_{a_i}\right) \cdot I_i(t) + m_{a_i} \cdot I_{a_i}(t-1) \qquad (3)$$

where $I_i(t)$ is the momentary intensity of stimulus i at the individual's *xyz*-position at time t, $I_{a_i}(t)$ is the intensity of stimulus i to which the individual is habituated or, in other words, the background intensity. We assume the memory parameter m_{a_i} is a non-changing coefficient within the range [0, 1] that determines how quickly the individual habituates and becomes desensitized to new intensities of the stimulus (Bush and Mosteller, 1955).

Sensory experience is the basis we use to encode a cognitively-inspired mechanistic account of the salmon's changing environmental context for momentary decisions (Goodwin et al., 2006, 2014), which we describe as the third step in the next sections.

2.1.3. Context-based behavioral choice—with a single factor

Contrary to the notion that context is important in decision-making only for higher trophic level organisms, contextual awareness resulting in different responses to the same stimulus is a factor even in single cells (Kramer et al., 2022). An organism's behavioral choice depends on the context of its momentary decision (Bak-Coleman et al., 2013; Coombs et al., 2020; Ikeda et al., 2020; Mann, 2020; Oram and Card, 2022). Sensory experience informs the decision context. Animal decisions are based on the simple notion of whether perceived conditions are better or worse than preceding experience (McNamara et al., 2013). In our approach, preceding experience is encoded through habituation, I_{a_i}.

In our approach, the previously experienced stimulus intensities provide the decision context when a single environmental factor is at play. We encode the momentary stimulus relative to the context of previous sensory experiences using the perceived change in intensity E_i.

Behavioral choice such as a change in movement orientation and speed within our approach is based on the notion of whether E_i exceeds a pertinent threshold, k_i, where k_i is a characteristic that must be determined in the analysis. Describing behavioral decisions using accumulated sensory evidence crossing a threshold (Bahl and Engert, 2020) is a common approach across a variety of organisms (Dragomir et al., 2020).

2.1.4. Context-based behavioral choice—with multiple factors

The natural world is composed of many factors, some known and many unknown, whose stimulus quantities are continuously integrated over time by an animal. Each stimulus competes for the individual's selective attention. Determining the decision context of behavioral choice requires not only integrating intensities over time for multiple abiotic and biotic factors but also finding a common currency to combine the diverse sensory experiences toward a singular decision for the moment. Our approach to multiple factors is to use thresholds, k_i, for each factor or stimulus i. We combine the sensory experiences across multiple factors by converting threshold exceedances into Boolean values [0 or 1], which we can use as a common currency to combine diverse sensory experiences to inform momentary choice.

An animal's movement strategy in natural settings may consist of a large repertoire of behavior responses. A stimulus operates on a spectrum, so the concept of a threshold helps in interpreting at what point does the factor warrant attention relative to competing factors. When the animal experiences a diverse array of environmental stimuli and conditions, behaviors within a repertoire may take varying precedence in different phases of a movement sequence (Sogard and Olla, 1993; New et al., 2001).

In our approach, an individual perpetually updates and compares their *nsd* values at time t, $E_i(t)$, to corresponding thresholds, k_i, for each stimulus i. When $E_i(t)$ crosses k_i we assume the neural activity, $a_B(t)$, in the animal's brain increases their propensity or motivation – mathematically, what we call *accumulated evidence*, $e_B(t)$ – to respond with behavior $B(t)\{r\}$ using one of the available responses, r, within the evolved repertoire, $r = \{1, 2, 3, \ldots\}$. Put simply, when $E_i(t)$ crosses k_i we assume the corresponding stimulus i warrants attention, even if no movement response is yet required; stimulus i begins to climb in the hierarchy of competing other stimuli. Mathematically, when the threshold is crossed then the Boolean measure switches from 0 to 1. When the Boolean measure is 1, then activity $a_B(t)$ takes on a value within the range $[0.0 < a_B \leq 1.0]$ that does not change with time and whose value is determined in the analysis. The constant a_B is based on a subjective assessment of the response's value to the animal relative to the other behaviors in the larger repertoire. Activity $a_B(t)$ is zero whenever the threshold is not crossed.

The evidence, e_B, supporting each behavior B accumulates based on inputs $a_B(t)$ through a cognitive algorithm and results in the selection of a singular movement orientation and speed response for the duration of time increment Δt. The temporal integration of evidence supporting different choice options — each behavior response B — is a computational process generally thought to underlie decision-making (Ossmy et al., 2013) and accurately describes paradigms with multiple sensory modalities across various organisms (Dragomir et al., 2020). The exact currency of evidence that is accumulated (e.g., sensory versus behavioral output) is an active area of neurophysiological study (Dragomir et al., 2020).

In our present approach, following the sensory integration paradigm, we use the Mutual Inhibition Model or Leaky Competing Accumulator model (Usher and McClelland, 2001) to temporally accumulate perceived evidence and select the behavior B. To decide behavior transitions, the sensory evidence accumulators, e_B, integrate the activity, a_B, supporting each behavior B as:

$$de_B = \left(a_B - \lambda e_B - \eta \sum_{\substack{j=1 \\ j \neq B}}^{S} e_j \right) dt + c dW_B \tag{4}$$

or as a complete equation in discrete form:

$$e_B(t + \Delta t) = e_B(t) + \left(a_B(t) - \lambda e_B(t) - \eta \sum_{\substack{j=1 \\ j \neq B}}^{S} e_j(t) \right)$$

$$\Delta t + c\zeta_B \sqrt{\Delta t} \tag{5}$$

where $e_B(t = 0) = 0$. The behavior $B(t)\{r\}$ implemented at time t is the response r associated with the greatest accumulator value e_B at the beginning of increment Δt. e_B is a leaky integrator that accumulates evidence from a drifting input with mean activity a_B (Bogacz et al., 2006). Activity a_B corresponds to a general, inherent urgency to respond to the stimulus with a particular behavior B (Schurger et al., 2012). Each behavior B is associated with an activity a_B that causes it to be implemented in the face of other available responses. An individual executes behavior B when the activity a_B supporting it accumulates over time in the form of accumulator e_B from Equation 4 or 5 and overtakes the accumulators, e, of the other available behaviors that could otherwise be implemented.

λ is the exponential decay rate of activity a_B where the leak term $-\lambda e_B$ causes e_B to decay to zero in the absence of inputs a_B. When $\lambda > 0$, the net effect is decay toward zero that produces stability in the activation whereas for $\lambda < 0$ the activation tends to self-amplify and is not stable (Schurger et al., 2012). The accumulators e_B mutually inhibit each other through a connection weight, η, where S is the number of accumulators e_B. The variable having uppercase W may be thought of as random fluctuations in the signal, intrinsic accumulator noise, or unmodeled inputs and can be represented as independent, identically distributed Wiener processes with unit variance (McMillen and Holmes, 2006).

In the discrete form, ζ_B is Gaussian noise sampled from a standard normal distribution $N(0, 1)$ with zero mean and variance $\sigma^2 = 1$, c is a noise-scaling factor, and Δt is the discrete time increment of the simulation (Usher and McClelland, 2001; Bogacz et al., 2007; Schurger et al., 2012; Tsetsos et al., 2012). λ and η are all assumed to be nonnegative. The activity scale can be chosen so that zero represents baseline activity in the absence of inputs, hence integration starts from $e_B(t = 0) = 0$ (Bogacz et al., 2006). The major simplification of the model here compared to that of Usher and McClelland (2001) is the removal of nonlinearities (Bogacz et al., 2006). e_B accumulation rates depend linearly on their present values. To account for the fact that neural firing rates in the brain are never negative, Usher and McClelland assumed that e_B is transformed via a threshold-linear activation function:

$$e_B\,(t\ +\ 1)\ \ =\ \max\left(0, e_B\,(t) + de_B\right) \tag{6}$$

or more simply:

$$e_B \rightarrow \max\,(0, e_B) \tag{7}$$

Usher and McClelland (2001) propose that a multi-decision process can be modeled by a direct extension of the Mutual Inhibition Model in which each e_B inhibits and receives inhibition from all other e_B. This implements a max-versus-average procedure where evidence favoring the most supported alternative is compared with the average of the evidence in support of all other alternatives (Bogacz et al., 2006). Usher and McClelland (2001) show the approach performs best among several alternative models. Behavior selection is an ongoing decision process, perpetual in time, and cross-inhibition robustly improves its efficiency by reducing the frequency of costly transitions (Marshall et al., 2015).

2.1.5. Multiplex signal disentanglement via multi-timescale perceptions

Animals must be responsive to information that changes locally as well as broader environmental shifts. Both local short-term and broader longer-term information inform the next behavioral choice through shifts in the decision context. Animals sample their landscape from a single position per unit time. Discerning whether a perceived change stems from updated positioning or broader environmental shifts is straightforward when the stimuli are relatively steady (unchanging with time) as the animal samples the space. When the landscape itself changes with time at nearly the same temporal scale that the animal samples its surroundings, disentangling self-guided and external factor contributions to perceived shifts in environmental context is less straightforward.

Distinguishing local versus larger-scale change is relatively straightforward from a Eulerian (outside human observer) point-of-view compared to the Lagrangian perspective of an individual limited in sensory range and to a single sample per unit time. Multiple perceptions operating at different timescales can disentangle environmental factors occurring at more than one spatiotemporal scale using only a single sample per unit time. In our approach, the animal serially samples its local surroundings once per unit time but can generate one or more parallel images of the environment at different spatiotemporal scales by tracking serial samples with multiple concurrent habituations (memories). Multiple memories, or habituations, encode information that the animal can later use to discern perceived environmental shifts at different spatiotemporal scales.

The notion of multiple timescales is not new (**Table 1**). Existing theory already suggests that animals integrate fluctuating sensory cues over multiple timescales relevant to the temporal features of their environment. Multiple integrations or memory timescales, such as in habituation, are frequently categorized as short- and long-term (**Table 1**). Shorter forms may be as fast as hundreds of milliseconds (Szyszka et al., 2012) and longer forms as slow as days (Sharpless and Jasper, 1956).

In behavioral analyses, multiple memory streams are a powerful means to account for the tracking of time-varying information (**Table 1**). While questions remain regarding the specific relationship between short- and long-term memory processes (McGaugh, 2000), it is generally recognized that slower-updating (longer-term) and faster-updating (shorter-term) memories can coexist (Bernacchia et al., 2011; Murray et al., 2014; Iigaya et al., 2019).

We expand Equation 3 to now include two timescales of integration for cognitively tracking long-term (slower) and short-term (faster) habituations to a stimulus i, denoted as $I_{a_i}^{slow}$ and $I_{a_i}^{fast}$, respectively:

$$I_{a_i}^{slow}\,(t)\ =\ \left(1 - m_{a_i}^{slow}\right) \cdot I_i\,(t)\ +\ m_{a_i}^{slow} \cdot I_{a_i}^{slow}\,(t-1) \tag{8}$$

$$I_{a_i}^{fast}\,(t)\ =\ \left(1 - m_{a_i}^{fast}\right) \cdot I_i\,(t)\ +\ m_{a_i}^{fast} \cdot I_{a_i}^{fast}\,(t-1) \tag{9}$$

with the memory values $m_{a_i}^{slow} \gg m_{a_i}^{fast}$ bound within the range of [0, 1], where superscript *slow* indicates the quantity updates at a slower rate since a larger m value more heavily weighs the past. We treat timescale integration (memory) parameters $m_{a_i}^{slow}$ and $m_{a_i}^{fast}$ as fixed but, in reality, they could themselves be context-dependent.

The dual timescale approach is a simple computational method for encapsulating the notion of multiple timescales that, in reality, are complex neural phenomena (Thompson, 2009; Bi and Zhou, 2020; Shen et al., 2020; Spitmaan et al., 2020). Two timescales of integration allow an individual with serial sampling of the landscape or waterscape to disentangle dual overlapping contexts occurring simultaneously; for example, detecting a spatial gradient amid rapid time-varying changes while immersed in a media that itself is moving, such as water.

The material discussed thus far does not stem primarily from fish or the aquatic realm and, therefore, is likely applicable to movement ecology questions in terrestrial, avian, and subterranean environments. Next, we describe the details of our tidal river salmon study before revisiting the general cognition characteristics tailored specifically to our analysis. Note that, at field scale, it is not yet possible to disentangle the relative contributions of all the potential abiotic and biotic factors that might be responsible for observed salmon movement. Therefore, our notion of *cognition* likely inadvertently encapsulates other factors that influence a fish's hydrodynamic response such as physiological condition, internal or bioenergetic state, change in risk disposition, etc.

3. Tidal river salmon movement behavior

In this section, we introduce the diverse and time-varying river conditions of our tidal system and the data available. Then, we describe the details of our cognitive approach to mechanistic behavior modeling tailored specifically to interpreting and predicting salmon movement and passage/entrainment.

3.1. California's Bay-Delta

The Sacramento-San Joaquin Rivers Delta that, together with San Francisco Bay, is often referred to as California's Bay-Delta supplies drinking water to 27 million people, fuels a $32 billion agricultural industry, and is habitat for more than 750 animal and plant species (California Department of Water Resources, 2022). The tidally influenced Sacramento River bifurcation at Georgiana Slough in Walnut Grove (**Figures 1**, **2**) is part of the managed water supply system. A management goal at the bifurcation is to direct juvenile salmon so their movement continues downriver using the Sacramento River, which leads more directly to the Pacific Ocean where these fish mature to adults. Salmon migrating through the alternate route, Georgiana Slough, take a longer path to the ocean that may also be associated with reduced survival probability (Perry et al., 2018).

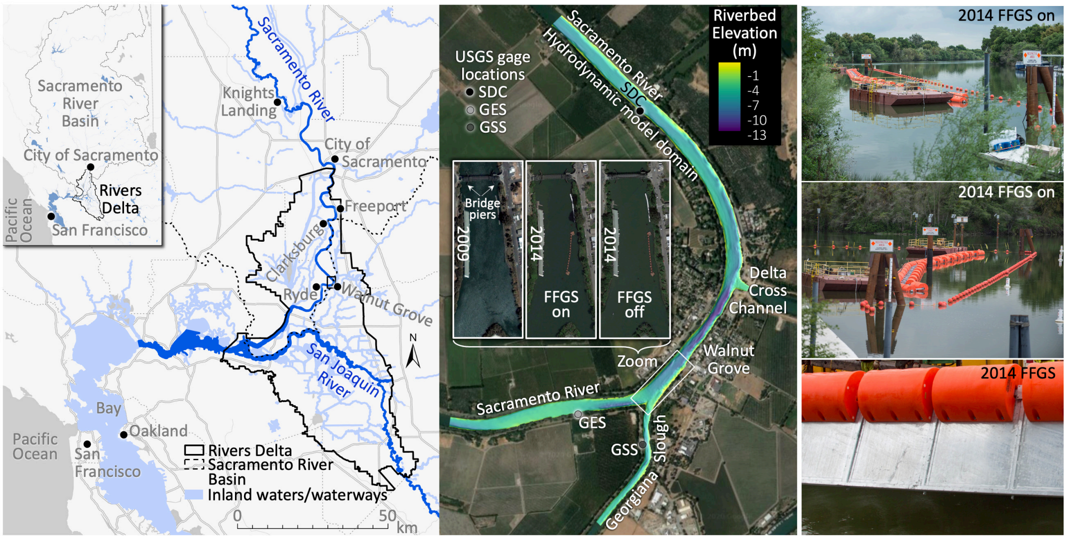


FIGURE 1

The Sacramento River reach between the Delta Cross Channel and Georgiana Slough in Walnut Grove, California used for our analysis is located between river miles 26 and 28. The reach is located between the cities of Sacramento and San Francisco within the Sacramento-San Joaquin Rivers Delta **(left panels)**. The floating fish guidance structure or surface guidance boom (FFGS) is deployed only during year 2014 (**middle** and **right panels**). FFGS field photo credit: California Department of Water Resources. Bathymetry data: U.S. Geological Survey, California Water Science Center. Map data: Google, Maxar Technologies, U.S. Geological Survey, USDA Farm Service Agency.

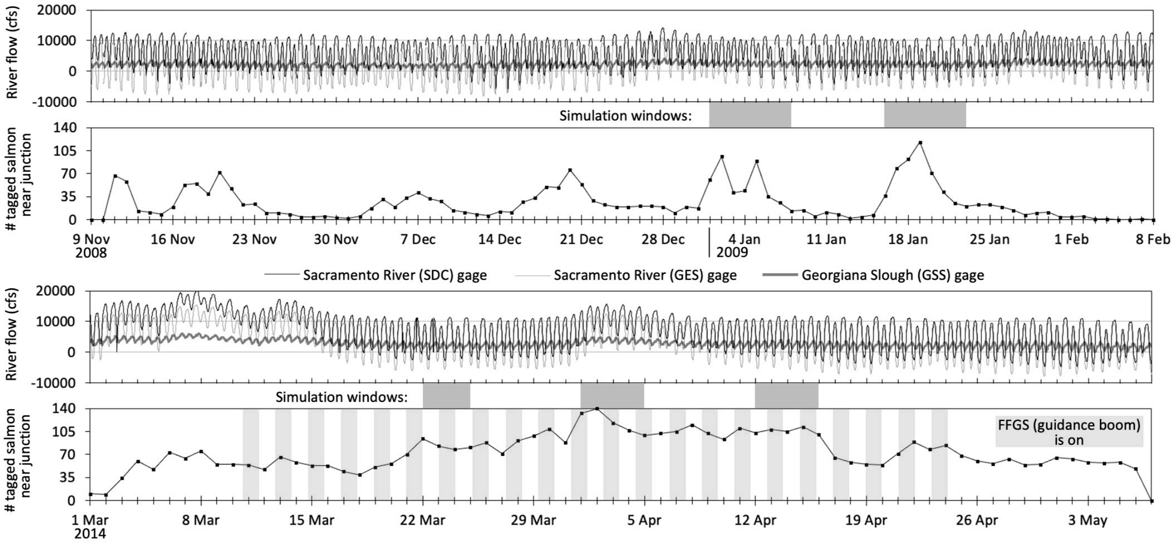


FIGURE 2

The tidally influenced flow of the Sacramento River bifurcation at Georgiana Slough during the 2008–2009 and 2014 studies. Negative river flows move upriver away from the ocean. The graph of tagged salmon counts from acoustic-tag telemetry (Romine et al., 2013, 2017; California Department of Water Resources, 2016) depicts the number of unique individuals observed at the junction with at least four consecutive detections within a day. Our analysis timeframes, or simulation windows (darker grayed blocks), correspond to the dates with the largest number of tagged salmon observed near the junction. FFGS is the floating fish guidance structure or surface guidance boom (**Figure 1**). Flow gage locations (SDC, GES, GSS) shown in **Figure 1**. cfs is cubic feet per second. Gage flow data from the U.S. Geological Survey (2020).

We use salmon acoustic-tag telemetry and hydrodynamic data from the Sacramento River between the Delta Cross Channel and Georgiana Slough to better understand and predict the stimuli-response behaviors of the fish that result in their ultimate fate (passage, entrainment) and movement patterns. We use data within five analysis or simulation windows (**Figure 2** and **Table 2**) from two field study seasons. We use year 2009 data (two windows: 1–7 and 16–22 January) to fully build and parameterize the fish behavior model. Later, we then apply the model without any modification to year 2014 flow conditions that include a novel surface guidance boom (three windows: 22–24 March, 1–4 and 12–15 April) to assess predictive performance on out-of-sample data.

3.1.1. Salmon field data details

The fish used in the 2008–2009 and 2014 studies are juvenile late fall-run Chinook salmon obtained from the Coleman National Fish Hatchery operated by the US Fish and Wildlife Service. The mean fork length of the 3,551 tagged salmon in 2008–2009 is 149.9 mm (Romine et al., 2013), and in year 2014 the average is 157 mm with a range of $109 - 213$ mm across the 5,461 individuals with acoustic transmitters (California Department of Water Resources, 2016; Romine et al., 2017).

Of the 3,551 tagged salmon in 2008–2009, 1,772 (49.9%) are released downriver of the Georgiana Slough junction with the Sacramento River; specifically, 690 downriver in Ryde in the Sacramento River (river mile 24) and 1,082 in Georgiana Slough (**Figure 1**). All other tagged salmon are released upriver approximately 53 km (33 miles) in the City of Sacramento at the Tower Bridge (river mile 59). In year 2014, 826 of the 5,461 tagged salmon (15.1%) are released in Georgiana Slough approximately 5 km (3 miles) downriver of the junction with the Sacramento River, and all others are released upriver in the City of Sacramento.

We filter out the following tag detections:

- known predator tags as well as tagged salmon that at any point during their observation are assigned a predator probability greater than or equal to 0.85 in the range [0, 1] based on previous work by Romine et al. (2014), where 1.0 suggests a predator and 0.0 a salmon. Some tagged individuals are released as known predators, and any fish released dead is classified as a predator. All fish released into Georgiana Slough during the 2008–2009 study and later observed near the junction are assumed to be predators (Romine et al., 2014). One predator during the 2008–2009 study ate five tagged salmon, and these tags are classified as predator;
- spatial positioning errors greater than 10 m. Georgiana Slough is only about 45 m wide near the junction;
- consecutive tag detections less than 2 s apart in order to sample the telemetry data as analogous as possible to the time step of modeled salmon described later;
- consecutive tag detections that would require a speed over ground greater than 2.5 m s^{-1}, a threshold cutoff slightly stricter than would be calculated (2.65 m s^{-1}) by combining the maximum water speed during our simulation windows of about 0.65 m s^{-1} (from the hydrodynamic modeling described later) and a generic $200 -$ mm fish with a short-duration *burst* swim speed of 2 m s^{-1} or 10 *body lengths per second* (Beamish, 1978).

3.1.2. Salmon movement patterns

Tagged salmon in the Sacramento River exhibit several distinct movement modes. We classify every tagged salmon path in the Sacramento River reach between the Delta Cross Channel and Georgiana Slough during our simulation windows using visual inspection according to the following predominant patterns (**Figure 3**):

(1) direct path — no milling or zig-zag movements greater than 1/3 of the river's width;

(2) zig-zagging — at least one cross-stream excursion sustained for more than 1/3 of the river's width. Path can include brief, intermittent milling and/or shoreline movement but no appreciable double-backing within the reach between the Delta Cross Channel and Georgiana Slough;

(3) reach milling — milling predominant throughout the reach between the Delta Cross Channel and Georgiana Slough;

(4) pier milling — distinct milling near the Walnut Grove Bridge piers;

(5) riverbank — movement and milling predominantly near the riverbank;

(6) mode combination — combination of two or more of (1) direct path, (2) zig-zagging, (3–4) milling, and (5) riverbank;

(7) unclassified — mode not readily classifiable, typically because the swim path has few detections, spatial gaps in key areas, a massive number of detections in a small area that persist for a while, or does not span the majority of the reach between the Delta Cross Channel and Georgiana Slough. Tag detections in the upriver portion of the reach during 2014 have, at times, more gaps and imperfections than 2008–2009 data, resulting in more contributions to this class.

Tagged fish released downriver of the junction may not swim upriver into the Sacramento River as far as the Delta Cross Channel during our simulation windows and, thus, often contribute to the unclassified count. Our classifications are analogous to those developed independently in prior work by the U.S. Geological Survey in a turning point analysis of the tagged fish; see page 3–215 of California Department of Water Resources (2016).

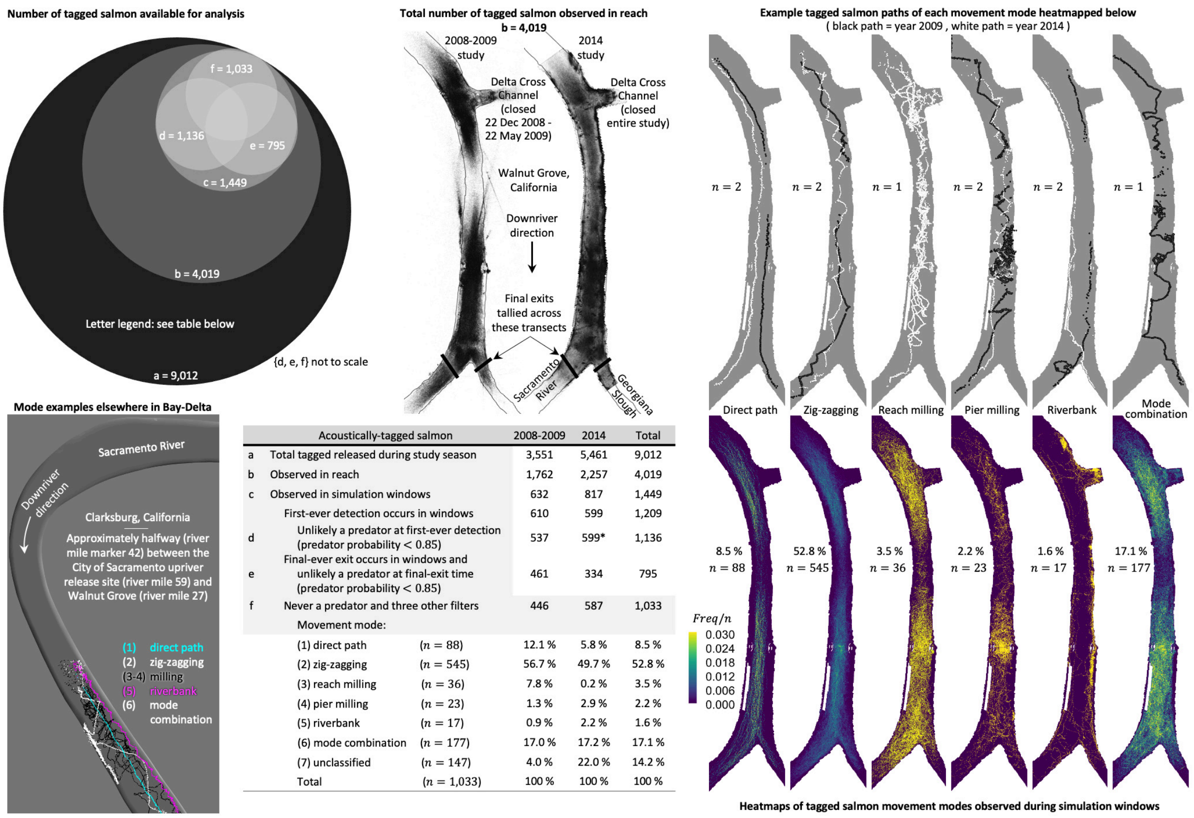
Heatmaps of the movement modes (**Figure 3**) illustrate the pattern of all mode-classified tagged salmon. A heatmap is the number (frequency, *Freq*) of unique individuals visiting a $1 - $m square grid cell filling the domain, normalized by the total tagged salmon in the movement mode category (*n* in **Figure 3**). Only detected tag positions are heatmapped, that is, paths are not implied from the position sequence.

Zig-zagging is, by far, the predominant movement mode in the Sacramento River reach between the Delta Cross Channel and Georgiana Slough in Walnut Grove. Salmon zig-zagging is not unique, however, to the Walnut Grove reach in the Bay-Delta. Zig-zagging and other movement modes are also observed upriver in Clarksburg (Dinehart and Burau, 2005) about halfway between the City of Sacramento release site and Walnut Grove (**Figures 1**, **3**).

TABLE 2 Tagged salmon data in analysis.

Date	Number of tagged salmon			
	First detected during simulation window	Permanently pass/exit (entrained) downriver during simulation window		
		Total exits (%: total exits/first detections)	Georgiana Slough (% of exits)	Sacramento River (% of exits)
Jan	2009			
1	56	40	8	32
2	75	62	21	41
3	20	20	5	15
4	24	22	7	15
5	67	60	14	46
6	10	12	4	8
7	9	10	2	8
Total	261	226	61	165
		(86.6 %)	(27.0 %)	(73.0 %)
16	32	21	9	12
17	64	46	10	36
18	62	45	13	32
19	76	64	19	45
20	28	35	14	21
21	10	15	5	10
22	4	9	2	7
Total	276	235	72	163
		(85.1 %)	(30.6 %)	(69.4 %)
Mar	2014			
22	53	21	8	13
23	49	22	6	16
24	40	18	2	16
Total	142	61	16	45
		(43.0 %)	(26.2 %)	(73.8 %)
Apr				
1	87	39	5	34
2	74	41	8	33
3	67	35	5	30
4	53	29	5	24
Total	281	144	23	121
		(51.2 %)	(16.0 %)	(84.0 %)
12	42	27	10	17
13	41	31	6	25
14	47	27	5	22
15	46	44	6	38
Total	176	129	27	102
		(73.3 %)	(20.9 %)	(79.1 %)

A single salmon exhibiting more than one movement mode in a short period of time can be observed in two examples within Figure 3. First, just upriver of Georgiana Slough (Figure 3, upper right) a salmon alternates between zig-zagging, pier milling, and the riverbank movement modes. Second, upriver, a salmon can be seen zig-zagging, transitioning to a riverbank mode, and then back again to zig-zagging (Figure 3 inset of Clarksburg, California—white fish trajectory).



	Acoustically-tagged salmon		2008-2009	2014	Total
a	Total tagged released during study season		3,551	5,461	9,012
b	Observed in reach		1,762	2,257	4,019
c	Observed in simulation windows		632	817	1,449
	First-ever detection occurs in windows		610	599	1,209
d	Unlikely a predator at first-ever detection (predator probability < 0.85)		537	599*	1,136
e	Final-ever exit occurs in windows and unlikely a predator at final-exit time (predator probability < 0.85)		461	334	795
f	Never a predator and three other filters		446	587	1,033
	Movement mode:				
	(1) direct path	($n = 88$)	12.1 %	5.8 %	8.5 %
	(2) zig-zagging	($n = 545$)	56.7 %	49.7 %	52.8 %
	(3) reach milling	($n = 36$)	7.8 %	0.2 %	3.5 %
	(4) pier milling	($n = 23$)	1.3 %	2.9 %	2.2 %
	(5) riverbank	($n = 17$)	0.9 %	2.2 %	1.6 %
	(6) mode combination	($n = 177$)	17.0 %	17.2 %	17.1 %
	(7) unclassified	($n = 147$)	4.0 %	22.0 %	14.2 %
	Total	($n = 1,033$)	100 %	100 %	100 %

FIGURE 3

Available acoustic-tag telemetry data (**upper-left, upper-middle,** table in **lower-middle**), movement mode heatmaps **(lower-right)**, example tagged salmon swim paths of each mode **(upper-right)**, and the modes exhibited elsewhere in the Bay-Delta **(lower-left)**. Tabulated are the (a) total tagged salmon released during the 2008-2009 and 2014 studies, (b) the number detected in the Sacramento River reach between the Delta Cross Channel and Georgiana Slough, (c) within our simulation windows, and (d–f) unlikely a predator at moments the data is used in our analysis. Heatmaps are computed after removing suspected predators, tag detections with spatial error greater than 10 m, and consecutive positions either less than 2 s apart or require a speed over ground in excess of 2.5 m s^{-1} (f). n equals the total tagged salmon in the movement mode category. Example constituent paths of each movement mode are plotted above the respective heatmap. Movement modes (1)–(6) are observed elsewhere in the Bay-Delta (gray inset) in a supplemental 2014 hydrophone array (California Department of Water Resources, 2016). We assume all tagged fish detected for the first time ever during our 2014 simulation windows are salmon (*) whereas year 2009 predator probabilities are formatted differently and allow us to identify and remove suspected predators at a tag's initial detection (d). We use transects immediately downriver of the junction to determine tagged salmon final exits downriver (e) (**Table 2**) also referred to as passage or entrainment. The Delta Cross Channel is closed during our simulation windows (**Figure 2**).

Habitat refuge, vision (Leander et al., 2021; Müller et al., 2021), and explicit response to spatial structure (Braithwaite and Burt de Perera, 2006; Miles et al., 2023) may play modulating roles in salmon movement. Also, behavioral variation among individuals of the same species is common (Bolnick et al., 2002; Bierbach et al., 2017; Cresci et al., 2018; Campos-Candela et al., 2019; Harrison et al., 2019; Honegger et al., 2020; Bailey et al., 2021; Daniels and Kemp, 2022) as it has distinct survival value (Humphries and Driver, 1970). We do not attempt to disaggregate or prioritize the relative contribution of all internal and external factors. Here, we focus on understanding the predominant zig-zagging swim path pattern and how it with smaller proportions of other movement modes might be hydrodynamically mediated.

3.1.3. Protean movement decisions and optimality

Movement is a behavior that operates within a hierarchy of needs, where predation is a constant threat for prey species. Predation complicates the analyses of behavioral choice in real-world environments because rote responses easily discerned by an outside observer may also be predictable from a predator's perspective. Protean movement in which a prey's path changes frequently, helps evade predators (Humphries and Driver, 1970; Godin, 1997; Richardson et al., 2018). Selective evolutionary pressure suggests that predators exploit repeated fixed patterns of prey (Humphries and Driver, 1970; Domenici et al., 2008), although perhaps not universally (Szopa-Comley and Ioannou, 2022). Peculiarities in observed movement that appear sub-optimal from an outside observer's perspective may be anti-predatory characteristics whereby optimality is realized at the much larger scale of species persistence. It is increasingly recognized that perceptual decision-making at the individual level in natural settings with multiple alternatives is suboptimal (Yeon and Rahnev, 2020).

3.1.4. Zig-zagging

Salmon persist in the "predator-prey arms race" (Humphries and Driver, 1970; Kelley and Magurran, 2006) of California's Bay-Delta, which suggests that they may have an anti-predatory characteristic to their downriver navigation strategy. When visual cues are limited underwater, zig-zagging keeps a prey's average position within the river channel unpredictable from the perspective of an immersed predator (Humphries and Driver, 1970). Prey zig-zagging is a protean movement pattern often thought to occur in small arenas where it lowers a predator's targeting accuracy (Furuichi, 2002; Jones et al., 2011; Richardson et al., 2018; Gazzola et al., 2021), however, juvenile salmon zig-zag also in the large spatial domains of dammed reservoirs; see telemetry data references in the supporting information appendix of Goodwin et al. (2014).

3.2. Fish movement behavior and hydrodynamics

3.2.1. Determining fish movement behavior starting with particles and particle tracking

To understand the relationship between salmon movement and hydrodynamics, we must first understand how the river environment itself is described and the assumptions that are involved. Water flow is described by the Navier–Stokes equations but conceptualizing a river's advective contribution to a fish's displacement in space (x, y, z Cartesian coordinate positions) is not trivial, especially when hydrodynamics changes with time and location.

The movement of an 'active' particle that is moving under its own motivation contributes volitionally to its spatial position (Patlak, 1953; Siniff and Jessen, 1969; Kareiva and Shigesada, 1983), e.g., a fish locating within a river via swimming. In water, the change in spatial position of a swimming fish can be described mathematically between time step t and $t + 1$ as follows:

$$x(t+1) = x(t) + (u + u_{volitional}) \cdot \Delta t$$

$$y(t+1) = y(t) + (v + v_{volitional}) \cdot \Delta t$$

$$z(t+1) = z(t) + (w + w_{volitional}) \cdot \Delta t \tag{10}$$

where x, y, and z are the individual's spatial position (m), u, v, and w are the water velocity vectors (m s^{-1}), $u_{volitional}$, $v_{volitional}$, and $w_{volitional}$ are the volitional contribution from swimming (m s^{-1}), and Δt is the time step increment (s).

A fish that does nothing (no volitional movement) is transported by the surrounding water flow while, in contrast, an individual with an unbiased, uncorrelated random walk within a non-advective environment such as a static lake typically exhibits some form of diffusion in its location over time. In an advective environment, such as a river or estuary, the diffusive property of a random walk can be appreciably altered by the advection.

In general terms, the movement path of a volitional random walk is stretched in the direction of the water flowline and the degree to which this happens depends on the strength and complexity of flow (river hydrodynamics). A "passive" particle that is neutrally buoyant and massless will follow the water flowline and provides a means to conceptualize and mathematically determine the contribution of physical water flow to an entity's movement (displacement) in a river. The movement of a simulated passive particle, however, depends inherently on the accuracy and spatiotemporal resolution of the available water flow data (Déjeans et al., 2022). Therefore, determining an entity's volitional movement behavior (which equals the measured total movement minus what a passive particle would do) depends also on the accuracy and spatiotemporal resolution of the available water flow data. As there are numerous methods for describing hydrodynamics within a river, with different tradeoffs, we provide a brief synopsis before describing the stimuli that we use in our analysis.

3.2.2. Describing river hydrodynamics via numerical modeling and measurement

Fish in rivers experience turbulence that may be thought of as water flow composed of a wide continuum of eddy sizes where larger eddies spawn smaller ones, passing on kinetic energy, down to the scale where viscous forces dampen or dissipate the phenomenon (Tritico and Cotel, 2010; Rodi, 2017; Crowley et al., 2022). In rivers, where width is often much larger than depth, the eddy size continuum has two ranges. Smaller-scale motions are fairly random whereas larger fluctuations interact with the mean flow and often have some order and correlated pattern (coherent structures). In each range, the largest eddies that contain the most energy are limited by the size of the river dimension (Rodi, 2017).

The straightforward approach to simulating the Navier–Stokes equations in order to describe river water flow dynamics is direct numerical simulation or DNS (Orszag and Patterson, 1972; Moin and Mahesh, 1998). DNS does not require any model assumptions and accounts for fluid phenomena across the many spatiotemporal scales relevant to fish, down to the smallest dissipation scale. DNS simulation of river flow, however, is impractical with present-day computing. For instance, a relatively low energy water domain just 0.1 m deep moving slowly at 0.1 m s^{-1} requires approximately one billion computational mesh points (Keylock et al., 2005), and the required grid size grows quickly with increasing flow complexity and energy. All other approaches to the Navier–Stokes equations involve approximating their full complexity (Keylock et al., 2012).

There are numerous approaches to modeling river hydrodynamics, and every method involves tradeoffs (Lane et al., 1999; Keylock et al., 2012; Rodi, 2017; Robinson et al., 2019; Brunner et al., 2020). A simple way to gain information about the time-varying nature of hydrodynamics is an unsteady Reynolds averaged Navier–Stokes (RANS) approach where motions and variations in the mean flow field account for eddy-shedding at scales greater than the integral timescale (Keylock et al., 2005). RANS renders a smoothed, or averaged, version of the water flow field and, presently, is a common workhorse of river hydrodynamic modeling.

An intermediate approach between DNS and RANS (Rodi, 2017) is large eddy simulation or LES (Smagorinsky, 1963; Bedford and Babajimopoulos, 1980; Mahesh et al., 2004; Khosronejad et al., 2016, 2020; Le et al., 2019; Flora, 2021; Flora and Khosronejad, 2021, 2022). LES resolves eddy phenomena larger than a given filter scale, not just above the integral timescale as in unsteady RANS (Keylock et al., 2005). LES resolves eddies down to the mesh element size, and smaller scale phenomena are approximated with a subgrid-scale model (Keylock et al., 2012; Rodi, 2017).

LES is more sensitive to the treatment of the river's boundary conditions than RANS (Rodi, 2017), which is one reason why hybrid LES-RANS approaches have emerged such as detached eddy simulation or DES (Spalart and Allmaras, 1992; Spalart et al., 1997; Constantinescu et al., 2011a; Keylock et al., 2012). LES and DES require more nodes and are more computationally expensive than RANS. The river flow field described by LES or DES is closer to what a fish experiences (**Figure 4**), but the temporal sequence of LES or DES outputs can be challenging to synchronize with a specific calendar date-time. In other words, it is not straightforward to determine whether an ephemeral eddy feature of interest from LES or DES occurred before, during, or after a measured fish passed through that part of the river.

For most rivers, water depth is shallow relative to width so the vertical acceleration is negligible compared to gravitational acceleration (Lai, 2010). In shallow water situations, the Navier–Stokes equations can be vertically averaged (Rodi, 2017). Two-dimensional, depth-averaged modeling of the Navier–Stokes equations provides the next level of accuracy when 3-D is not required, and the approach is practical for many river applications with a more typical desktop computer. 2-D depth-averaged approaches require considerably less computational resources. Numerous modeling approaches occupy the spectrum between RANS and simpler 2-D and 1-D methods, often covering much larger spatial domains (Zhang et al., 2016; Savant et al., 2018; Robinson et al., 2019; Brunner et al., 2020).

The selection of hydrodynamic model involves accounting for whether the additional required resources are balanced by the needed improvements in predictive ability and utility (Lane et al., 1999; Lai, 2010; Robinson et al., 2019; Brunner et al., 2020). The field of hydrodynamic modeling continues to rapidly evolve, and emerging methods such as *physics-informed neural networks* (Karniadakis et al., 2021; Kochkov et al., 2021) and other forms of machine learning (Margenberg et al., 2022; Vinuesa and Brunton, 2022; Zhang et al., 2022) are expanding the viable approaches.

Generally, one can measure river hydrodynamics at finer spatiotemporal scales than modeling can render them, but at the expense of spatial coverage (**Figure 4**). Acoustic Doppler velocimeters (ADVs) measure water velocity many times a second at a single point. Acoustic current profilers now commonly referred to as acoustic Doppler current profilers or ADCPs (Muste et al., 2004; Dinehart and Burau, 2005) measure the flow field many times a second at multiple distance intervals from the aimed instrument and are often able to span much of a river's width or depth. Particle image velocimetry or PIV (Soo et al., 1959; Adrian, 2005; Tritico et al., 2007) and large-scale particle image velocimetry or LSPIV (Fujita, 1997; Fujita et al., 1998; Muste et al., 2008) measure instantaneous velocities in a 2-D plane using tracers present in the flow. Infrared quantitative image velocimetry or IR-QIV (Schweitzer and Cowen, 2021) measures instantaneous velocities at the 2-D water surface without tracers or illumination and can be used both day and night. A continuing active area of research is developing methods to estimate 3-D subsurface hydrodynamics from river-wide measurements at the water surface (Johnson and Cowen, 2016, 2017a,b, 2020). Increasing the spatial coverage of river measurements can be accomplished by deploying multiple instruments or, in some cases, moving the instruments to capture different flow field regions.

To date, no measurement or modeling technique can accurately describe hydrodynamics down to the finest scale that fish detect throughout a 3-D river reach. We use field measurements of the river's flow and bathymetry to build and validate a RANS model of the time-varying 3-D hydrodynamics for year 2009 (Lai, 2000; Lai et al., 2003, 2017). Later, for year 2014, we use a 2-D depth-averaged model (Lai, 2010). For both models, we output river hydrodynamics at $3-min$ intervals because the water flow field at the junction of the Sacramento River and Georgiana Slough can change noticeably within a few minutes and frequently reverses direction (**Figure 2**). Our 3-D RANS and 2-D depth-averaged model mesh domains (**Figure 1**, middle plot) are approximately 550,000 and 50,000 vertices, respectively, for each $3-min$ time increment.

3.2.3. Eulerian-Lagrangian-agent method (ELAM)

River hydrodynamics output from our 3-D RANS and 2-D depth-averaged modeling determines the river's advective contribution (u, v, and w water velocity vectors) to the fish's spatial displacement during an increment of time (Equation 10). To compute the fish's volitional swimming contribution to its own displacement, we must first gain an understanding of the stimuli available to our modeling that can influence its behavior. Then, we must determine how the multiple available competing and simultaneous stimuli may be perceived at a moment in time by the animal and inform a repertoire of evolved behaviors that mathematically result in a movement response behavior, specifically, a 3-D orientation and speed ($u_{volitional}$, $v_{volitional}$, and $w_{volitional}$).

Fish are simulated as an "active" particle within our hydrodynamic model grid. A 3-D fish orientation and speed ($u_{volitional}$, $v_{volitional}$, and $w_{volitional}$) together with the u, v, and w water velocity vectors from the hydrodynamic model complete Equation 10 and allow us to update the fish's spatial displacement each time increment.

We employ an Eulerian-Lagrangian-agent method (ELAM) to conceptually understand the movement behavior of salmon by mathematically resolving the differences between passive particle and tagged fish movement path and passage/entrainment patterns (Goodwin, 2004; Goodwin et al., 2006, 2014). The ELAM acronym stems from the constituent numerical frameworks involved (**Figure 5**):

- Eulerian — computational mesh (static or time-varying 2-D or 3-D) composed of nodes used to describe the environmental domain;
- Lagrangian — continuous directional trajectory composed of computationally discrete locations used to describe individual movement trajectories and directional sensory perception;
- agent — algorithm ensemble used to describe the behavioral cognitive decision-making of animals.

We simulate each salmon individually in order to gain their Lagrangian perspective. Each individual has agent-based perceptual responses to the Eulerian-meshed river hydrodynamics. A sensory ovoid around each simulated salmon (**Figure 5**), described in detail later, limits the spatial extent of stimulus information available for making movement decisions. Simulated

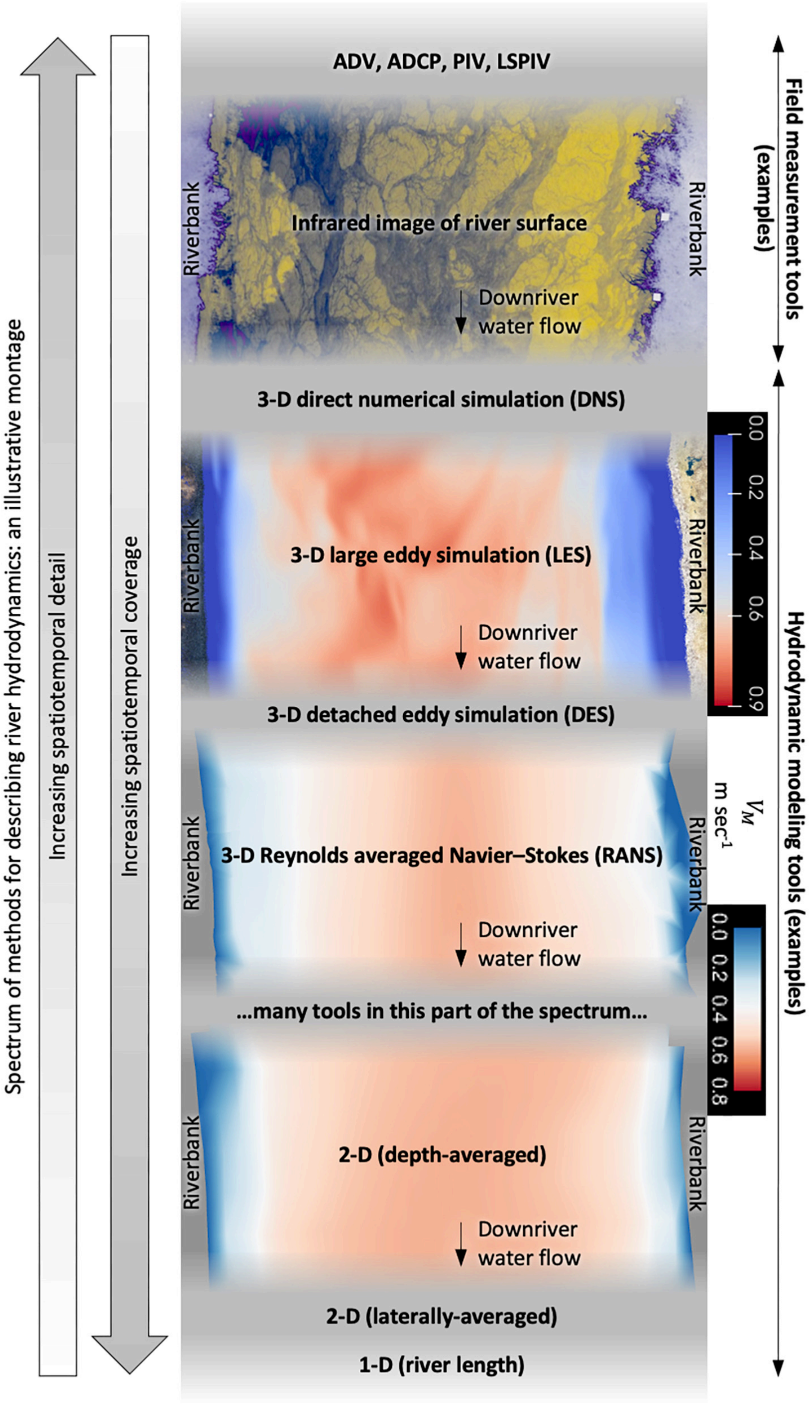


FIGURE 4

Rivers have more hydrodynamic heterogeneity than can be readily captured by any single measurement device or computational model. Here, we use a conceptual montage to illustrate some of the general tradeoffs in spatiotemporal detail vs coverage associated with different approaches to measuring/modeling river hydrodynamics. The fidelity of hydrodynamic information available influences the factors attributed to 3-D/2-D fish movement trajectories and behavior. Water flow heterogeneity within a river at the surface can be measured in detail via an infrared camera that reflects underlying hydrodynamic phenomena, illustrated here near Sacramento River mile 34 in Sutter Slough (courtesy of Seth Schweitzer; Schweitzer and Cowen (2021)). Water flow heterogeneity can also be modeled in great 3-D detail throughout the river column using LES, illustrated here near Sacramento River mile 89.5 (courtesy of Kevin Flora; Flora and Khosronejad (2022)). Describing river hydrodynamics with infrared quantitative image velocimetry (IR-QIV, Schweitzer and Cowen (2021)) or LES (Khosronejad et al., 2016; Flora and Khosronejad, 2022) provides more spatiotemporal detail than is possible using the 3-D RANS or 2-D depth-averaged methods in our study. In 3-D LES and RANS modeling, the hydrodynamic variable values are provided explicitly at multiple depths whereas 2-D depth-averaged models provide only a single value for each horizontal (*xy*-plane) location. However, RANS and even 2-D models render more spatial heterogeneity than other, courser forms of hydrodynamic modeling. The 3-D RANS and 2-D depth-averaged illustrations of the river flow field here are of similar conditions in the Sacramento River near mile 27 between the Delta Cross Channel and Georgiana Slough upriver of the bridge piers. ADV is an acoustic Doppler velocimeter; ADCP is an acoustic current profiler now commonly referred to as an acoustic Doppler current profiler; PIV is particle image velocimetry; LSPIV is large-scale particle image velocimetry.

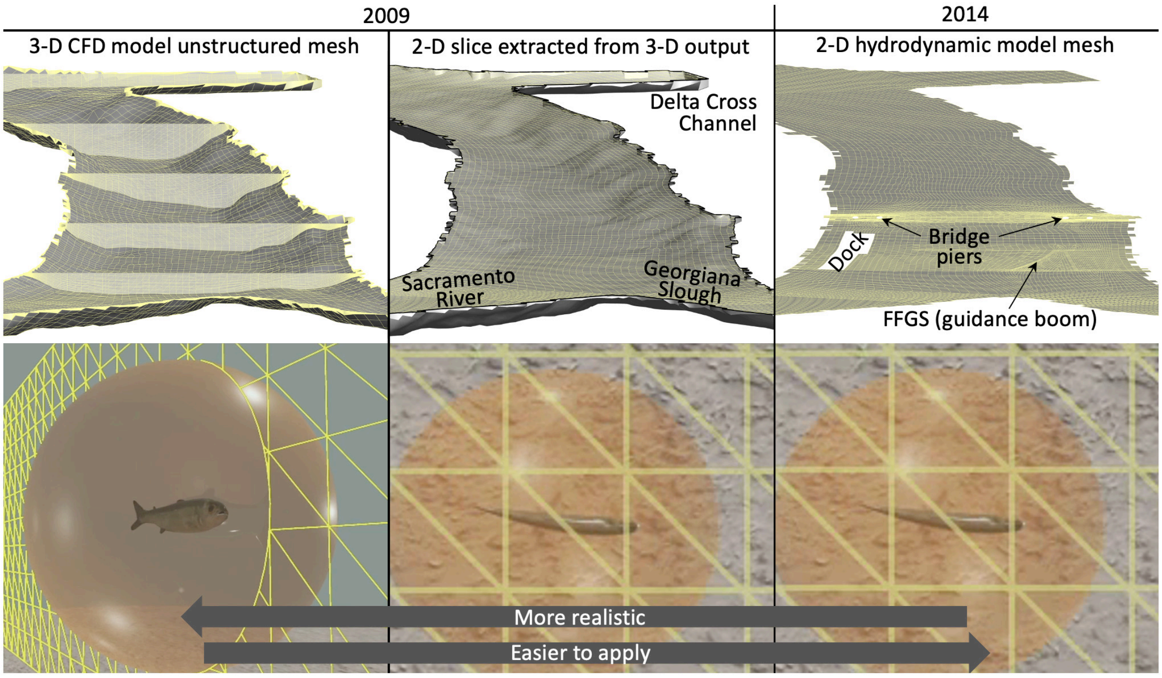


FIGURE 5
To implement our cognitive approach to mechanistic salmon movement behavior modeling we use a numerical scheme called the Eulerian-Lagrangian-agent method, or ELAM. We use three different forms of river hydrodynamic model mesh output: explicit 3-D hydrodynamics **(left panels)**, 2-D *xy*-plane horizontal slice extractions from just under the water surface for each output in the original 3-D flow field time series **(middle panels)**, and 2-D depth-averaged water flow fields **(right panels)**. In the 2-D analyses (**middle** and **right panels**), both the vertical *z*-coordinate (depth-oriented) hydrodynamics and fish swim orientation/speed are eliminated. No 3-D model is used for year 2014. Only a 2-D depth-averaged river hydrodynamic model is available for year 2014 ELAM simulations. A sensory ovoid **(lower panels)** around each simulated salmon limits the spatial extent of stimulus information available for making movement decisions.

fish neither have global information nor know downriver from upriver.

In our study, the agent framework encodes our cognitive representation of a salmon's perceived local hydrodynamic environment and resulting behavioral choices. Fish movement decisions (agent framework) are composed of a swim orientation and speed (Lagrangian framework) implemented in the spatial mesh data output from the hydrodynamic model (Eulerian framework).

3.2.4. ELAM model development and parameterization

To build a hypothesis for the salmon's behavior repertoire, we identify possible strategic and tactical solutions (Anderson, 2002) that individuals of the population may have evolved over time to confront common and critical challenges in order to survive and persist. Behavioral choice observed in one setting may not be relevant to a repeat encounter. Identifying the motivation of animals is an unavoidably subjective exercise with present technology yet important for understanding which modalities may inform a specific movement decision, how their behavior will vary with context, and for extrapolating existing observations to make predictions in other environmental conditions (Mann, 2018, 2020).

We use a systematic, manual exploratory process to develop and parameterize the behavior repertoire. We start by overlaying the time-dynamic environment with fish movement trajectories. Separate, but related, we also plot each trajectory in its entirety atop the most representative water flow condition. The two overlays are then viewed many times repeatedly, leveraging human visual acuity and intuition. The goal of the initial exploratory process is to find and discern repeated movement patterns — and changes in movement patterns — that cannot be readily explained with how passive particles move. The manual process takes time. Ever-maturing tools are getting better at automating the identification of trajectory patterns and change phenomena (Romine et al., 2014; Gurarie et al., 2017; Vilk et al., 2022). However, we find that to date automated methods cannot yet fully match the performance of human visual acuity and intuition. One reason is that key patterns we find useful for discerning a behavior repertoire are obvious only in the context of — that is, contrasted with — movement dynamics that happen elsewhere either spatially in the domain or in time within the available data.

Unfortunately, we find that key movement patterns and attributes (e.g., changes in swim path orientations) are rarely evident at first and emerge to the human eye/intuition after gaining a gist of the movement patterns and changes. Complicating the process of identifying key patterns and changes is that one must keep in mind the underlying hydrodynamics and what passive particles would do. In rivers, hydrodynamics can vary quickly in both space and time.

An observed real-world fish movement pattern (or change) may have a place in the behavior repertoire if it occurs analogously among multiple individuals. We often observe patterned phenomena of interest to our analysis where hydrodynamic features are more complex. A pattern or change may not have a place in the repertoire if the trajectory could be attributed to inherent animal movement stochasticity, observed in very few individuals, or not coincident with any nearby rendered environmental feature. More complicated is when water flow pattern changes in time, switching from identifiable hydrodynamic features at one moment to perhaps none at all, for instance, during slack tide; in such circumstances, movement pattern changes might be related to the temporal and not spatial domain. Further complicating the process, but where manual acuity and intuition are helpful, is when patterns are obscured by imperfect real-world sampling of the trajectory, common in the aquatic realm. Despite the above challenges, we anticipate that tools in the near-future will automate the present manual process in a way that is more on par with human visual acuity and intuition.

After key distinct patterns are discerned within the trajectory data, typically about a half-dozen, trial-and-error exploration commences whereby one pattern or change is selected and work begins to reproduce that phenomenon using the available environmental data. Once successful, a scaffolding process begins whereby the next distinct pattern or change is reproduced whilst not losing the model's ability to also reproduce the first behavior phenomenon. Each addition to the model's behavior repertoire typically involves nuancing the algorithms and parameterization of already-described phenomenon. The exploratory model development process ends with a behavior repertoire, algorithms, and parameterization when all of the identified trajectory pattern and change phenomena can be reproduced with a single structure.

We use prior ELAM model findings as a starting point and guide (Goodwin, 2004; Goodwin et al., 2006, 2014) for how hydrodynamic stimuli might relate to fish movement patterns and changes. We also leverage findings — both old and new — from fish-flow research (**Tables 1, 3**). In this study, we identify the following four movement patterns and changes in the 2009 data that, once reproduced via simulation, result in the fully developed and parameterized version of the ELAM model described herein:

- a salmon changing its zig-zag within the Sacramento River in front of the Delta Cross Channel junction during relatively steady (unchanging with time) ebb tide flow, suggesting the riverbank per se may not explicitly be solely responsible for the swim path re-orientation pattern;
- nine salmon near-concurrently zig-zagging within the Sacramento River with little-to-no milling in the reach from the Delta Cross Channel to downriver of the Georgiana Slough junction during relatively steady ebb tide flow, in which both flow and fish continue primarily via the Sacramento River;
- two salmon milling, in part, with zig-zag movements during relatively slow flood tide flow, one in the thalweg near the bridge piers and, at the same time, the other along the Sacramento River bank opposite the Delta Cross Channel;
- two salmon milling, in part, with zig-zag movements during relatively slow ebb tide flow into Georgiana Slough, one of the fish in the thalweg just downriver of the Delta Cross Channel junction and the other near the bridge piers that does not enter (e.g., seems to avoid) Georgiana Slough dissimilar from a passive particle. At the same time, two salmon swim upriver

TABLE 3 Candidate hydrodynamic stimuli: abbreviated synopsis of historical and more recent works.

Candidate hydrodynamic stimulus	Fish behavior response
Water velocity gradient	Dijkgraaf, 1963; Royce et al., 1968; Fausch and White, 1981; Kalmijn, 1988, 1989; Fausch, 1993; Fletcher, 1994; Hayes and Jowett, 1994; McLaughlin and Noakes, 1998; Braun and Coombs, 2000; Crowder and Diplas, 2000; Montgomery et al., 2000; Kemp et al., 2003; Goodwin, 2004; Goodwin et al., 2006; Sweeney et al., 2007; Nestler et al., 2008; Russon and Kemp, 2011; Abdelaziz et al., 2013; Vowles et al., 2014; Oteiza et al., 2017; Albayrak et al., 2020; Beck, 2020; Swanson et al., 2020; Zhu L. et al., 2021; Li et al., 2022; Tan et al., 2022; Li et al., 2023
Turbulence	MacKinnon and Hoar, 1953; Pavlov et al., 1982; Pavlov and Tyuryukov, 1993; Pavlov et al., 1995; Skorobogatov et al., 1996; Coutant, 1998; Coutant and Whitney, 2000; Crowder and Diplas, 2000; Pavlov et al., 2000; Cada and Odeh, 2001; Coutant, 2001; Crowder and Diplas, 2002; Enders et al., 2003; Smith, 2003; Lupandin, 2005; Smith et al., 2005; Cotel et al., 2006; Liao, 2006, 2007; Enders et al., 2009b; Tiffan et al., 2009; Tritico and Cotel, 2010; Silva et al., 2011; Lacey et al., 2012; Silva et al., 2012; Abdelaziz et al., 2013; Liao and Cotel, 2013; Smith et al., 2014; Cotel and Webb, 2015; Elder and Coombs, 2015; Gao et al., 2016; Kerr et al., 2016; Kirk et al., 2017; Quaranta et al., 2017; Tan et al., 2018; Kerr and Kemp, 2019; Silva et al., 2020; Zhu et al., 2020; Ben Jebria et al., 2021; Kulić et al., 2021; Lewandoski et al., 2021; Li P. et al., 2021; Prada et al., 2021; Syms et al., 2021; Szabo-Meszaros et al., 2021; Zhu L. et al., 2021; Zielinski et al., 2021; Gisen et al., 2022; Li et al., 2022; Tan et al., 2022; Li et al., 2023; Wiegleb et al., 2023
Relative water velocity/speed	MacKinnon and Hoar, 1953; Brett and Alderdice, 1958; Schwartz, 1974; Montgomery et al., 1997; Standen et al., 2002; Standen et al., 2004; Sweeney et al., 2007; Chagnaud et al., 2008; McElroy et al., 2012; Mussen et al., 2013; Langford et al., 2016; Romine et al., 2021; Gisen et al., 2022; Li et al., 2022; Liao et al., 2022; Maddahi et al., 2022; Tan et al., 2022; Zeng, 2022; Kerr et al., 2023; Li et al., 2023; Renardy et al., 2023
Water acceleration, deceleration, and inertial factors	Jones, 1956; Brett and Alderdice, 1958; von Baumgarten et al., 1971b; Ducharme, 1972; Arnold, 1974; Denton and Gray, 1988, 1989; Kalmijn, 1989; Kroese and Schellart, 1992; Bleckmann, 1994; Pavlov and Tjurjukov, 1995; Haro et al., 1998; Coombs and Montgomery, 1999; Coutant and Whitney, 2000; Johnson et al., 2000; Montgomery et al., 2000; Kanter and Coombs, 2003; Kemp et al., 2005; Liao, 2007; Sweeney et al., 2007; Bleckmann, 2008; Enders et al., 2009a; Johnson et al., 2009; Enders et al., 2012; Chagnaud and Coombs, 2013; McHenry and Liao, 2013; Montgomery et al., 2013; Goodwin et al., 2014; Vowles et al., 2014; Arenas et al., 2015; Gisen et al., 2022; Zeng, 2022; Wiegleb et al., 2023
Water pressure (registered by fish swim bladder)	Moreau, 1876; Jones, 1949, 1951, 1952; McCutcheon, 1966; Alexander, 1982; Coutant and Whitney, 2000; Goodwin, 2004; Strand et al., 2005; Goodwin et al., 2006; Govoni and Forward, 2008; Nestler et al., 2008; Weitkamp, 2008; Brown et al., 2012; Goodwin et al., 2014

in Sacramento River flood flow from downriver of the slough junction and these fish readily enter Georgiana Slough akin to passive particles.

We identify one additional pattern, i.e., two salmon zig-zagging into Georgiana Slough, but are able to reproduce this last example as an emergent outcome of reproducing the previous four examples. The example patterns and changes above are found multiple times in the field telemetry data. Reproducing the above movement patterns via simulation by adding them to the model mix, one by one, is how we develop and parameterize the ELAM in this study.

In due diligence, we rigorously evaluate the model structure and all our parameters that we describe in the coming sections via genetic algorithm and simulated annealing optimization schemes. We evaluate model structure by eliminating (zeroing-out) different components and stochasticity required to initially meet our goal. We also evaluate adding in (activating) stochasticity permissible from the algorithms in our model but not leveraged in the original manual development. Lastly, we explore the model's parameter space to find optima that may have eluded the manual means of development. Optimization schemes result in no further model or performance improvements but remain an area of study. We anticipate that automated methods will be superior in the future, so the exploratory process leading to the model structure described in the following sections can be accomplished faster and cheaper in later works.

3.3. Hydrodynamic stimuli

Identifying variables of the river flow field relevant to fish movement behavior has been an ongoing process for almost a century (**Tables 1**, **3**). Fish have multiple sensory modalities to inform movement (Liao, 2007), and the context-dependencies in multisensory information are important even for the relatively simple case of rheotaxis (Bak-Coleman et al., 2013; Coombs et al., 2020).

Selecting stimuli for analysis is still unavoidably subjective as the metrics available change with measurement scale. Also, hydrodynamic variables are often correlated. Not surprisingly, different hydrodynamic variables have been attributed to fish movement behavior. We select five candidate hydrodynamic stimuli from the literature for evaluation in our study (**Table 3**).

3.3.1. Variable physical quantities

A nerve response in fish can be stimulated with relative flow field currents as small as 0.025 mm s^{-1} (Schwartz, 1974) and water particle movement of less than 0.5 μm (Suckling and Suckling, 1964; Anderson and Enger, 1968; Popper and Carlson, 1998). Fish detect and interact with hydrodynamics at scales far smaller than are rendered in a river reach size RANS model (Borazjani and Sotiropoulos, 2008, 2009, 2010; Windsor et al., 2010a,b; Oteiza et al., 2017; Khan et al., 2022). However, animals also constantly integrate momentary, noisy stimuli sensory evidence over time and space to infer the state of their environment (Bahl and Engert, 2020; Dragomir et al., 2020; DiBenedetto et al., 2022).

We assume fish can generate a hydrodynamic image of its nearby river environment not dissimilar from RANS-level spatiotemporal resolution by integrating sensory experience over time. We do not explicitly account for how a fish upscales minuscule hydrodynamic experiences to form a RANS-level perception of its localized river flow field. However, later, we describe parameterization of Equation 3 that can upscale point measurements of the RANS solution to perceive much larger, bulk flow changes within the river due to the tides. The minuscule-to-RANS and RANS-to-tidal perception upscaling processes could be analogous. Leveraging our assumptions, we formulate candidate stimuli (**Table 3**) using output from our RANS hydrodynamic model.

The spatial gradient of water speed or velocity (magnitude, G_M, s^{-1}) represents the amount of mechanical distortion in the water flow field (Nestler et al., 2008). Mathematically, G_M is computed as the Frobenius or Euclidean norm of the pure normal strain (linear deformation), angular velocity (rotation), and shearing strain (angular deformation) tensors. We compute G_M on the Eulerian mesh of the hydrodynamic model with u, v, and w representing the mean or average water velocity vectors at time t:

$$G_M(t) = \sqrt{\begin{array}{l}\left(\frac{\partial u}{\partial x}\right)^2+\left(\frac{\partial u}{\partial y}\right)^2+\left(\frac{\partial u}{\partial z}\right)^2+\left(\frac{\partial v}{\partial x}\right)^2+\left(\frac{\partial v}{\partial y}\right)^2\\ +\left(\frac{\partial v}{\partial z}\right)^2+\left(\frac{\partial w}{\partial x}\right)^2+\left(\frac{\partial w}{\partial y}\right)^2+\left(\frac{\partial w}{\partial z}\right)^2\end{array}} \tag{11}$$

Turbulence is hard to describe mathematically with a single metric (Tennekes and Lumley, 1972; Tritico and Cotel, 2010; Liao and Cotel, 2013; Crowley et al., 2022). For instance, in the x-coordinate direction, turbulent flow can be conceptually viewed as the instantaneous random fluctuation u' about the mean u where the total water velocity at a moment in time, $u^{momentary}$, is:

$$u^{momentary} = u + u' \tag{12}$$

where u', v', and w' represent the instantaneous water velocities relative to the mean velocities. Of the many options for describing turbulence, we select the metric of turbulent kinetic energy (TKE, $m^2\ s^{-2}$) to include in our analysis. TKE is computed as follows:

$$TKE(t) = \frac{1}{2}\left(\overline{(u')^2} + \overline{(v')^2} + \overline{(w')^2}\right) \tag{13}$$

TKE is computed within our 3-D RANS model using the $k - \varepsilon$ turbulence closure method (Harlow and Nakayama, 1968; Launder and Spalding, 1974).

Water speed (V_M, m s^{-1}) is simply the magnitude of the mean velocities:

$$V_M(t) = \sqrt{u^2 + v^2 + w^2} \tag{14}$$

Fish are sensitive to gravity and, thus, also to other acceleratory and inertial stimuli (von Baumgarten et al., 1971a), which we define with the spatial, convective acceleration of water (magnitude, A_M, m s^{-2}) as:

$$A_x = u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} + w\frac{\partial u}{\partial z}$$

$$A_y = u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} + w\frac{\partial v}{\partial z}$$

$$A_z = u\frac{\partial w}{\partial x} + v\frac{\partial w}{\partial y} + w\frac{\partial w}{\partial z}$$

$$A_M(t) = \sqrt{(A_x)^2 + (A_y)^2 + (A_z)^2} \tag{15}$$

Lastly, we assume water pressure registered by the salmon's swim bladder varies proportionally with depth below the surface (D, m).

3.3.2. Spatial velocity gradient (G_M) vs. turbulent kinetic energy (TKE)

The magnitude of the spatial velocity gradient tensor, G_M, is the sum of linear deformation (pure normal strain rates), rotation (angular velocities), and angular deformation (shearing strain rates) mechanisms. While the mathematics are more involved, in simple conceptual terms, G_M can be viewed as a precursor to turbulence. A velocity gradient, G_M, may or may not result in turbulence. *TKE* reflects turbulence that has actually materialized. The velocity gradient may exist in areas with little-to-no *TKE* but turbulence is less likely without G_M. Variables G_M and *TKE* can be highly correlated. Fish may be attuned not only to turbulence but also the distortion that precedes it (Goodwin, 2004; Nestler et al., 2008).

In our hydrodynamic modeling, turbulence represented as *TKE* exhibits spatial patterns similar to our velocity gradient metric, G_M. The spatial pattern similarities between *TKE* and G_M occur throughout our river domain and tidal phases. From a stimulus modeling point-of-view, the similarities suggest only one of the variables is needed. We select the velocity gradient because, in our modeling and post-processing, the spatial G_M patterns are more pronounced than *TKE* across tidal phases. More specifically, the velocity gradient G_M illuminates a marked stimulus in areas where tagged salmon re-orient whilst little-to-no *TKE* signature exists (i.e., down to the lowest practical numerical precision) (**Figure 6**).

Given that fish movement is commonly analyzed in the context of turbulence (**Table 3**), we illustrate *TKE* for visual comparative purposes. A full accounting of the tradeoffs between *TKE* and G_M as a behavioral stimulus is beyond the scope of the work herein. We recognize that our *TKE* finding may be attributable to nuances and idiosyncrasies of our hydrodynamic modeling that, if done differently, might result in a different conclusion regarding the value of turbulent kinetic energy for modeling salmon swimming behavior. The tradeoffs between *TKE* and G_M are worthy of future, more in-depth analysis.

3.3.3. Acute vs. nonacute

We select four hydrodynamic variables to continue our analysis, and introduce the notion of acute and nonacute to conceptually differentiate how the stimuli contribute to and rank in precedence order within a repertoire of multiple competing behaviors:

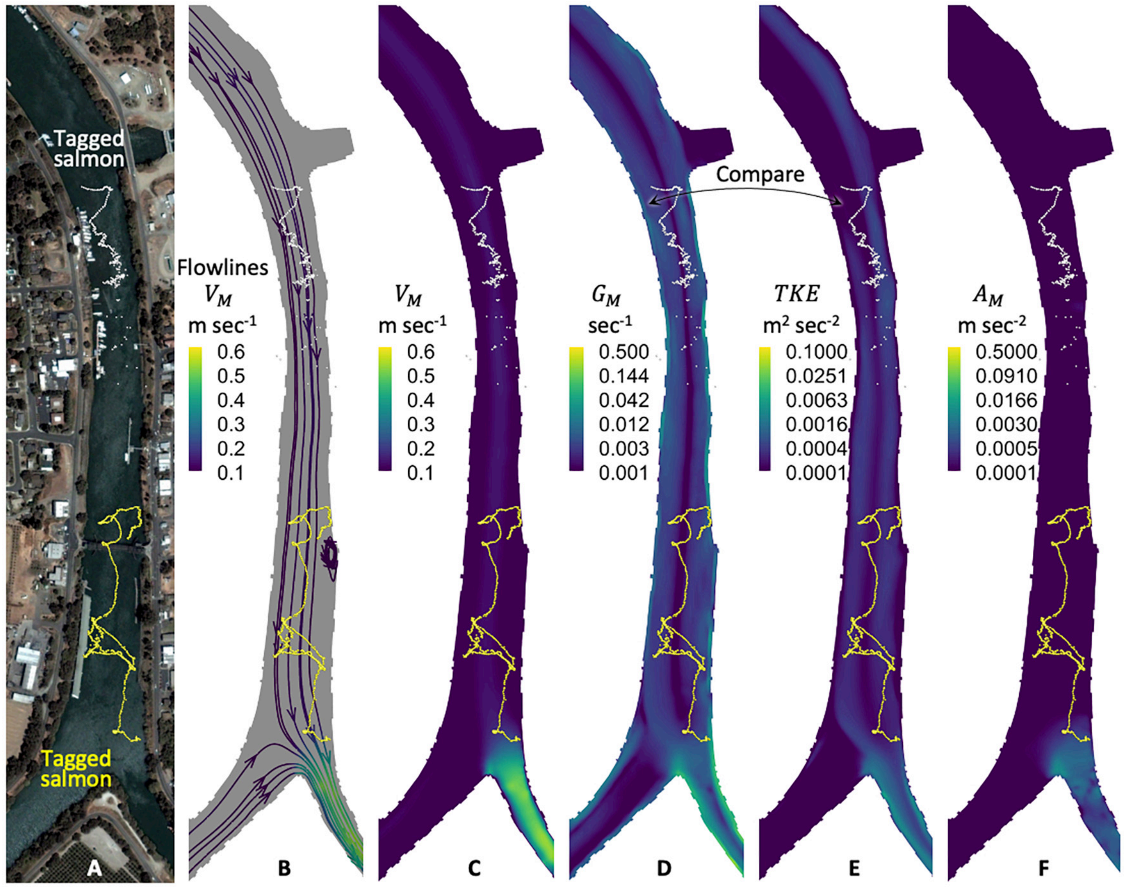


FIGURE 6

Tagged salmon and candidate hydrodynamic stimuli. Depicted are two tagged salmon **(A)**, water flowlines **(B)**, and the physical quantities of our candidate hydrodynamic stimuli **(C–F)** in a river scenario with both ebb and flood flows. Spatial patterns in our velocity gradient metric G_M are similar yet more pronounced than turbulent kinetic energy, *TKE*, [compare panels **(D)** and **(E)**]. Across tidal phases, G_M illuminates a hydrodynamic stimulus in areas where tagged salmon re-orient even where little-to-no *TKE* signature exists down to the lowest practical numerical model precision available. Map data: Google, Maxar Technologies, U.S. Geological Survey, USDA Farm Service Agency.

- spatial gradient of water speed, G_M, stimulus $i = 1$ (nonacute)
- water speed, V_M, stimulus $i = 2$ (nonacute)
- water acceleration, A_M, stimulus $i = 3$ (acute)
- fish swim bladder pressure, D, stimulus $i = 4$ (acute)

We consider a variable to be acute if the stimulus has a surmised inherent value to the animal across different contexts. Examples include an approaching predator or a physiologically damaging hydraulic condition. In our approach, acute stimuli require a timely response and quickly dominate other, nonacute factors. We consider a stimulus to be nonacute if the behavior's value to the animal depends mostly on the present context of competing stimuli. The behavior response to an acute stimulus will be more consistent across different environmental contexts as it is less sensitive to competing stimuli. We describe in detail later how competing acute stimulus responses are resolved.

3.4. Stimuli: physical vs. perceived intensity

In rivers, G_M and A_M quantities span orders of magnitude, so we convert the intensities to log form analogous to the decibel scale using Equation (1):

$$I_{i=1}(t) = \log_{10}\left(\frac{G_M(t)}{G_o}\right) \tag{16}$$

$$I_{i=3}(t) = \log_{10}\left(\frac{A_M(t)}{A_o}\right) \tag{17}$$

where $G_o = 1e^{-6}$ and $A_o = 1e^{-6}$ are arbitrary reference values. Values of V_M and D do not span orders of magnitude, so they remain unmodified from their physical quantities:

$$I_{i=2}(t) = V_M(t) \tag{18}$$

$$I_{i=4}(t) = D(t) \tag{19}$$

3.5. Stimuli: perceived change in intensity

We compute the derivative stimulus quantities of G_M, V_M, and A_M on the Eulerian mesh (Equations 11–15), then transform them to perceived intensity I_i (Equations 1, 16–19), and lastly compute the temporal rate of change in I_i at the fish centroid via Equation 2. To be clear, note that we are first computing the derivative quantities of G_M, V_M, and A_M throughout the entire spatial domain as a preprocessing step, in other words, via a global Eulerian perspective. Second, we interpolate each physical derivative quantity from the Eulerian mesh to the precise fish centroid location and transform G_M, V_M, and A_M to their perceived intensity via Equations 16–19. For the last step, we compute one more rate of change (derivative, differential) that is of the temporal domain and conducted only at the fish centroid location. The last derivative uses a local (Lagrangian) perspective in which the individual compares the momentary experience at the fish centroid to a habituated memory integrating all preceding experiences (Equation 2). We describe the last derivative (rate of change, differential) computed at the individual level next, in the following paragraphs.

We find that the perceived change in stimuli $i = 1, 2, 3$ follow Equation 2 as expected, reinforcing the notion that proportional differencing (signal-to-background ratios) influence behavioral choice. We find again here — as in prior work (Goodwin, 2004; Goodwin et al., 2006, 2014) — that the perceived change in swim bladder pressure (D, m, stimulus $i = 4$) for eliciting the needed vertical movement dynamics in our approach is best described without the denominator. Specifically, we find that using the denominator results in an asymmetric response to perceived depth changes that biases the modeled fish to move up more than down in the water column. The bias makes it difficult to reproduce observed salmon swim paths. Thus, here as in previous work, we use a simpler formulation that does not bias vertical movement either up or down in the water column:

$$E_4(t) = \left|I_4(t) - I_{a_4}(t)\right| \tag{20}$$

Alternative methods exist for translating physical (measured/modeled) variables into perceived quantities, E_i, but to date our evaluations have not found better formulations for our stimuli $i = 1 - 4$ that work across our multiple environmental contexts.

3.6. Multiplex signal disentanglement via multi-timescale perceptions

In our approach, simulated salmon make decisions every 2 s even if the choice is no change from the previous time increment. The $2 - \mathrm{s}$ time increment is mandated by a goal of keeping individuals responsive to hydrodynamic features that can come-and-go in a matter of a few seconds, e.g., as a fish rapidly transits through infrastructure. Also, we want to limit the number of interactions with the boundary of the hydrodynamic model Eulerian mesh. Regardless of the boundary interaction heuristics employed, e.g., at riverbanks, these features of the model are nonetheless more physical than hydrodynamically-mediated and can, if left unchecked, influence the fate of simulated fish. Our goal is to maintain as much a hydrodynamically-mediated fish swim behavior as possible.

We use memory timescales, m_{a_i}, to mathematically develop a context for behavioral choice. A timescale is one part of a process that determines the spatiotemporal scales within which a simulated salmon can robustly discern hydrodynamic feature changes. The sequence of perceptual processing (model variables) that results in a behavior decision B is as follows:

$$\frac{m_{a_i}}{\text{memory}} \rightarrow \frac{I_{a_i}}{\text{habituation}} \rightarrow \frac{E_i,\ k_i}{\text{perceived change in stimulus intensity}}$$

$$\rightarrow \frac{a_B}{\text{sensory activity}} \rightarrow \frac{e_B}{\text{evidence accumulator}} \rightarrow \frac{B}{\text{behavior}}$$

In the remaining portion of this section, we describe the first half of the sequence: $m_{a_i} \rightarrow I_{a_i} \rightarrow E_i$. We start with the construct of one timescale for each stimulus i that we refer to arbitrarily as *slow*. We set $m_{a_i}^{slow} = 0.9999$ ($T_{50} = 3.85$ h) where T_{50} is the half-life of the habituation indicating how long it takes for the level to decline 50% after the last non-zero stimulus acquisition. The memory value is pulled directly from prior work that focused on simplifying the parameter (Goodwin et al., 2014).

We find the single timescale is sufficient for activating a response to our acute stimuli (**Table 4**) across diverse contexts. We describe the behaviors fully in the next section (**Table 5**), but for the purposes of illustrating the first part of the perceptual processing sequence we note that one of our behaviors, $B\{4\}$, is a response to water acceleration. Most often the behavior $B\{4\}$ is triggered in the context of simulated salmon avoiding Georgiana Slough, that is, repulsed by the water acceleration enveloping the entrance to the slough. The $B\{4\}$ response is relatively consistent so long as the water acceleration stimulus, A_M, is present at sufficient intensity.

In contrast, we find that responses to our nonacute stimuli — behaviors $B\{2\}$ and $B\{3\}$ also referred to with the notation $B\{2,3\}$ — require additional context quantification. $B\{2\}$ is a reaction to G_M that results in an orientation toward (attraction to) the fastest nearby water, V_M. Behavior $B\{3\}$ is similar but inverted, in which the response to V_M results in an orientation toward the largest nearby spatial gradient in water speed, G_M (**Table 5**). By *nearby* we mean within the perceptual range of the sensory ovoid (**Figure 5**) described in detail later. We highlight $B\{2,3\}$ here because of their unique dependence on multiple timescales. $B\{2,3\}$ must be responsive to both local spatiotemporal features such as riverbank-induced hydrodynamic patterns of elevated G_M and low V_M as well as to, at the same time, bulk water flow speed changes due to the tides. $B\{2,3\}$ take on a very different character — visual trajectory appearance — near the riverbank when bulk river flow changes due to the tides.

TABLE 4 Relationship between hydrodynamic stimuli, memory timescales (*slow* = longer-term; *fast* = shorter-term), and behavior response.

		Original physical (measured/modeled) quantity, φ	
		Unmodified, $I_\varphi = \varphi$	Log-transformed, $I_\varphi = \log_{10}\left(\frac{\varphi}{\varphi_o}\right)$
Memory (habituation)	**Single timescale** $I_{a_i}^{slow}$	**Fish's swim bladder pressure** **D (t)**, meters Stimulus $i = 4$ (acute) Triggers behavior $B\{5\}$ Response type I	**Water acceleration** $\mathbf{A_M}$ **(t)**, m s^{-2} Stimulus $i = 3$ (acute) Triggers behavior $B\{4\}$ Response type II
	Dual timescales $I_{a_i}^{slow}, I_{a_i}^{fast}$	**Water speed** $\mathbf{V_M}$ **(t)**, m s^{-1} Stimulus $i = 2$ (nonacute) Triggers behavior $B\{3\}$ Response type II	**Spatial gradient in water speed** $\mathbf{G_M}$ **(t)**, s^{-1} Stimulus $i = 1$ (nonacute) Triggers behavior $B\{2\}$ Response type II

Type I is triggered by stimulus i, response orients to *same* stimulus. Type II is triggered by stimulus i, response orients to *different* stimulus.

TABLE 5 Engineering design relevance of each behavior in the repertoire of downstream-migrating salmon responses to river hydrodynamics.

	Context-based behavioral choice/decision		
Engineering design relevance How each stimulus might be used to trigger a managed movement of fish in a river channel	**Behavior notation** Type I or II *Swim path/trajectory color*	**Orientation** Alignment Attraction Repulsion Modulation	**Trigger** Sensory evidence accumulator, e_B, integrates the activity, a_B, supporting behavior B when the following occurs:
Guide salmon with the bulk water flow *toward an area*	**B {1}** N/A *Cyan*	**Flowline alignment** swim with flow	Absence of other triggers
Separate (guide) salmon away from the bulk water flow *toward/away from an area*	**B {2}** II *Yellow*	**Velocity ($\mathbf{V_M}$) attraction** swim toward fastest water	Small or decreasing perceived change in spatial gradient of water speed G_M (↓ E_1^{fast}) in large G_M (↑ E_1^{slow})
	B {3} II *Blue*	**Gradient ($\mathbf{G_M}$) attraction** swim toward largest spatial gradient in water speed	Small or decreasing perceived change in water speed V_M (↓ E_2^{fast}) in fast water (↑ E_2^{slow})
Repulse salmon *away from an area*	**B {4}** II *Gray*	**Acceleration ($\mathbf{A_M}$) repulsion** swim against flowline, away from large A_M	Large perceived change in water acceleration/deceleration A_M (↑ E_3^{slow})
In deep environments: Separate (guide) salmon away from the bulk water flow *toward/away from an area*	**B {5}** I *Green*	**Pressure (depth, D) modulation** swim toward habituated/acclimatized depth	Large perceived change in swim bladder pressure or depth D (↑ E_4^{slow})

N/A is not applicable. ↓ = small or decreasing values; ↑ = large values.

We find that $B\{2,3\}$ cannot be responsive to both localized and tidally-driven bulk flow hydrodynamics at the same time with only a single timescale.

The inadequacy of a single timescale for $B\{2,3\}$ precipitates our need for a second that can facilitate perception at a different scale. Equation [3] with timescale $m_{a_i}^{slow} = 0.9999$ ($T_{50} = 3.85$ h) forms the basis we need for a simulated fish to perceive bulk flow changes within the river due to the tides; this is the process we alluded to earlier (Section 3.3.1) that may have analogies for how a fish could upscale minuscule hydrodynamic experiences to form a RANS-level perception of its localized river flow field. We pursue a second timescale that can operate at smaller spatiotemporal scales. For simplicity, we start with the length of time between consecutive behavioral choices in our fish model ($T_{50} = 2$ s, $m_{a_i}^{fast} = 0.5$) and then evaluate values higher and lower than our initial guess. We find that $T_{50} = 2$ s provides the most robust perception of local hydrodynamic features needed to activate $B\{2,3\}$. The superior performance of $T_{50} = 2$ s stems, in part, from the intrinsic relationship to our model's time step that, in turn, is related to the spatial resolution of the Eulerian mesh data. Therefore, $T_{50} = 2$ s is not reflective of real fish memory of local hydrodynamic features but, rather, an artifact that is inseparable from our river hydrodynamic description. The dual timescales facilitate perception of hydrodynamic features in our river reach at two different spatiotemporal scales, simultaneously.

Sensory experience for each stimulus i is integrated over time in the form of habituation, $I_{a_i}^{slow}$ and, for $B\{2,3\}$, also $I_{a_i}^{fast}$. A simulated fish detects perceived changes E_i^{slow} and E_i^{fast} by comparing the perceived stimulus intensity at momentary time t to an integrated value over time that corresponds to longer-term (slower, $I_{a_i}^{slow}$) and shorter-term (faster, $I_{a_i}^{fast}$) habituations, respectively.

A change in water acceleration A_M ($i = 3$) is perceived using the *slow* timescale (Table 4) via Equation 2:

$$E_3^{slow}(t) = \frac{I_3(t) - I_{a_3}^{slow}(t)}{I_{a_3}^{slow}(t)} \qquad (i = 3) \qquad (21)$$

and swim bladder pressure ($i = 4$) changes are perceived via Equation 20 using the variation of:

$$E_4^{slow}(t) = \left| I_4(t) - I_{a_4}^{slow}(t) \right| \qquad (i = 4) \qquad (22)$$

We use two timescales to perceive the velocity gradient G_M ($i = 1$) and water speed V_M ($i = 2$). We expand Equation 2, one for the *slow* and another for the *fast* timescale. Perceived changes in G_M and V_M are perceived in both *slow* and *fast* timescales as:

$$E_1^{slow}(t) = \frac{I_1(t) - I_{a_1}^{slow}(t)}{I_{a_1}^{slow}(t)} \qquad (i = 1) \qquad (23)$$

$$E_2^{slow}(t) = \frac{I_{a_2}^{fast}(t) - I_{a_2}^{slow}(t)}{I_{a_2}^{slow}(t)} \qquad (i = 2) \qquad (24)$$

$$E_i^{fast}(t) = \frac{I_i(t) - I_{a_i}^{fast}(t)}{I_{a_i}^{fast}(t)} \qquad (i = 1, 2) \qquad (25)$$

Note the difference between Equations 24 and 2, 21, 23, 25. Equations 2, 21, 23, 25 all follow the same logic structure where the momentary perceived intensity I_i is located in the first position of the numerator. In contrast, Equation 24 places the fast memory (shorter-term) habituation, $I_{a_2}^{fast}$, in the position. In other words, for V_M (Equation 24 only) we modify the *slow* memory structure of E_2 by substituting $I_{a_2}^{fast}$ in lieu of I_2 in the numerator. Through trial-and-error, we find that Equation 24 is superior within our modeling approach for an immersed individual to perceive meaningful large spatiotemporal scale changes in river water speed due to the tides.

The floor of habituated intensities for G_M and A_M are set to 0.001 and 0.0001, respectively. In other words, $I_{a_{i=1}} \geq 0.001$ and $I_{a_{i=3}} \geq 0.0001$. Note the numerical floors here are different than the arbitrary reference values of $G_o = 1e^{-6}$ and $A_o = 1e^{-6}$ used in log-transforming these physical quantities to perceived intensities $I_{i=1}$ and $I_{i=3}$, respectively, in Equations 16,17.

3.7. Repertoire of hydrodynamic response behaviors

In this section, we describe the behaviors so that in the next section we can describe the second half of the perceptual processing (model variables) sequence: $E_i,\ k_i \rightarrow a_B \rightarrow e_B \rightarrow B$. We refer to the behaviors $B\{1\}$, $B\{2\}$, $B\{3\}$, $B\{4\}$, and $B\{5\}$ using the notation $B\{1,2,3,4,5\}$ and analogously for any subset of responses. Our salmon behaviors $B\{1,2,3,4,5\}$ are repulsion, alignment, attraction, and modulation responses to the river's hydrodynamic field (Table 5). The default behavior, $B\{1\}$, is swimming oriented aligned with (parallel to) the river flowline facing downstream. $B\{1\}$ is a negatively rheotactic response that occurs in the absence of stimuli supporting other actions. Behaviors $B\{2,3\}$ are both attraction responses, towards faster water and larger spatial gradients in water speed, respectively. Behavior $B\{4\}$ is also aligned parallel to the river flowline but in the opposite direction facing into, instead of with, the water current where the fish's head is upstream of the tail. $B\{4\}$ is a positively rheotactic response to avoid (repulsion from) elevated A_M. Behavior $B\{5\}$ modulates swim depth, D, to mitigate rapid changes in swim bladder pressure.

Only one behavior from the options of $B\{1,2,3,4\}$ is implemented per time increment $\triangle t$. The exception is $B\{5\}$, which is a vertical-only behavior and always acts in concert simultaneously with one of the behaviors from $B\{1,2,3,4\}$ that provides the xy-plane orientation. Behavior $B\{5\}$ is a vertically-oriented response inclined off the horizontal xy-plane. The horizontal xy-plane is perpendicular to the direction of gravity. Since $B\{5\}$ confers no orientation within the xy-plane — and the fish must always be oriented in some way within the xy-plane — that information is provided by one of the behaviors from $B\{1,2,3,4\}$. The orienting process works as follows: first, the simulated fish chooses one of the behaviors from $B\{1,2,3,4\}$ using the process steps in Table 6 and described in the sections that follow. Second, the simulated fish determines whether a vertically-oriented $B\{5\}$ inclination is warranted; if so, then $B\{5\}$ overrides (supersedes) the vertical angle inclination off the xy-plane set by the chosen behavior from $B\{1,2,3,4\}$. For example, assume the simulated fish chooses $B\{4\}$ and this behavior turns (re-orients) their body 5° to the left from the present heading and upward vertically 10° off the xy-plane. Then assume the fish

TABLE 6 Cognitive-based mechanistic fish movement behavior model: algorithm ensemble, steps, equations, and parameters.

Step	Component	Term(s), Equation(s)	Equation #	B {1}	B {2}	B {3}	B {4}	B {5}
1	Stimuli (behavior triggers) $i = 1, 2, 3, 4$	G_M, V_M, A_M, D	1, 11, 14–19	Absence of other triggers	G_M $i = 1$	V_M $i = 2$	A_M $i = 3$	D $i = 4$
2	Memory timescales	*slow* = longer-term *fast* = shorter-term	3, 8, 9		$m^{slow}_{a_{i=1,2,3,4}} = 0.9999\ (T^{slow}_{50} = 3.85\ hours)$			
	Memory (habituation) I_{a_i}	Exponentially weighted moving average, EWMA (Bush and Mosteller, 1955)			$m^{fast}_{a_{i=1,2}} = 0.5\ (T^{fast}_{50} = 2\ seconds)$			
3	Perceived change in stimulus intensity E_i	Variant of the *just noticeable difference*, *jnd* (Weber, 1846; Fechner, 1860)	2, 20–25		$k^{slow}_{i=1} = 0.001$ $k^{fast}_{i=1} = 0.01$	$k^{slow}_{i=2} = 0.001$ $k^{fast}_{i=2} = 0.001$	$k^{slow}_{i=3} = 0.6$	$k^{slow}_{i=4} = 0.5$
	Environmental context (of behavioral choice/decision)	Perception (multi-timescale) E^{slow}_i, E^{fast}_i						
4	Behavioral choice/decision	Mutual Inhibition Model or Leaky Competing Accumulator model (Usher and McClelland, 2001)	4–7, 26–29	$c_{B\{1,2,3,4,5\}} = 0$ $a_{B\{1\}} = 0.30$	$\lambda_{B\{1,2,3\}} = 0.1$ $\eta_{B\{1,2,3\}} = 0.01$ $a_{B\{2\}} = 0.40$	$a_{B\{3\}} = a_{B\{2\}} - 0.01$	$\lambda_{B\{4\}} = 0.005$ $\eta_{B\{4\}} = 0$ $a_{B\{4\}} = 0.6$	$\lambda_{B\{5\}} = 0.1$ $\eta_{B\{5\}} = 0$ $a_{B\{5\}} = 0.7$
5	Swim orientation	Codling et al., 2004	32, 33	$\delta_{B\{1,2,3,4,5\}} = 1.0, \kappa_{B\{1,2,3,4,5\}} = 10000.0$				
6	Swim orientation (step length)	Weibull distribution	34	$\alpha_{B\{1,2,3,4\}} = 1.5, \gamma_{B\{1,2,3,4\}} = 0.3$	$k_{Weibull_{B\{1,2,3\}}} = 0.1$		$k_{Weibull_{B\{4\}}} = 0.7$ $k_{Weibull_{B\{4\}}} = 0^*$	
7	Movement	x, y, z Cartesian coordinates	10					

The ELAM model is designed to minimize the number of parameters, facilitate parameter simplicity, eliminate all permissible stochasticity, and plug-and-play alternative algorithms; however, future applications may find value in deviating from this initial baseline approach. We constrain a_B between [0, 1] in order to compare the performance with other, alternative algorithms that operate in the range of [0, 1] for their analogous parameters. Activity $a_{B\{3\}}$ is set just below the value of $a_{B\{2\}}$ so that in a tie-breaker scenario then $B\{2\}$ is the behavior implemented. a_B values can play a role in determining the response precedence, so we set $a_{B\{5\}} > a_{B\{4\}} > a_{B\{2\}} > a_{B\{3\}} > a_{B\{1\}}$. Behaviors $B\{4\}$ and $B\{5\}$ are an acute stimulus response, so we set them as uninhibited by the others via $\eta = 0$.

$^*k_{Weibull_{B\{4\}}} = 0$ when the fish is facing more with (than against/into) the water flow vector, which makes the individual re-orient.

determines $B\{5\}$ is warranted with a downward angle of 20°. Behavior $B\{4\}$ and $B\{5\}$ orientations are integrated as follows: the $B\{5\}$ downward angle of 20° supersedes the upward 10° inclination of $B\{4\}$. Behavior $B\{5\}$ does not modify the xy-plane 5° left turn (re-orientation) of $B\{4\}$. For reference, 0° in the localized xy-plane used in decision-making always points in the direction from the fish's tail to head.

Behaviors $B\{2, 3\}$ often operate in tandem, in opposing fashion, yielding emergent properties that we describe next.

3.7.1. Emergent properties from opposing behaviors

Juvenile Pacific salmon are prey that must reach the ocean in limited time. We propose that a salmon's downstream migration strategy involves balancing the opposing goals of:

(i) concealing their presence with $B\{3\}$ by leveraging G_M associated with turbulence, acoustic noise, low visibility (elevated turbidity), and physical cover (Anjum and Tanaka, 2020);
(ii) seeking faster water, $B\{2\}$, that expedites the salmon's downriver journey to the ocean.

Behaviors $B\{2\}$ and $B\{3\}$ are at odds as $B\{2\}$ orients the salmon toward the thalweg, e.g., river center, while $B\{3\}$ leads toward the river's edge.

Note that from the Lagrangian perspective of an individual fish, the orientation toward faster water does not have to correspond with the water flow direction and often they do not coincide; for example, near the riverbank, water flow may point downriver (parallel to the riverbank) while the direction pointing toward faster water is in line with the shortest path to the thalweg (perpendicular to the riverbank).

Behaviors $B\{2, 3\}$ work in combination by mutually inhibiting each other, a dynamic that confers the advantageous emergent properties of keeping salmon responsive to rapidly changing conditions, maintaining downstream progress, and a generally unpredictable position within the river. While the fish does not benefit from the optimum river position of fastest water for downriver migration, the salmon increases its survival probability (Sabal et al., 2020). At an evolutionary scale, the $B\{2, 3\}$ combination increases the probability of salmon life cycle completion and promotion of the species.

The notion of emergent properties arising from opposing and mutually-inhibiting dynamics is not a novel concept. The mutually inhibiting nature of $B\{2, 3\}$ shares an analogy with the neural inhibitions that operate at much smaller scale within an animal's brain (Usher and McClelland, 2001; Sukenik et al., 2021). At a very different scale, turbulence both attracts and repulses fish (Smith, 2003; Smith et al., 2005; Liao and Cotel, 2013). In socially-driven animal swarms, attraction and repulsion dynamics are the basis of individual movement (Couzin et al., 2002, 2005; Ballerini et al., 2008; Lemasson et al., 2009, 2013; Katz et al., 2011).

3.8. Context-based behavioral choice

In this section, we describe the second half of the perceptual processing (model variables) sequence: $E_i,\ k_i \rightarrow a_B \rightarrow e_B \rightarrow B$. Multiple stimuli compete to influence movement, so we must organize the hierarchical repertoire of stimulus-responses for the changing phases of a behavioral sequence (Sogard and Olla, 1993; New et al., 2001). In our mechanistic approach, using the Mutual Inhibition Model or Leaky Competing Accumulator model (Usher and McClelland, 2001), the perceived changes E_i are translated into a common currency for comparison across all the different sensory modalities, stimuli i. The common currency is activity, a_B, from Equation 5. Activities a_B are accumulated as sensory evidence e_B that support the triggering of its corresponding behavior. Sensory evidence e_B is compared across all the behaviors each time step to choose the response. The behavior with the greatest evidence e_B is chosen for the next time increment $\Delta t = 2$ s (**Figure 7** and **Table 6**).

In mathematical form, the activity a_B — and therefore evidence e_B — that supports each behavior B getting triggered increases when the corresponding perceived changes E_i^{slow} and E_i^{fast} cross their respective thresholds k_i^{slow} and k_i^{fast}. In this way, the fish's movement decision (swim orientation and speed) is informed by comparing the momentary perceived change to memories of preceding experience. A succinct description of the environmental condition that activates a_B and contributes to e_B for triggering each behavior B is provided in the right column of **Table 5** and illustrated in **Figure 7**. The process is described in **Table 6**. We describe the mathematics of how activities a_B are computed in the paragraphs that follow.

We constrain the activity constants a_B to the range $[0.0 < a_B \leq 1.0]$. The advantage of constraining activity values is that we can, if ever warranted, compare the cognitive algorithm separate from other parts of our model to other decision methods with parameters also able to operate in the range [0, 1]. We describe the activities a_B of the decision-making process starting with behavior $B\{5\}$, then $B\{4\}$, and lastly the more complicated $B\{2, 3\}$.

Activity a_B supporting $B\{5\}$ occurs when the perceived change in depth, D, representing the perceived change in swim bladder pressure exceeds threshold $k_{i=4}^{slow}$ as:

$$a_{B\{5\}}(t) = a_{B\{5\}} \quad if \quad E_{i=4}^{slow}(t) \geq k_{i=4}^{slow} \\ = 0 \quad \text{otherwise} \tag{26}$$

Activity a_B supporting behavior $B\{4\}$ occurs when the perceived change in A_M exceeds threshold k_3^{slow} as:

$$a_{B\{4\}}(t) = a_{B\{4\}} \quad if \quad E_{i=3}^{slow}(t) \geq k_{i=3}^{slow} \\ = 0 \quad \text{otherwise} \tag{27}$$

$B\{4\}$ and $B\{5\}$ are acute stimulus responses, and we are able to set these behaviors as uninhibited by the others ($\eta = 0$ in Equation 5, **Table 6**). Note that for the acute stimulus responses we are able to simplify the decision process in two ways: first, $B\{4, 5\}$ require only a single timescale and, second, we are able to eliminate inhibition ($\eta = 0$).

The activation of the nonacute behaviors $B\{2\}$ and $B\{3\}$ is more complex in three ways. First, $B\{2, 3\}$ require evaluation at two timescales. The *slow* timescale resolves hydrodynamic features that are generally attributable to the tidal cycle. The *fast* timescale resolves local features such as riverbank-induced hydrodynamics. Local features can come-and-go with the tides

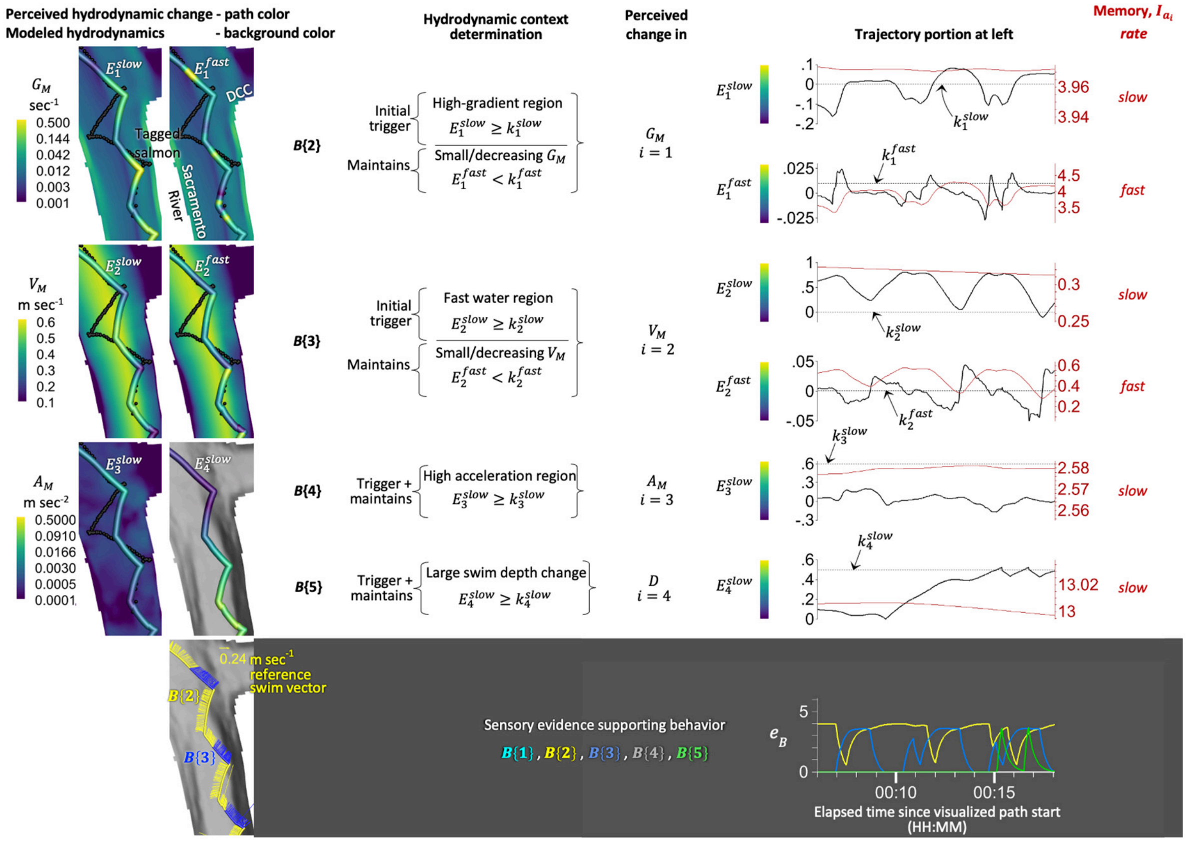


FIGURE 7

Graphical illustration of a simulated salmon's perception of river hydrodynamics versus the pattern output by a numerical flow field model, together with the underlying cognitive dynamics of our mechanistic behavior modeling approach. To simplify the illustration, the ELAM salmon is simulated with steady hydrodynamics (unchanging with time) using a snapshot extracted from the flow field time series that is representative of the river flow conditions when the tagged fish was actively swimming. Illustrated are the momentary experiences and behavioral choices of a zig-zagging simulated salmon. The simulated salmon qualitatively resembles the zig-zag movement of a tagged salmon (black path) via behaviors $B\{2, 3\}$ that arise from perceived changes in V_M and G_M (**Tables 4**, **5**). Perceived hydrodynamics (E_i, colored path) differ from the river flow field stimulus patterns output from the hydrodynamic model (background color). Additional detail including *TKE* contours available in **Supplementary Figure 1**.

so, for instance, the riverbank-induced hydrodynamic feature of elevated G_M and low V_M may be negligible or imperceivable during slack tide whereas the pattern is pronounced in ebb tide. Therefore, the pattern of elevated G_M and low V_M are reliable for indicating a riverbank and/or shallower habitat only under certain environmental conditions (contexts). Second, activating $B\{2, 3\}$ depends on the existing behavioral state, B, of the salmon. Third, we find the activities a_B need to be inhibited by the other behaviors ($\eta = 0.01$) to operate properly within the overall repertoire.

To switch to $B\{2\}$ from any other *xy*-plane response from the options of $B\{1, 3, 4\}$, the salmon must perceive a high-gradient region where the longer-term (*slow*) perceived increase in G_M is $E^{slow}_{i=1}(t) \geq k^{slow}_{i=1}$ while simultaneously perceiving a very small or decreasing short-term (*fast*) change in G_M of $E^{fast}_{i=1}(t) < k^{fast}_{i=1}$, and this latter condition will sustain $B\{2\}$ once initiated.

$$\begin{aligned} a_{B\{2\}}(t) = a_{B\{2\}} \ & if\ B(t-1) \neq 2\ and\ E^{slow}_{i=1}(t) \geq k^{slow}_{i=1} \\ & and\ E^{fast}_{i=1}(t) < k^{fast}_{i=1} \\ & = 2\ and\ E^{fast}_{i=1}(t) < k^{fast}_{i=1} \\ = 0 \quad & otherwise. \end{aligned} \tag{28}$$

Similarly, the initial switch to $B\{3\}$ from any other *xy*-plane response, $B\{1, 2, 4\}$, requires the salmon perceive a longer-term (*slow*) environmental shift to faster water described mathematically as $E^{slow}_{i=2}(t) \geq k^{slow}_{i=2}$ while simultaneously perceiving a very small or decreasing short-term (*fast*) change in V_M of $E^{fast}_{i=2}(t) < k^{fast}_{i=2}$ and the latter condition will sustain $B\{3\}$ once triggered:

$$\begin{aligned} a_{B\{3\}}(t) = a_{B\{3\}} \ & if\ B(t-1) \neq 3\ and\ E^{slow}_{i=2}(t) \geq k^{slow}_{i=2} \\ & and\ E^{fast}_{i=2}(t) < k^{fast}_{i=2} \\ & = 3\ and\ E^{fast}_{i=2}(t) < k^{fast}_{i=2} \\ = 0 \quad & otherwise. \end{aligned} \tag{29}$$

We set the value of activity $a_{B\{3\}}$ just below that of $a_{B\{2\}}$ so that in a tie-breaker scenario where both $B\{2, 3\}$ dominate other behaviors, then $B\{2\}$ is the one implemented.

Activity a_B values play a role in determining the response precedence so we set $a_{B\{5\}} > a_{B\{4\}} > a_{B\{2\}} > a_{B\{3\}} > a_{B\{1\}}$. Acute stimulus responses are the highest priority. $B\{5\}$ is valued higher in the precedence than $B\{4\}$ but recall that a vertical angle from $B\{5\}$ does not override a $B\{4\}$ *xy*-plane orientation so, in effect, $B\{4\}$ remains the highest priority in the horizontal plane.

3.8.1. Zig-zag example of context-based behavioral choice with steady river hydrodynamics

We use a single 3-D output, or snapshot in time, extracted from a river flow field time series in order to ignore, for this example, the additional complexity introduced by time-varying hydrodynamics. Simulated salmon swim orientation and speed responses at $2-$ s intervals (**Figure 7** bottom-left) correspond to momentary perceived changes in each stimulus. Habituation to each stimulus updates at multiple timescales described simply as *slow* and *fast*. The propensity, or evidence e_B, to respond to A_M or D increases when the perceived change in stimulus intensity, E_3^{slow} or E_4^{slow}, respectively, exceeds their corresponding threshold, k^{slow}.

The activation of $B\{2,3\}$, eliciting the zig-zag swim path (**Figure 7**), is more complex than either behaviors $B\{4,5\}$ that are responses to stimuli $i = 3, 4$, respectively, because perceived changes in the responsible stimuli G_M and V_M are integrated at both *slow* and *fast* timescales and the activities a_B supporting $B\{2,3\}$ depend on the existing behavioral state B. If a salmon is implementing a non-$B\{2\}$ behavior, then the simulated fish must experience a high-G_M region ($E_1^{slow}(t) \geq k_1^{slow}$) to initiate $B\{2\}$. Sustaining $B\{2\}$ requires only a small or decreasing perceived change in G_M ($E_1^{fast}(t) < k_1^{fast}$). Similarly, triggering $B\{3\}$ requires the salmon to experience fast water ($E_2^{slow}(t) \geq k_2^{slow}$) and maintaining $B\{3\}$ requires only a small or decreasing perceived change in water speed ($E_2^{fast}(t) < k_2^{fast}$). Initial activation, or triggering, of the behavior requires the maintenance criterion also be met at the initiation moment (**Table 5** and **Figure 7**). Whichever behavior B has the maximum accumulated evidence, e_B, is implemented for the $2-s$ time increment (**Figure 7** bottom). $B\{1\}$ is a default behavior that occurs during the absence of evidence supporting other behaviors.

3.9. Sensory ovoid and points

Simulated salmon sense their 3-D environment using a localized sensory ovoid (**Figure 5**) beyond which the fish has no knowledge of the virtual world. We represent the ovoid using six sensory points located at the cardinal positions (front, back, left, right, above, below) surrounding the fish. The simulated fish is at the center of the ovoid. We refer to the cardinal point distances on the outer edge of the ovoid as the sensory query distance, *SQD*. Sensory points, or *SQD*s, are a simple discretized version of the ovoid that simulated fish use to orient in relation to local spatial patterns in stimuli.

Our ovoid is not used to compute any of the trigger stimuli (**Table 5**). Recall that our hydrodynamic trigger stimuli are local rates of change in time computed at the fish centroid. Our sensory ovoid is used only for orienting the fish toward the fastest nearby water, $B\{2\}$, or toward the largest nearby G_M, $B\{3\}$, in the detectable range sensed by the cardinal points. Since the orienting stimuli V_M and G_M are scalar quantities, the direction toward higher values cannot be determined with a simple point measurement at the fish centroid. Orientation toward larger values is determined by comparing V_M and G_M at the available cardinal endpoint locations on the exterior shell of the sensory ovoid to their values at the fish centroid. Note that $B\{1,4\}$ orientations can be computed using just the water velocity vectors at the fish centroid, so the sensory ovoid is not used for these behaviors. $B\{5\}$ operates relative to the vertical (gravity) axis and, here too, the sensory ovoid is not needed.

In the real world, the sensory range of a fish depends on the stimulus (Giske et al., 1998) and the *SQD* would be proportional to fish size. In our model, for simplicity, ovoid size is the same for imaging V_M and G_M. The size of our simulated sensory ovoid is determined not by fish size but, rather, the spatial resolution of hydrodynamics within the Eulerian mesh. Sizing the sensory ovoid smaller than the spatial resolution of the river hydrodynamics available in the Eulerian mesh results in the situation where V_M and G_M have the same value at the outer edge (*SQD*) as at the fish centroid. When the difference in stimulus values between the centroid and outer edge of the sensory ovoid is less than the numerical precision available from the hydrodynamic model — meaning there are no significant digits — then the simulated fish cannot orient to spatial trends in V_M and G_M.

The limiting factor determining *SQD* in computer simulations is the numerical precision of hydrodynamic variable values stored in the time-varying Eulerian mesh of the hydrodynamic model. SQD_{CFD} is the distance between a fish and its sensory point location below which orienting stimulus differences have little-to-no significant digits (Goodwin et al., 2006). A spatial trend computed with $SQD < SQD_{CFD}$ is not only unreliable but often misleading. Therefore, simulated fish require $SQD \geq SQD_{CFD}$ for orientation, and it is preferable that $SQD \gg SQD_{CFD}$.

Our sensory ovoid is a construct that lets us leverage the hydrodynamic model information commensurate with the available spatiotemporal resolution. Orienting stimuli V_M and G_M increase and decrease in intensity at different spatial rates depending on where the fish is in the river. For instance, in the thalweg, V_M and G_M may not change much across several meters whereas near the riverbank these variables can often change appreciably in less than a meter. Varying the ovoid size each time step provides simulated fish the ability to discern V_M and G_M trends of different spatial scales. We find that varying the ovoid each time step is a better way to discern V_M and G_M spatial trends at different scales compared to, for instance, adjusting the size so that it is proportional to the Eulerian mesh element size at a location. Using our approach, we find that even though the *SQD* may not be optimally sized to detect a particular spatial trend at a given moment in time, the temporal variation in *SQD* allows a simulated fish to discern the necessary V_M and G_M spatial trends within a few time steps at most.

Through trial-and-error on our mesh, we set the *SQD* so that it changes each time step randomly according to a normal distribution with a mean in the *xy*-plane of 5.0 m, a standard deviation of 1.5, and a minimum radius of 0.1 m. The vertical (*z*-coordinate) radius has a mean of 0.4 m and a standard deviation of 0.1. In our approach, a more sophisticated sensory ovoid is not particularly useful unless accompanied with a concomitant improvement in hydrodynamic resolution. Thus, our use of a sensory ovoid is trivial compared to the fundamental concept in Oteiza et al. (2017).

When orienting in relation to V_M and G_M spatial trends, one or more of the four *xy*-plane sensory points must have a $|jnd| \geq 1\%$ in that variable's value relative to the fish (centroid), otherwise orientation remains unchanged from the previous time increment. A *jnd* is used here, as opposed to the *nsd*, because this is a discrete comparison. The 1% rule is constant even as the ovoid size changes each time step. If all cardinal point $\left|jnd\right| < 1\%$, then we assume there is no relevant perceived difference or spatial trend in V_M or G_M around the fish at the scale of time t's sensory ovoid and hence no orientation change. Vertical sensory points and orientation are handled analogously to the xy-plane.

3.10. Swim orientation

Behavior B determines the preferred orientation, θ_o. Before we describe the swim orientation algorithm that we use in this study, it is worth noting the Ornstein-Uhlenbeck (O-U) model (Uhlenbeck and Ornstein, 1930) for several reasons. The O-U model is a powerful, longstanding approach to orientation that is used frequently (Gurarie et al., 2017), and remains a constant source of evaluation in our own work. The O-U model has attributes similar to Equations 4 and 5 used in other parts of our algorithm ensemble for cognitively deciding individual behavior transitions. The O-U model describes and produces a stochastic movement orientation that is implemented in the model, θ, based on the idealized preferred direction θ_o from behavior B as follows:

$$d\theta = \psi\left(\theta_o - \theta'\right) dt + c dW \tag{30}$$

or as a complete, first-order approximation of the stochastic differential equation in discrete form (Gillespie, 1996; Natvig and Subbey, 2011):

$$\theta\left(t + \Delta t\right) = \theta'\left(t\right) + \psi\left(\theta_o\left(t\right) - \theta'\left(t\right)\right)\Delta t + c\zeta\sqrt{\Delta t} \tag{31}$$

where ζ is a sample value from a standard normal distribution $N\left(\mu = 0, \sigma^2 = 1\right)$ with mean μ and σ standard deviation, ψ is the drift term describing the strength of attraction to the preferred orientation θ_o, $\theta'\left(t\right)$ is the orientation at time t, c is a noise-scaling factor analogous to its use in Equations 4 and 5 or it can be thought of as a diffusion term where $c\zeta\sqrt{\Delta t}$ is the white noise, Brownian motion, or a Wiener process describing randomness. When $\psi = 0$, then there is no attraction to the preferred orientation θ_o, only diffusion.

We find the mechanics of the Codling et al. (2004) algorithm integrate better with our overall methodology. We use the Codling et al. (2004) algorithm to compute the movement orientation that is actually implemented in the model for a given time step, θ, based on the idealized preferred direction θ_o from behavior B. In our approach, we use the Codling et al. (2004) algorithm to set the initial movement orientation θ whenever there is an updated preferred direction θ_o due to a change in behavior B. Since one of our goals is to eliminate all permissible stochasticity, we do not use the algorithm during consecutive orientations when the behavior B is not changing. Should stochasticity during consecutive orientations be required in future work, we find the Codling et al. (2004) and O-U algorithms both suffice.

In the Codling et al. (2004) algorithm, the swim orientation is randomly drawn from a von Mises distribution $T\left(\theta, \theta'\right)$ that is dependent on a concentration parameter, κ, and mean turning angle, $\mu_{\theta-\theta'}$, as follows:

$$T\left(\theta, \theta'\right) = \left(2\pi J_o\left(\kappa\right)\right)^{-1} \exp\left[\kappa \cos\left(\theta - \theta' - \mu_{\theta-\theta'}\right)\right] \tag{32}$$

where $J_o\left(\kappa\right)$ is the modified Bessel function of order zero, and the mean turning angle is:

$$\mu_{\theta-\theta'} = -\delta_{\Delta t}\left(\theta' - \theta_o\right) \qquad \left(-\pi < \theta', \theta_o, \mu_{\theta-\theta'} \leq \pi\right) \tag{33}$$

where θ is the movement orientation at time $t + \Delta t$, θ' is the movement orientation at time t, and $0 < \delta_{\Delta t}$ is the amplitude of the mean turning angle. $\delta_{\Delta t}$ controls how quickly the swimming orientation returns to the preferred direction θ_o during the re-orientation process, which is a proxy for the sensing ability of the animal (Codling et al., 2004). κ controls the amount of randomness in the choice of each new orientation and is a proxy for the orienting ability of the animal. A low value of κ corresponds to a poor orientating ability, for instance, in a highly turbulent environment. Setting $\kappa = 0$ collapses the von Mises distribution to a wrapped uniform distribution. $\mu_{\theta-\theta'} > 0$ biases the random walk in the preferred direction θ_o (Codling et al., 2004).

3.10.1. Swim orientation (step length)

Swim orientation in our model is further influenced by step length, or re-orientation probability (Okubo, 1980). We use the Weibull distribution to determine the fish's propensity to maintain the same orientation (step length). The Weibull distribution is often used in fatigue (time-to-failure) analysis as well as in ecology for the analyses of step length in animal movement and correlated random walk models (Morales et al., 2004; McClintock et al., 2012, 2014). We describe the Weibull probability density function (random number) as:

$$Weibull = \frac{\alpha}{\gamma}\left(\frac{\zeta}{\gamma}\right)^{\alpha-1} e^{-\left(\frac{\zeta}{\gamma}\right)^{\alpha}} \qquad \left(\zeta \geq 0\right) \tag{34}$$

where α is the shape and γ is the scale parameter, respectively, and ζ is a sample value from a standard normal distribution $N\left(\mu = 0, \sigma^2 = 1\right)$ with mean μ and σ standard deviation (**Table 6**).

Our use of the Weibull distribution is simple. In our approach, the fish's orientation is allowed to change based on the preferred direction θ_o of behavior B if the Weibull random number is greater than or equal to a threshold value, $k_{Weibull}$, that does not change with time. If $Weibull < k_{Weibull}$, then the simulated fish's orientation is not changed (i.e., continues straight-ahead) although the movement trajectory may not be straight because of the contribution from advection due to river hydrodynamics.

We do not apply the step length treatment to the vertical-only behavior, $B\{5\}$, but it is applied to the vertical orientation component of all other behaviors that act in 3-D whenever the Eulerian mesh is three-dimensional. Shape and scale parameters of the Weibull distribution as well as the threshold values are set as part of model development and parameterization.

3.11. Swim speed

Simulated fish swimming speed is modulated by both behavior and the environmental condition. The swimming speed for each behavior B is based on a surmised interpretation of the stimulus-response's value to the animal. For instance, swim speed may be slow, or otherwise bioenergetically efficient, for a *default* behavior that is executed merely because there is a lack of important stimuli.

In contrast, the swim speed may approach the species' burst propulsion limit for an avoidance response in fast water.

We set swim speed as *body lengths* (*BL*) *per second*, or $BL\ s^{-1}$, according to *drift*, *cruise*, and *burst* swimming modes (Beamish, 1978) with an assumed juvenile salmon size of 0.12 m (120 mm). The swim speed of each behavior is set initially as:

- $B\{1\}$ is a *drift* swim mode (0.25 BL s^{-1}, 0.03 m s^{-1});
- $B\{2, 3, 4\}$ are *cruise* modes (2.0 BL s^{-1}, 0.24 m s^{-1}).

If water flow is faster than *cruise* swimming during an A_M avoidance response, $B\{4\}$, then swim speed instantly increases to 1.9 V_M up to the *burst* maximum of 10.0 BL s^{-1}, 1.2 m s^{-1}. The *burst* speed is near the maximum BL s^{-1} measured in Bay-Delta juvenile salmon (Lehman et al., 2017).

Vertical swimming, $B\{5\}$, depends on the *xy*-plane behavior where speed is initially set from one of the following $B\{1, 2, 3, 4\}$ but is increased up to 1.9 V_M, but no more than the *burst* maximum, whenever the fish is failing to alleviate recent perceived change in swim bladder pressure. Vertical overrides of the *xy*-plane behavior speed typically occur when the simulated fish must counteract strong vertical water currents, most common in deep environments near infrastructure.

We simulate all fish identically as 120 mm in length even though the mean fork length of tagged fish is slightly higher than 150 mm. Our reason is that salmon management is concerned with fish as small as 60 mm (California Department of Water Resources, 2016). We arbitrarily select a single fish size between 60 and 150 mm, slightly closer to 150 mm. We do not use a distribution of fish sizes in order to reduce heterogeneity and stochasticity in the model wherever permissible. The assumed salmon size by itself is not a critical assumption in the model. The same swim speed (m s^{-1}) can be obtained for a different sized fish with simple counterbalanced shifts in the assumed *drift*, *cruise*, and *burst* swimming *body lengths per second* (BL s^{-1}) values.

3.12. Swim orientation and speed integration

We find one last nuance required of $B\{2, 3\}$ using the aid of steady ebb tide flow hydrodynamics and the transit times of tagged and modeled salmon within our river reach (**Figure 8** upper-right dyad). During ebb tide flow, tagged salmon zig-zag at a travel rate that can only be qualitatively reproduced in simulation if the ELAM fish is partially positive rheotactic, that is, the modeled individual orients their swimming facing slightly into (against) the oncoming water current (see the orientation of the swim vectors in **Figure 7** lower-left). Whenever water speed exceeds the fish's *cruise* swim speed of 2 *body lengths per second* (Beamish, 1978) we prescribe that the rheotactic orientation of $B\{2\}$ and $B\{3\}$ increases positively by 10%. The 10% is only a rheotactic increase in the preferred orientation θ_o and not an absolute angle relative to the water flow vectors.

In behavior rule computations thus far, the simulated fish's 3-D orientation is based on a local coordinate system tied to the direction in which the salmon is pointing its head, which can change every time increment. In the *xy*-plane of the local (fish heading) coordinate system, 0° is straight-ahead, 180° is behind the individual, 90° is to the left, and 90° (or 270°) is to the right of the individual. Water pressure (depth) varies parallel with gravity, so we maintain the local and global vertical coordinate systems as the same. When the local 3-D orientation and swim speed is computed, we can then use how the salmon is oriented in the global Cartesian mesh of the Eulerian-based hydrodynamic model to compute the component swim vectors $u_{volitional}$, $v_{volitional}$, and $w_{volitional}$, which completes the spatial displacement Equation 10.

3.13. Model time step

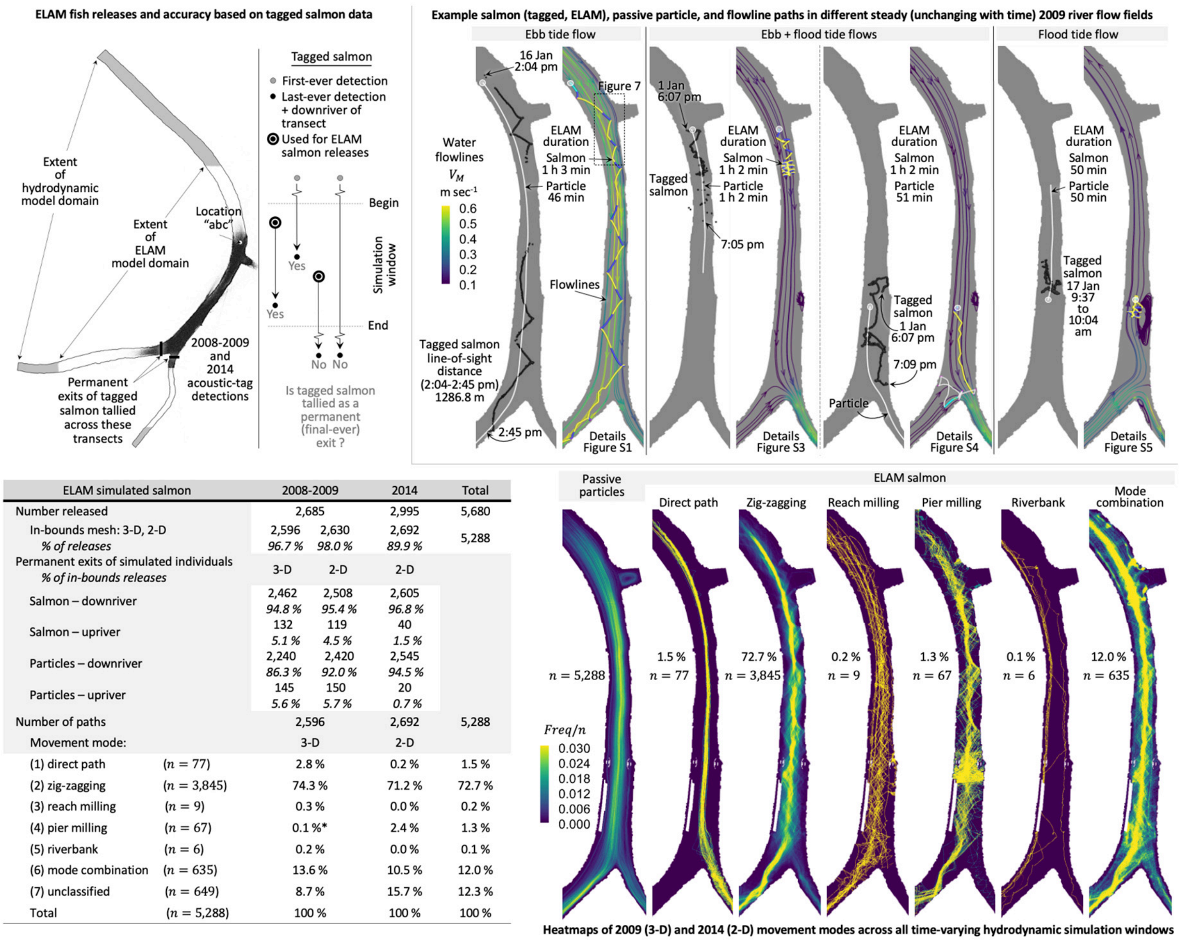
We find that simulated salmon need to make movement decisions at $2-s$ increments in order to react quickly in fast water. Longer time steps increase the number of mesh boundary encounters as well as scenarios where simulated salmon are hydrodynamically captured (entrained) that, by contrast, tagged fish successfully avoid. Depending on the scenario, our cognitive algorithm ensemble generally requires several discrete time steps for an acute stimulus response to rise within the hierarchy of competing behaviors and enable the simulated fish to successfully realize an aversive maneuver before capture. We find that 2 s is the longest increment permissible for the requisite number of time steps to occur that allow acute stimulus responses such as $B\{4\}$ to achieve the avoidance observed in tagged salmon in rapidly-changing hydrodynamics near infrastructure. Thus, the $2-s$ time step is an upper-bound on the increment length for our river analysis. We forgo smaller time increments because it increases model runtime without a needed benefit for our study setting.

All hydrodynamic values are linearly interpolated spatially from their nearby mesh storage locations (e.g., cell vertex/node, cell center, or cell face center) to the precise fish centroid location and seven surrounding sensory points every 2 s. First, all stimulus values are interpolated spatially in linear fashion to the precise fish position and seven sensory points for each of the adjacent $3-min$ intervals on either side in time from the available hydrodynamic model output. Then, second, stimulus values are linearly interpolated to the $2-s$ increment of the fish's decision moment from the adjacent $3-min$ interval values.

Most parameters of the fish cognition algorithm ensemble (**Table 6**) are intrinsically linked to the time step increment in their present form. Changes to increment length require counterbalancing other parameter values in order to compensate and retain the same cognitive dynamics achieved with another step length. Parameter re-balancing, however, occurs in a nonlinear, multidimensional space that can be challenging to negotiate. Practically, changing the time increment length usually involves recalibrating the model. Insulating model performance from increment length may be possible as a future improvement and, presently, may be found in limited form in components such as swim orientation step length.

3.14. Lagrangian encounters with the Eulerian mesh boundary

A key but often overlooked issue that can arise and have large, unintended effects on the destination of simulated volitional



ELAM simulated salmon		2008-2009		2014	Total
Number released		2,685		2,995	5,680
In-bounds mesh: 3-D, 2-D *% of releases*		2,596 *96.7 %*	2,630 *98.0 %*	2,692 *89.9 %*	5,288
Permanent exits of simulated individuals *% of in-bounds releases*		3-D	2-D	2-D	
Salmon – downriver		2,462 *94.8 %*	2,508 *95.4 %*	2,605 *96.8 %*	
Salmon – upriver		132 *5.1 %*	119 *4.5 %*	40 *1.5 %*	
Particles – downriver		2,240 *86.3 %*	2,420 *92.0 %*	2,545 *94.5 %*	
Particles – upriver		145 *5.6 %*	150 *5.7 %*	20 *0.7 %*	
Number of paths		2,596		2,692	5,288
Movement mode:		3-D		2-D	
(1) direct path	(n = 77)	2.8 %		0.2 %	1.5 %
(2) zig-zagging	(n = 3,845)	74.3 %		71.2 %	72.7 %
(3) reach milling	(n = 9)	0.3 %		0.0 %	0.2 %
(4) pier milling	(n = 67)	0.1 %*		2.4 %	1.3 %
(5) riverbank	(n = 6)	0.2 %		0.0 %	0.1 %
(6) mode combination	(n = 635)	13.6 %		10.5 %	12.0 %
(7) unclassified	(n = 649)	8.7 %		15.7 %	12.3 %
Total	(n = 5,288)	100 %		100 %	100 %

FIGURE 8
Setup of the ELAM analysis **(upper-left)**, example tagged and simulated salmon paths with a passive particle **(upper-right)**, movement mode heatmaps **(lower-right)**, and tabulated downriver entrainment and movement mode proportions **(lower-left)**. Spatial extent of the hydrodynamic model is based on available river gage (**Figure 1**) and bathymetric data. ELAM model spatial domain is based on the extent of salmon acoustic-tag telemetry data from 2008 to 2009 (Romine et al., 2013) and 2014 (California Department of Water Resources, 2016; Romine et al., 2017). Tagged salmon exits are used to assess the accuracy of simulated individual (particle, salmon) entrainment. Example swim paths of tagged salmon (black path) and ELAM fish (path colored by behavior B, **Tables 4**, **5**) are provided in dyads for different tidal environments (ebb, flood, ebb+flood tide flows), which can be compared to the passive particle (white path). The example simulated particle and salmon paths within each dyad are released from the same location (white circle) near where the tagged fish is first detected. The ELAM salmon and particle are simulated with steady hydrodynamics (unchanging with time) using a snapshot extracted from the flow field time series that is representative of the river flow conditions when the tagged fish was actively swimming. The underlying cognitive dynamics of each example ELAM salmon are illustrated in greater detail in **Supplementary Figures 1**, **3**–**5** along with candidate stimulus *TKE*. Heatmaps are generated from the simulated individuals (particles, salmon) responding to time-varying hydrodynamics changing every 3 *min* across all simulation windows. Heatmap values are computed the same as in **Figure 3** and, just as in **Figure 3**, only modeled fish detections are heatmapped, that is, the paths are not implied from the position sequence. Note that modeled individuals are detected perfectly at $2-s$ increments throughout the domain, unlike tagged salmon. One reason why simulated salmon exhibit less milling near the piers (movement mode #4) in year 2009 (*) compared to year 2014 may be that the bridge is not rendered in the 2009 mesh (**Figure 5**) and, thus, its hydrodynamic impact on the river is not perceivable to ELAM salmon.

individuals in bounded 2-D or 3-D environmental domains is their interaction with the boundary of the computational Eulerian mesh. River hydrodynamic modeling generates the mesh as part of the development process. We simulate fish within the original mesh of the hydrodynamic model in all of our work regardless of element type and geometric mesh tessellation. The hydrodynamic domain has boundaries at the water surface, riverbank, and river bottom. The domain tessellation can change each $3-min$ timestep, and this is relatively common in modern hydrodynamic models that use adaptive meshing methods.

The behavior repertoire is built and parameterized to make every attempt within reason so that simulated salmon respond only to hydrodynamic stimuli including near boundaries such as the riverbank and bottom bathymetry. Limiting interaction with physical boundaries is a key reason why our timestep is 2 s. As a backup for when our simulated fish do physically interact with a boundary, every practical attempt is made to recover hydrodynamically-mediated decisions within a single timestep of the behavior model.

When a fish's sensory ovoid runs up against a physical boundary in the Eulerian mesh, compressing one of the cardinal point distances toward the fish, the individual is re-oriented away from the feature for that timestep alone. Our model works in double precision, yet even still the numerical processes within a computer are neither infinite nor perfect. Situations arise where double precision calculations store a fish adjacent to a boundary by an infinitesimal distance on the other (dry, non-water) side. Then, at the next timestep, the model interprets the same position as outside the meshed domain. We employ heuristics in an attempt to recover fish violating the boundary by repositioning the individual to the nearest mesh cell center, typically, a very short distance from the point of violation. Hydrodynamic models typically use tessellation methods in which there is a graded approach to cell sizes where they are small near physical boundaries and larger nearer the thalweg or wide unobstructed water flow regions. Therefore, our heuristics generally result in very small location displacements while recovering hydrodynamically-mediated behavior within a single timestep. As a third backup, when the boundary interaction heuristics are insufficient, then the modeled fish is removed from simulation. Removals are seldom. Next, we provide examples of boundary interaction scenarios that do not always have obvious conceptual or computational heuristic solutions.

Mesh boundary encounters in the following scenarios can result in the loss of simulated individuals, at times, depending on the exact circumstances. First, the scenario of a simulated individual in 3-D located near the water surface and riverbank. At the next time step, the water surface drops but simulated movement behavior (an imperfect abstraction of the real world) keeps the individual near the previous *xy*-position where there is no longer water, or even a mesh if the grid is adaptive. Second, the scenario of two individuals at the same *xy*-position but at different depths, one at the water surface and one at the river bottom. At the next time step, the water surface drops. If we lower the individual at the water surface to maintain its depth, the one at the bottom cannot be handled similarly because it would then be placed under the river. If we chose to do nothing for the one at the bottom yet lower the individual at the water surface, then the ELAM model now treats simulated individuals differently according to depth — a model complexity that can have unintended consequences. Third, and similar but not exactly the same example as described earlier, the scenario of an individual at the riverbank an *n*-th decimal place (spatially) inside the river domain. At the next time step, computer precision/truncation results in the individual now an *n*-th decimal place outside the meshed domain. If the mesh has adapted during the timestep change, then sometimes there is no clear solution heuristic for identifying the most appropriate interior cell in which to place the fish. Fourth, the scenario of an individual in a wetting-and-drying scenario (Lai, 2010) where the Eulerian mesh changes with river inundation and water may not be spatially contiguous at all times near a riverbank or in the floodplain. A simulated individual near the riverbank or in the floodplain can be cut off from the river during drying cycles and find itself trapped with no way out when its refuge dries entirely.

Some of the above issues have robust solutions for passive particles and/or certain types of mesh geometries (tessellations). We want the same boundary encounter heuristics applied across all simulated fish, particles, and 2-D/3-D mesh element shapes to prevent such attributes from contributing to differences between applications. To date, we have found neither an optimum nor computationally-efficient solution heuristic for all combinations of possible mesh tessellation, element shapes, boundary topologies, and time-varying mesh/element/boundary changes that can arise in 2-D and 3-D.

3.15. Synchronizing observed and modeled passage/entrainment

Passage (entrainment) is often a critical biological criterion determining the engineering success of water operations management or the design of an in-river structure. To assess the performance of our approach, we want to quantitatively reproduce the passage/entrainment proportions of tagged salmon using the ELAM model. Synchronizing real and simulated worlds for comparative analysis, however, is not straightforward. Tagged salmon in 2008–2009 (Romine et al., 2013) and 2014 (Romine et al., 2017) may occupy our spatial domain prior to the simulation window and/or remain in the area afterward (**Figure 8**).

Transects immediately downriver of the junction (**Figures 3**, **8**) are used in our analysis to determine the final passage/entrainment (permanent exits) of tagged salmon (**Table 2**). The available telemetry data does not afford us the ability to move the transects further downriver. Tagged fish that occupy our domain before the simulation window and remain in the area afterward are not part of our analysis as these individuals represent a movement mode that our model does not attempt to reproduce. Non-downriver movement may be rooted in the tag being eaten by a predator not perfectly filtered previously (Romine et al., 2014), in a dead salmon on the riverbed, or long-duration milling/riverbank movement modes. We only use tagged fish with a predator probability less than 0.85 in the range $[0, 1]$ (Romine et al., 2014) at the time of their final, permanent exit for comparison with modeled entrainment (**Figure 3**e and **Table 2**). We do not count tagged fish that linger beyond our simulation window as part of the real-world entrainment proportion regardless of when they enter the domain (**Figure 8**). However, we do count tagged salmon that permanently exit during our simulation window even if they occupy the area beforehand.

Year 2009 predator probabilities from Romine et al. (2014) are formatted such that we can identify and remove suspected predators at a tag's first-ever detection (**Figures 3**d, **8** and **Table 2**). Year 2014 probabilities are formatted differently, so we assume all initial tag detections are salmon. Tagged salmon detected for the first time in our domain during the simulation windows, but that are not part of the passed/entrained tally are often fish released into Georgiana Slough that remain downriver of the transect; that is, these tagged fish reveal themselves in our domain only within the small spatial region downriver of the transect in Georgiana Slough. Our conceptual tradeoffs result in tagged salmon passage/entrainment into Georgiana Slough and downriver into the Sacramento River that total 100%.

Simulated salmon are tallied as they exit the ELAM model domain downriver of the junction (**Figure 8**) instead of the transect to allow individuals the opportunity to move upriver back into the junction area and select a different route from their first choice. In this way, the modeled and empirical passage proportions are comparable as it is the final passage decision of the observed (telemetry) fish that are factored. The spatial extent of the ELAM model domain is shortened from the river flow field mesh to more closely align with available telemetry field data (Figure 8). Simulated individuals, salmon or particles, that do not exit downriver (Figure 8) result from one of the following reasons:

- out-of-bounds release;
- mesh boundary interaction requiring removal;
- exits upriver;
- freely remains in the domain.

Simulated salmon exiting the domain at the upstream boundary are not factored into modeled passage/entrainment, which considers only downriver entrainment. Simulated salmon released on a particular day are allowed up through the end of the following day to exit after which they are removed from simulation and labeled as remaining in the domain. We do not attempt to capture the dynamics of salmon that linger in the domain longer than $24 - 48$ *h*. Simulated individuals that remain in the domain are often releases near the end of the simulation window. However, some non-exiting particles are caught in an eddy and swirl in the cul-de-sac of the Delta Cross Channel inlet region, and some salmon exhibiting a riverbank movement mode are removed downriver of the junction due to drying mesh elements.

Simulated individual exits are equivalent to measuring their passage/entrainment at the transects so long as they do not incur a mesh boundary interaction between the transect and domain extent necessitating its removal from simulation. Fish removed due to boundary interaction issues are not considered in passage/entrainment proportions. Our conceptual tradeoffs result in simulated entrainment into Georgiana Slough and downriver into the Sacramento River totaling 100%.

3.16. Release of simulated individuals

Five simulated individuals are released at the location (*xy*-position) and time of each initial tag detection within our simulation window (Figure 8). We avoid releases associated with tagged fish that have been in the area for days or weeks. Releasing five simulated individuals per tagged salmon is an arbitrary judgment based on balancing model runtime and the replicates needed to average out the required/unavoidable stochasticity in our cognitive algorithm ensemble (Table 6). Replicates also serve as a contingency against losing individuals during simulation from mesh boundary interactions. We believe the above approach makes the best use of our limited field data (Figure 3).

Vertical positions from the underwater acoustic-tag telemetry (*z*-coordinate values) are not accurate enough to determine water column locations, so we have to artificially generate the release depths at each *xy*-position. We assume the Sacramento River's depth is too shallow for salmon to exhibit a lognormal depth profile (Smith et al., 2010; Goodwin et al., 2014). Instead, here, we use a simple normal, or Gaussian, distribution $N\left(\mu, \sigma^2\right)$ with a mean depth $\mu = -2.5$ m and a standard deviation $\sigma = 0.75$ as follows:

$$\textit{Release depth} = \mu + \sigma\zeta \qquad (35)$$

where ζ is a value drawn from the standard normal distribution $N\left(\mu = 0, \sigma^2 = 1\right)$. In some cases, a release is out-of-bounds due to a depth (*z*-coordinate) generation that is under the river or imprecision in the field telemetry *xy*-position placing the fish outside the river channel in the *xy*-plane (Figures 3, 8). In 3-D simulations for year 2009, a release is out-of-bounds if not within the river domain in the horizontal plane at the fish's depth. In 2-D modeling for year 2009 and 2014, a release is out-of-bounds if not located within the horizontal plane of the river channel as depth does not factor into the simulations. We do not manually modify out-of-bounds release locations to convert them into in-bounds positions. Simulated individuals (salmon or particles) released out-of-bounds are immediately removed from simulation and play no further role in our results.

A minimum proportion of simulated individuals (salmon or particles) must exit the domain downriver within the simulation window for modeled entrainment to be valid in our analysis, either in comparison with real-world patterns or, later, as part of a prediction about the future. We arbitrarily require that the proportion of simulated individuals exiting the domain downriver be greater than the proportion of total tagged salmon exits (Table 2), less ~10%. In other words, since 86.6% and 85.1% of tagged salmon permanently exit during each seven-day simulation window for year 2009 we require that $\geq 75\%$ of simulated individuals must exit the domain downriver. We require $\geq 35\%$ of simulated fish must exit within each 2014 three- or four-day window (Figure 8) since only 43.0% of tagged salmon permanently exit during the timeframe of 22–24 March. The criteria we use is arbitrary but a useful way to flag and eliminate the use of outcomes where, for example but not encountered in this work, too many modeled fish are removed from simulation due to boundary violations described earlier. If the proportion of downriver domain exits does not meet the minimum thresholds, then there may be reason to doubt the synchrony of the simulation relative to the real world and, therefore, invalidates model results regardless of the accuracy achieved. In our study, the downriver exit proportions of simulated individuals (salmon and particles) always exceed 86% (Figure 8).

4. Results

Once the ELAM model is built and parameterized, in this case using the 2009 data alone, we simulate salmon and passive particles through the river reach. Later, we run the same model without any modification to year 2014 river conditions that include a novel fish guidance structure not present in year 2009 (Figure 1). To assess our stimuli responses (Tables 4, 5) and cognitive algorithm ensemble (Table 6), we first compare the movement swim paths of tagged and simulated salmon. Then, second, we compare the key quantitative metric at our location for water operations engineering and management: the proportion of salmon that enter Georgiana Slough versus continue downriver using the Sacramento River. Third and last, since near-term future predictions generally do not have the advantage of knowing beforehand how fish will enter the domain spatially or temporally, we evaluate many different spatiotemporal release distributions.

As passive particles are subject to the same analysis assumptions as modeled salmon, they can tell us whether simulated outcomes (paths, entrainment) are primarily due to our model setup idiosyncrasies such as the release assumptions and transect locations. Simulated particles also serve another important purpose in waterways engineering design. Passive particles are analogous to the historical use of colored dye in scaled physical models of river infrastructure, which has long served as an important engineering method for assessing in-river hydraulic structure design and management alternatives. To simulate passive particles, all the behavior computations still occur just as with modeled salmon, but we override the computed volitional swim speed vectors ($u_{volitional}$, $v_{volitional}$, $w_{volitional}$) to 0 m s^{-1} just prior to the implementation of equation [10]. Overriding the swim speed to zero eliminates the volitional movement contribution of all behavioral stimulus responses.

4.1. Swim paths

4.1.1. Year 2009 hindcast

Our first comparison of model versus real-world data leverages information about when and where tagged salmon enter the domain. We compare simulated individual (particle, salmon) movement paths with tagged fish two different ways: qualitative comparisons and heatmaps of their movement modes.

First, to qualitatively illustrate simulated behavior and paths across diverse tidal (ebb, flood, ebb+flood) environments without the complexity of varying hydrodynamics, we select date and time blocks when the river flow is relatively steady (unchanging with time) and tagged salmon are actively swimming. We use a single 3-D output, or snapshot in time, extracted from the original flow field time series for each example tidal (ebb, flood, ebb+flood) environment. Using the extraction (Figure 8 upper-right dyads), we simulate a passive particle (white path) and salmon (path colored by behavior B from Tables 4, 5) released at the same location (white circle) near where the tagged fish (black path) is first detected during the steady hydrodynamic window.

Tagged salmon paths and displacement differ markedly from passive particles across the diverse ebb, flood, and ebb+flood tide flow environments. Our stimuli responses (Tables 4, 5) and cognitive algorithm ensemble (Table 6) result in volitional swim speed vectors ($u_{volitional}$, $v_{volitional}$, $w_{volitional}$) that modify the particle path to more closely resemble that of tagged salmon in a variety of examples (Figure 8 upper-right dyads). In ebb tide flow, the simulated fish qualitatively resembles the zig-zag path of a tagged salmon via behaviors $B\{2, 3\}$ emerging from responses to V_M and G_M.

Eulerian-Lagrangian-agent method modeled fish qualitatively reproduce other, different movement patterns of tagged salmon during ebb+flood and reversing (flood) river conditions near slack tide. In the combined ebb+flood flow condition, ELAM salmon exhibit zig-zagging in the upper portion of the reach where water flows downriver while closer to the junction the model reproduces fish avoidance of Georgiana Slough. In the flood tide condition, the model reproduces salmon location holding or milling near the bridge piers where water flow direction reverses and moves upriver.

An explanation for simulated salmon not following the flow during tidal shifts (i.e., both the ebb+flood and flood tide conditions) can be visualized in Supplementary Figures 3–5 (part G in the upper-right). Without the advective contribution from fast moving water, the dynamic of opposing behaviors $B\{2, 3\}$ results in the emergent property of milling. The additional 10% positive rheotactic orientations of $B\{2\}$ and $B\{3\}$ aid the simulated salmon in not being appreciably swept down- or up-river. The emergent result appears to be a simulated milling that can, at times, resemble a correlated random walk. Here, however, the movement pattern does not stem from a correlated random walk parameterization in the classic sense; instead, the movement emerges from two competing, opposing behaviors with often-contradictory orientations.

The 10% increase in positive rheotactic orientation of $B\{2\}$ and $B\{3\}$ aids, but is not solely responsible for preventing, the simulated fish from being swept with the water. Since the 10% is only an increase and not an absolute orientation angle, the addition is not sufficient to offset a preferred direction in line with downstream flow. Near-slack tide, when water is moving slowly either downriver (Supplementary Figures 3G, 4G) or upriver (Supplementary Figure 5G), the preferred orientations of $B\{2\}$ and $B\{3\}$ also aid the individual in not being appreciably swept down- or up-river. In the downriver water flow scenario near the junction with Georgiana Slough, milling is aided by repulsion to acceleratory stimuli, $B\{4\}$, as seen in Supplementary Figure 4G.

Second, we categorize all of the simulated salmon responding to time-varying hydrodynamics used to compute passage/entrainment according to their predominant swim path pattern using the same visual inspection process earlier for tagged fish. Heatmaps and the movement mode proportions of simulated fish (Figure 8) and tagged salmon (Figure 3) highlight the differences and similarities in the swim paths of individuals used to compute passage/entrainment. Heatmaps are based on detected positions, which are not sampled equally between real and simulated worlds. Detected positions from underwater telemetry in the real world are not perfect (Figure 3) whereas modeled fish locations are known with certainty at $2-s$ increments throughout the domain.

Simulated fish swim paths are more concentrated along the river thalweg than for tagged salmon (Figure 3 vs. Figure 8 heatmaps). The larger proportion of zig-zagging in simulated salmon is anticipated given that this movement mode is a focus of our behavior rule development because it is, by far, the most predominant pattern of tagged salmon in our river reach (52.8% of tagged fish). Note the bridge is not rendered in the 3-D year 2009 mesh (Figure 5) and, thus, the piers' hydrodynamic signature is not perceivable to ELAM salmon for these simulations. Nonetheless, in the reversing flood tide flow scenario, simulated salmon in year 2009 still resemble some forms of milling or location holding without the pier-induced hydrodynamics (Figure 8). The lack of the bridge piers in the rendered 2009 hydrodynamics, however, is likely one reason why simulated salmon exhibit less milling near the piers (movement mode #4, Figure 8) than modeled fish in year 2014.

4.1.2. Year 2014 out-of-sample prediction (engineered fish guidance)

We apply our cognitive algorithm ensemble (Table 6) developed and calibrated using year 2009 data to out-of-sample, year 2014, river conditions that include a floating wall or surface-oriented guidance boom called the "floating fish guidance structure" (FFGS, **Figures 1**, **9**). The surface guidance boom extends below the water surface to a depth of 5 ft or 1.52 m (California Department of Water Resources, 2016; Romine et al., 2017). The boom and year 2014 hydrodynamics are modeled with a 2-D depth-averaged model (Lai, 2010).

We find that year 2014 simulated salmon swim paths in 2-D are not as heterogeneous as 3-D trajectories from year 2009. At least two factors are responsible. First, year 2014 lacks vertical heterogeneity. Second, horizontally, the 2-D depth-averaged hydrodynamic model output has a more diffuse laterally-distributed high-velocity core compared to the flow field rendered with an explicit 3-D flow field model (**Figure 4**). That is, in our 2-D flow field simulation, the higher velocity core is less concentrated in the river thalweg and distributed across a wider portion of the river's width compared to 3-D rendering of the flow field. A 2-D representation of the river does not perfectly correspond with a particular depth from an explicit 3-D rendering of the flow field since 2-D and 3-D modeling assumptions are different. The more diffuse high-velocity core in 2-D flow field rendering has a concomitant impact on hydraulic derivatives, particularly G_M. The impact of a more diffuse high-velocity core on G_M results in wider cross-sectional excursions of the simulated fish. The greater amplitude of 2-D zig-zag paths can also be attributed to the physical domain of the river. Natural channel cross-sections are often u-shaped (**Figure 5** upper left), so simulated salmon deeper will have less width (amplitude) before encountering hydrodynamics that trigger re-orientation compared to fish nearer the water surface where the river is widest.

Despite inherent tradeoffs involved with 2-D hydrodynamic simulation relative to 3-D, we can still use year 2014 outcomes to explain how salmon guidance and entrainment operates in the context of a salmon's past hydrodynamic experiences integrated at multiple scales. The simulated salmon swim paths in **Figure 9** are responding to time-varying hydrodynamics at the same time when tagged fish are observed swimming through the river reach. Simulated salmon paths in **Figure 9** are included in the **Figure 8** heatmaps. Simulated salmon perceptually sense and respond only to river hydrodynamics associated with the boom's presence in the water flow field, that is, modeled fish do not physically interact with the FFGS structure rendered in the mesh and they can pass through to the other side by, conceptually, swimming under in 2-D.

We find that caution should be exercised when attributing observed salmon movement and entrainment to a surface guidance boom's configuration and alignment. When the FFGS is deployed (on), hydrodynamics that emanate from the structure result in a filament of G_M that starts at the boom downriver endpoint and extends to the riverbank apex at the junction point where the river bifurcates (**Figure 9**). Salmon initially deflected at the boom toward the Sacramento River can be subsequently attracted to the G_M filament, drawing them toward Georgiana Slough (**Figure 9A** dashed gray region). However, not all boom encounters are followed subsequent attraction to the G_M filament (**Figure 9D** dashed gray region). Salmon can be hydrodynamically deflected toward the Sacramento River at the boom (**Figure 9A**) and also by the G_M filament downriver of the structure (**Figure 9B** dashed gray region). If the perceptual context is different, however, the filament can attract salmon into Georgiana Slough (**Figure 9C** dashed gray region).

Entry into Georgiana Slough is not always a result of filament attraction, as river flow can re-orient a salmon toward Georgiana Slough even if the salmon is initially deflected toward the Sacramento River (**Figure 9E** dashed gray region). Salmon can also respond to the boom by milling behind the structure (**Figure 9F** dashed gray region) or in front between the FFGS and dock on the opposite riverbank (**Figure 9H** dashed gray region).

River flow alone can direct salmon into the Sacramento River when the boom is not deployed (**Figure 9G** dashed gray region). Also, the G_M filament exists in shorter form when the FFGS is off, extending upriver from the riverbank apex point of bifurcation. At times, the shortened filament can act in combination with G_M emanating from the riverbank near the boom to attract salmon into Georgiana Slough even when it requires the fish to cross the critical streakline or water flowlines entering separate routes downriver (**Figure 9I** dashed gray region).

In summary, G_M can both repulse, $B\{2\}$, and attract, $B\{3\}$, nearby salmon. Broadly, influence of the guidance boom on salmon depends on the context of the fish's decision-making at the time of the boom encounter. Specifically, perceived hydrodynamic stimuli depend not only on the fish's momentary sensing but also on its memories of past hydrodynamic experiences that are integrated at multiple scales.

Figure 10 summarizes all computational movements of simulated salmon. The increase in riverbank boundary interactions in 2-D (**Figure 10**) compared to 3-D and 2-D extractions of year 2009 hydrodynamics is a result of releasing simulated salmon where tagged fish are first detected. Some tagged fish show up for the first time at the riverbank where the geometric configuration of Eulerian mesh elements are complex because of wetting and drying. As the water surface rises and falls with river flow, mesh elements along the riverbank are identified as wet or dry by the 2-D hydrodynamic model. Since the ELAM model does not permit simulated fish to enter or cross dry mesh elements, the geometric configuration of wet elements at the river's edge can, at times, be complex and in a practical sense trap some individuals from moving into the river toward the thalweg. Simulated fish that remain trapped along the riverbank for the duration of the simulation window in year 2014 show up in **Figure 10** as mesh boundary encounters, but are otherwise not factored into our analyses. For instance, the trapped simulated individuals are treated as out-of-bounds releases and do not contribute to the swim path heatmaps.

4.2. Passage/entrainment

The model performs well in the quantitative performance metric of greatest interest to our study, passage/entrainment (**Figure 11**). Final passage/entrainment is the permanent, final exit of individuals into either Georgiana Slough or the Sacramento River downriver of the junction (**Figure 8**). Root-mean-square error (*RMSE*) is a simple yet robust metric that quantifies the difference in the final passage percentages (i.e., ultimate measured fate or entrainment) between the tagged and simulated salmon across $7-$day contiguous multi-day windows for year 2009 and $3-$ and $4-$day contiguous windows for year 2014. The ELAM

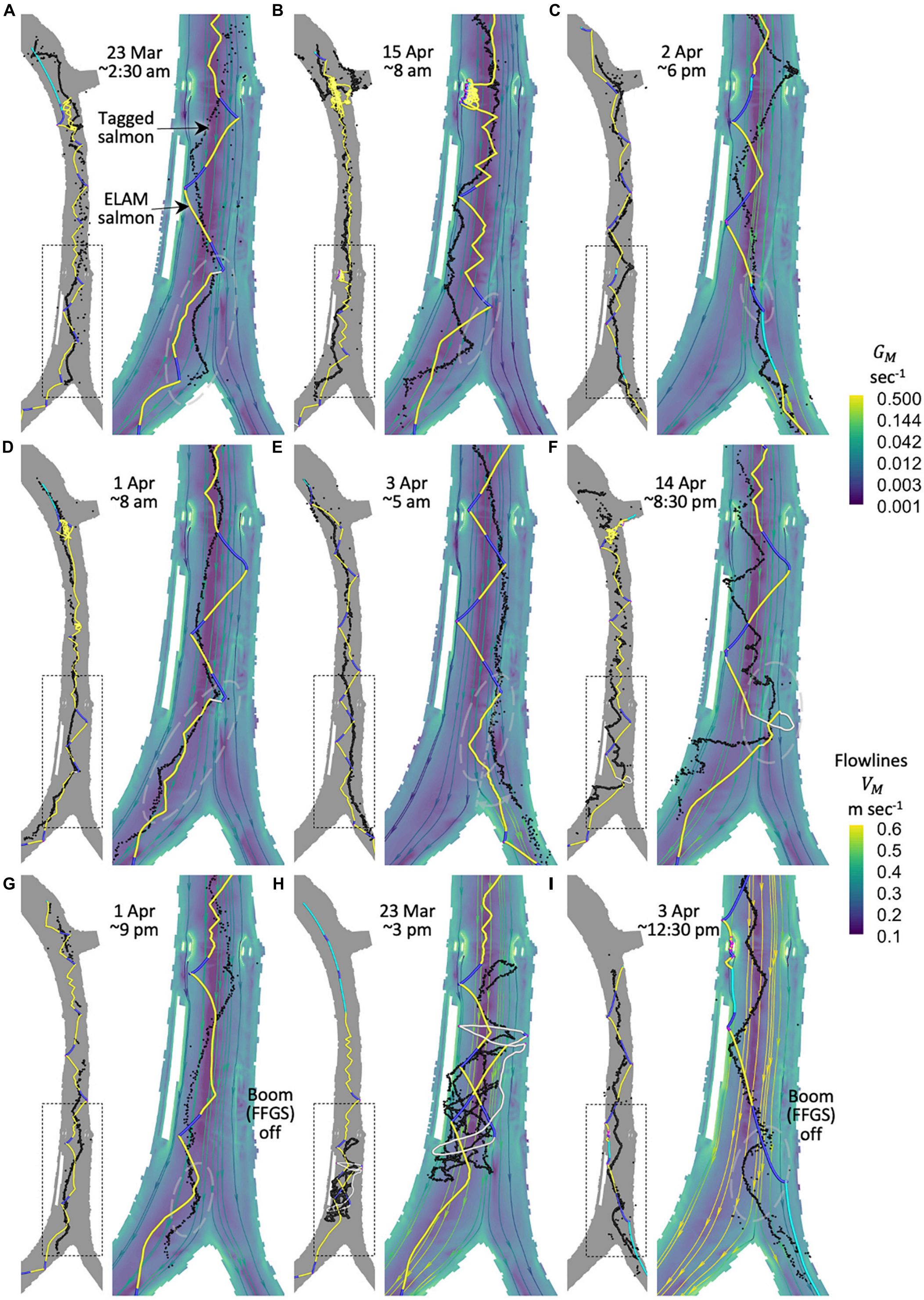


FIGURE 9

Year 2014 tagged and ELAM salmon response to the engineered surface guidance boom (FFGS) and the resulting entrainment. The ELAM model is built and calibrated with 2009 data, then applied without modification to year 2014 river conditions with the FFGS. Simulated salmon swim paths are responding to time-varying hydrodynamics at the same time that tagged fish are observed swimming through the river reach. Simulated salmon paths in the figure are included in Figure 8 heatmaps. Simulated salmon paths are colored by the behavior *B* (Tables 4, 5) and the tagged fish trajectory is colored black. Movement dynamics of simulated and tagged salmon near the FFGS are provided as dyads, where the left side is a zoomed-out view of the river reach and the right is a zoomed-in view of the FFGS with G_M contoured as a fill color and river water flowlines colored separately. Each dyad **(A–I)** represents a different category of context-based salmon response to surface boom hydrodynamics. Additional details: the tagged salmon in panel **(A)** returns later and the one in panel **(I)** several days later. Paths in panel **(B)** illustrate a tagged and ELAM salmon that begin around midnight while the hydrodynamics are plotted for 8 am when the fish pass the FFGS and junction. In panel **(E)**, we add a light gray geometric line and arc angle to ease visual interpretation of the tagged salmon direction before re-orientation toward Georgiana Slough. The tagged salmon path in panel **(H)** is longer than displayed and truncated here to ease visual comparison where primary similarities exist with the simulated fish.

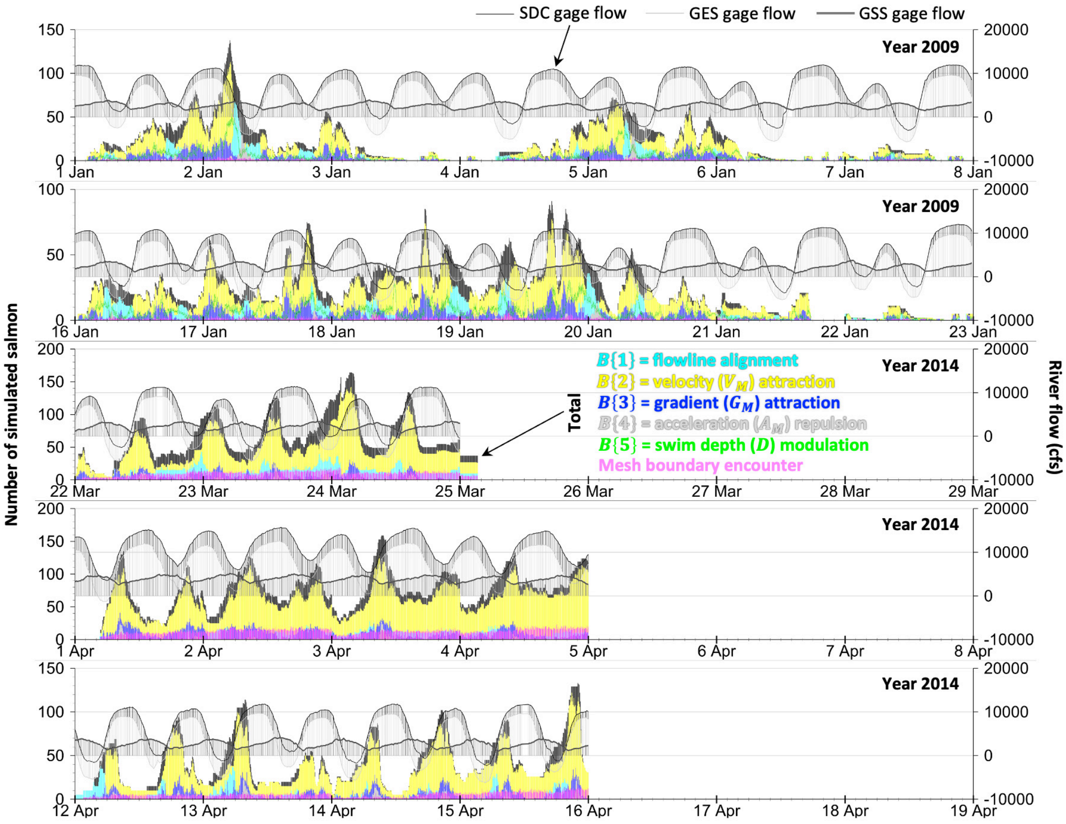


FIGURE 10

The distribution of behaviors $B\{1, 2, 3, 4, 5\}$ over time within the simulated salmon population throughout the river reach that underlie the movement mode heatmaps (Figure 8), simulated salmon paths near the FFGS in year 2014 (Figure 9), and modeled entrainment (Figure 11). The sum total of simulated salmon making decisions within the ELAM model domain at any given time (black) is decomposed into the number implementing each constituent behavior. Behavior proportions are overlaid, not stacked, with behaviors least represented in the population plotted overtop more predominant responses. Note how flow hydrodynamics as viewed by the gage stations (Figures 1, 2) change temporally and also by location within the river reach. Simulated salmon behaviors are updated every 2 s in response to river hydrodynamics that update at $3 - min$ intervals. Note that $B\{5\}$ is a vertical-only response that occurs simultaneously together with an xy-plane orientation set by one of the following behaviors from $B\{1, 2, 3, 4\}$ and can only be implemented in the year 2009 3-D mesh.

model generally reproduces past and predicts the near-future passage/entrainment with an $RMSE \leq 10$ (Figure 11).

We run sensitivity analyses to evaluate some key uncertainties in the model and its intended future use. Specifically, the standard deviation following the ± symbol (Figure 11) is generated by varying the random number generator seed that is part of the algorithm ensemble (Table 6) and, for 3-D, we also vary the random guesses of the release depth (z-coordinate).

Simulated salmon and passive particles that make up the passage/entrainment proportions are responding to time-varying hydrodynamics, and the classified movement modes of all these modeled individuals are heatmapped (Figure 8). A temporal distribution of behaviors (Figure 10) throughout the river reach underlies resultant passage/entrainment (Figure 11). No single hydrodynamically-mediated response behavior is solely responsible for the passage/entrainment pattern at the junction.

Passive particle passage/entrainment (Figure 11 blue shade background) represents neutrally-buoyant individual movement when the perceptual decision-making behavior is turned off. Passive particles are analogous to an entity merely following the flow/flowlines.

4.3. 3-D vs. 2-D

In 2-D simulations, both the vertical z-coordinate (depth-oriented) hydrodynamics and fish swim orientation/speed are eliminated. In the 2-D slice extractions for year 2009, a 2-D xy-plane horizontal slice is extracted from just under the water surface for each output in the original 3-D flow field time series. Simulated salmon passage/entrainment is resilient to the simpler 2-D descriptions of the river (Figure 11). Also, we provide an example comparison of a 3-D swim path (Supplementary Figure 1) and its 2-D counterpart within an extracted slice of the same hydrodynamic condition (Supplementary Figure 2).

The 3-D vs. 2-D passage/entrainment outcome suggests that the analysis of salmon with modeled perceptual decision-making may not always require the maximum permissible hydrodynamic resolution. Elimination of the vertical hydrodynamics and swim orientation/speed alone does not appreciably change the simulated salmon entrainment or trajectories, e.g., comparing Supplementary Figures 1 vs. 2, in our relatively shallow system domain. Nonetheless, modeling hydrodynamics as depth-averaged

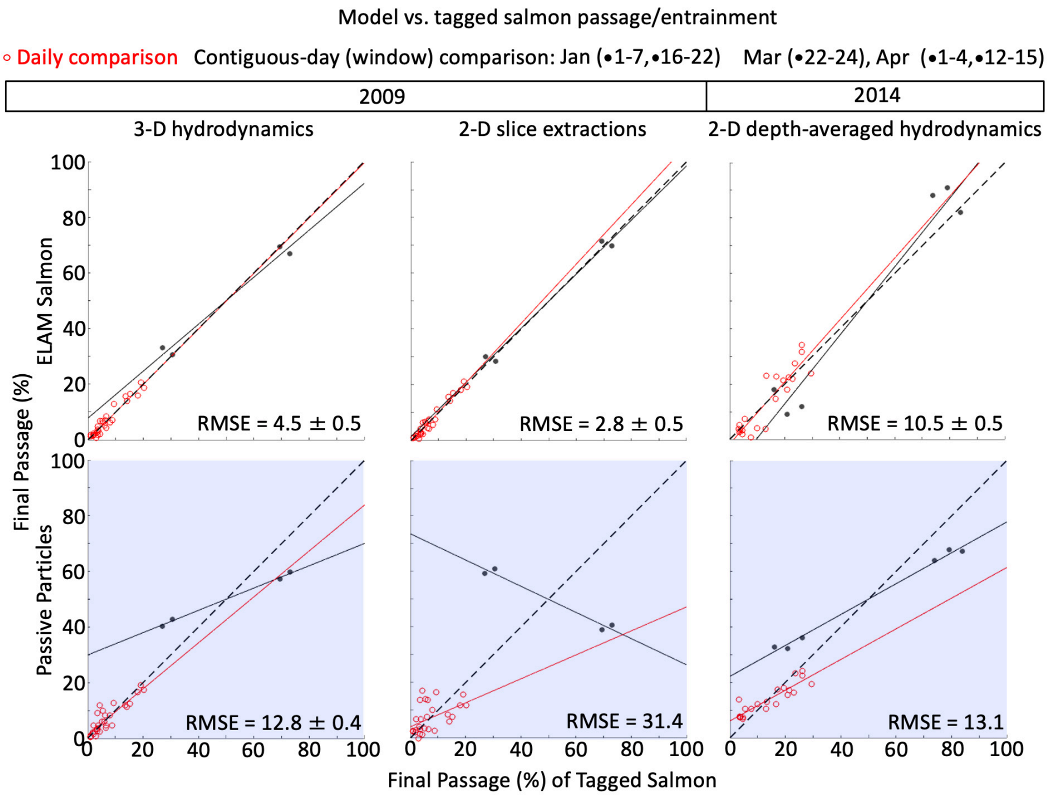


FIGURE 11

Comparison of tagged versus modeled salmon passage/entrainment. The ELAM model is developed with year 2009 data (**left** and **middle panels**), then applied without modification to out-of-sample, year 2014, river conditions that include a surface-oriented boom for guiding salmon **(right panels)**. Passive particle passage/entrainment is plotted with a blue shade background. Each dot represents a comparison of tagged salmon versus simulated individual (fish or particle) passage/entrainment on a percentage basis (%) downriver into either Georgiana Slough or the Sacramento River. There is one dot for the Georgiana Slough proportion and one for the Sacramento River. There are two black dots (Georgiana, Sacramento) for each simulation window (Figure 2), which represent the total cumulative passage/entrainment; for instance, in year 2009, there are two black dots for the cumulative passage during 1–7 January and another two black dots representing the total entrainment across 16–22 January, resulting in four total black dots. Red dots are smaller in magnitude because they represent the daily portion of the total (window) percent that went downriver in each route. The root-mean-square error (RMSE) is based on the cumulative passage/entrainment on a simulation window basis, i.e., the black dots. No 3-D model is used for year 2014; instead, a 2-D depth-averaged model is used to render year 2014 river hydrodynamics with the surface guidance boom.

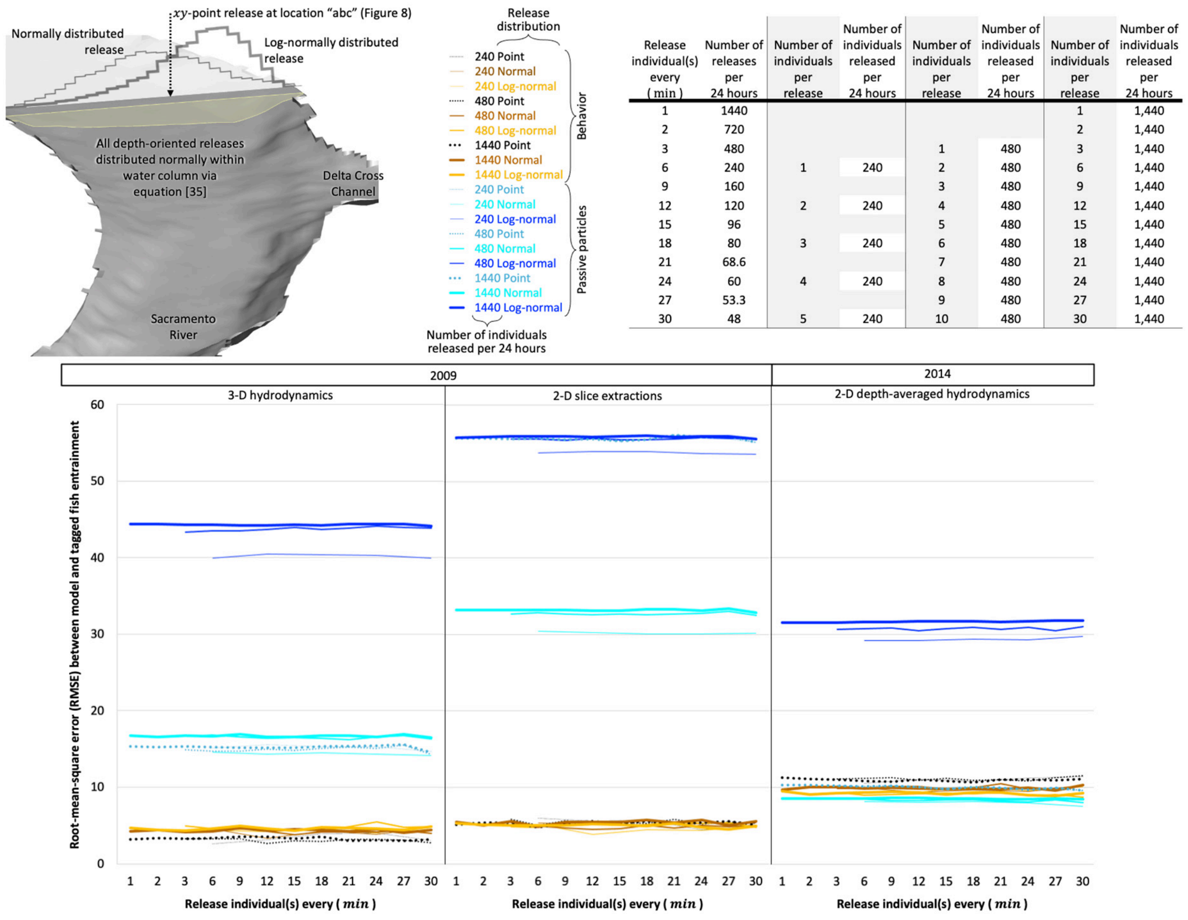
in lieu of 3-D phenomena does appear to influence the character of year 2014 swim path cross-sectional excursions compared to those in year 2009 regardless of whether the simulated salmon movement is generated from 3-D or 2-D slice representations of the water flow field.

4.4. When salmon entry pattern is unknown

Future predictions of fish movement behavior for informing water operations engineering and management do not always have the benefit of knowing how salmon will enter the domain of interest. We revisit year 2009 and 2014 passage/entrainment results without the benefit of tagged salmon to inform the release of simulated individuals (fish and passive particles) and with the added simplification that $B\{4\}$ is a *cruise* speed response regardless of the river flow field. The $B\{4\}$ simplification stems from more recent continuing efforts to simplify the model wherever possible, finding that the parsimony has an undetectable impact on simulated passage/entrainment.

While one can discount the timing of releases in steady (unchanging with time) hydrodynamics, e.g., Smith et al. (2010), when the environment itself varies with time then both the time sequencing and spatial distribution of individual entries into the domain could impact model outcome. To release simulated fish and passive particles into the domain without the aid of tagged salmon data, we arbitrarily use three different quantities of individuals per 24-*h* period, three spatial configurations (i.e., point, normal, log-normal distributions), and up to twelve different time intervals (**Figure 12**). Spatially, we release all simulated individuals within the same cross-sectional transect located at "abc" (Figure 8). Temporally, we release individuals separately and in clusters (**Figure 12** upper right). Simulated individuals are released irrespective of the river flow condition at the moment of release.

We plot the results of the sensitivity analysis in the form of root-mean-square error (*RMSE*) of the release alternative outcomes. The *RMSE* quantifies the difference in final exit passage/entrainment proportions (ultimate measured fate) between tagged salmon and the simulated individuals. A result is not plotted if the number of permanent exits downriver is less than 75% of the total attempted releases, which occurs only in two instances: point releases of 1, 440



Release individual(s) every (min)	Number of releases per 24 hours	Number of individuals per release	Number of individuals released per 24 hours	Number of individuals per release	Number of individuals released per 24 hours	Number of individuals per release	Number of individuals released per 24 hours
1	1440					1	1,440
2	720					2	1,440
3	480			1	480	3	1,440
6	240	1	240	2	480	6	1,440
9	160			3	480	9	1,440
12	120	2	240	4	480	12	1,440
15	96			5	480	15	1,440
18	80	3	240	6	480	18	1,440
21	68.6			7	480	21	1,440
24	60	4	240	8	480	24	1,440
27	53.3			9	480	27	1,440
30	48	5	240	10	480	30	1,440

FIGURE 12
Modeled passage/entrainment without the benefit of tagged salmon to inform the release of simulated individuals. Simulated individuals (fish and passive particles) are released using three different quantities per 24-h period, three spatial distributions (point, normal, log-normal) and, in time, up to twelve different ways **(upper right)**. All simulated individuals are released within the same cross-sectional transect located at "abc" **(upper left)**. Model accuracy in the form of root-mean-square error (*RMSE*) for each release alternative is plotted separately using a unique line and color combination **(upper middle)**. The *RMSE* of simulated fish passage/entrainment relative to tagged salmon is plotted using black or shades of orange while passive particles use shades of blue **(upper middle)**. *RMSE* quantifies the difference in final exit passage/entrainment proportions (ultimate measured fate) between tagged salmon and simulated individuals **(bottom half)**.

passive particles in the year 2009 3-D domain when released at intervals of 6 and 21 *min* apart.

Simulated fish passage/entrainment is resilient to alternative releases when *RMSE* is based on a contiguous passage/entrainment fate integrated over multiple days: 7 – day windows for year 2009 and 3– and 4 – day windows for year 2014 — the same method in Figure 11. Passive particles can resemble the passage/entrainment during 2014 hydrologic conditions when released using a point or normal spatial distribution, but log-normally distributed passive particles biased toward the outside bend of the river perform poorly for both year 2014 and 2009.

5. Discussion

We describe a cognitive approach to the mechanistic modeling of fish behavior responses to river hydrodynamics at the scale that water operations infrastructure is designed and managed. The ELAM model quantitatively describes and reproduces selective tidal stream transport patterns of downstream-migrating juvenile Pacific salmonids and predicts their guidance and passage/entrainment patterns in out-of-sample data across diverse environmental contexts. We find that a mix of behaviors (Figure 10) underlies our modeled swim paths (Figure 8) and passage/entrainment outcomes (Figure 11).

Our theoretical approach suggests that a behavioral mix is most likely to emerge in regions dominated by nonacute stimuli. ELAM analysis helps conceptualize the nuanced influence that engineered structures have on the movement of downstream-migrating salmon (Table 5: Engineering design relevance). The intended use of the ELAM model is to inform how future fish passage/entrainment outcomes may result from water operations infrastructure management and design. A numerical behavior model in which simulated fish quantitatively reproduce observed, tagged salmon passage/entrainment patterns (Figure 11) aligns with the tool's intended purpose.

Reproducing past animal movement patterns (hindcasting) is one way to establish confidence in a model's validity (Getz et al., 2018; Leitch et al., 2021). A model's accuracy should stem from the underlying mechanisms, and comparing quantitative predictions to new observational data is one of the strongest tests of scientific theory (Dietze et al., 2018).

Our goal at the outset of the study was to develop a decision-support tool capable of quantitatively reproducing passage/entrainment proportions within an arbitrary root-mean-square error (*RMSE*) of approximately ten, similar to previous work in other environmental contexts (Goodwin et al., 2006, 2014). In this system, ELAM model accuracy visibly degrades as *RMSE* exceeds approximately twelve (**Figure 11**) and *RMSE* much below ten has diminishing benefit.

A key finding of our work is that the repertoire of hydrodynamic responses in a tidal setting are theoretically consistent with — a superset of — the behaviors that juvenile Pacific salmonids exhibit in simpler, steady flow reservoir settings (**Figure 13**). Salmon often navigate both reservoirs and dams in the upper watershed (Martinez et al., 2021) followed by tidal environments closer to their ocean entry. The ability to mathematically describe, reproduce, and predict fish movement behavior across such diverse environments strengthens water operations decision-support in application to scenarios outside the range of conditions to which the tool is calibrated, a typical need of engineering and management design future forecasting.

The model herein is an abstraction of reality and the underlying mechanics are not a holistic description of salmon movement behavior or the cognitive architecture of fish. There is no such thing as a perfect ecological forecast (Dietze et al., 2018). Numerous questions remain for future study. In the model's minutiae, for instance, we identify at least two instances where practical functionality deviates from anticipated theory. First, E_4 differs from the *nsd* construct of other stimuli, Equation 20 vs. 2; that is, our current formulation for describing perceived changes in intensity does not appear to work as anticipated when using depth as a proxy for salmon swim bladder pressure. Second, $I_{a_2}^{fast}$ outperforms I_2 in E_2^{slow} from Equation 24; that is, we find that I_2 in E_2^{slow} does not work and that Equation 24 is the construct that works within our modeling approach for an immersed individual to perceive meaningful large spatiotemporal scale changes in river water speed due to the tides. Perhaps the deviations are the result of simulated abstraction and limited mensuration of the real world.

At a broader level, our work raises the question of how many timescales animals may use and how the number might be related to environmental and social complexity (Rodriguez-Santiago et al., 2022; Tump et al., 2022; Li et al., 2023). Our work provides a basis upon which further improvement and advancement is likely. Further improvement must confront nontrivial tradeoffs that we discuss next.

5.1. Model realism vs. usefulness

The ELAM is similar to other models in that it is a simple, finite, and abstract representation of reality. Perhaps the single biggest challenge of our work is finding the best balance between model realism and usefulness in the context of how the tool is to be used. Tradeoffs between model realism and complexity are a common problem (Getz et al., 2018). Increasing model complexity can come at the expense of concomitant deleterious impacts on tool transferability to settings beyond which the tool is calibrated (Yates et al., 2018).

Realism can be added in the form of more detailed hydrodynamics and/or behavior rules. The practical downside of increasing the model's complexity for realism alone is the additional computational burden incurred, which then reduces the resources available to explore and improve the model elsewhere. Determining the most important real-world features for a model to reproduce is paramount, yet rarely straightforward. The demands of scientific inquiry and engineering construction deadlines are rarely in perfect synchrony.

Hydrodynamic modeling impacts the realism of simulated trajectories. Additional flow field heterogeneity and stochasticity provided by DES or LES compared to RANS (**Figure 4**) would likely result in more heterogeneous, and thus realistic, simulated trajectories. As is, our modeled salmon entrainment predictions (**Figure 11**) are generally insensitive to vertical hydrodynamics and vertically-aligned movement behavior $B\{5\}$ in the relatively shallow Sacramento River. Nonetheless, secondary currents (Dinehart and Burau, 2005; Fong et al., 2009; Constantinescu et al., 2011a; Moradi et al., 2019; Yan et al., 2020; Schreiner et al., 2023) and water column heterogeneity should not be entirely discounted as a factor in salmon entrainment (Ramón et al., 2018). Selective tidal stream transport (Creutzberg, 1961) may be driven by multiple factors (Benson et al., 2021; Gross et al., 2021b) including vertically-aligned hydrostatic pressure (Tielmann et al., 2015) and horizontal, cross-sectional gradients in water turbidity (Bennett and Burau, 2015).

Adding explicit behavioral variation to our simulations through distributions of animal characteristics, such as size or orientation tendencies (movement modes), would likely improve the realism of simulated trajectories. Presently, we eliminate (zero-out) all permissible stochasticity and heterogeneity not explicitly required to meet our primary objective — reproduce and predict future passage/entrainment — in order to minimize the number of tunable parameters. We find that discerning meaningful parameter influences on key mechanics of the model is far more challenging when other forms of variability (stochasticity) are present in the model, e.g., attributes with the sole purpose of increasing the "wiggle" realism in simulated fish trajectories. While discerning parameter influence on model performance amid stochasticity is a challenge that can be met with Monte Carlo or similar methods, again, increasing the computational burden within a study has tradeoffs with those resources becoming unavailable elsewhere where they might have a greater overall impact. ELAM model parameter values herein do not change during simulation and are identical across all the analyses described, the only exception being the random number seed varied for computing the standard deviations in modeled entrainment (**Figure 11**).

There are many opportunities for future improvement relevant to the data presented herein and in application to other systems. For example, alternative algorithms exist for every ensemble constituent (**Table 6**). Continuing work can improve our understanding of fish and the mechanics required to meet fish passage research and water operations goals, just as this work builds upon previous work (**Figure 13** and **Tables 1**, **3**). In the next section, we discuss some of the more noticeable aspects

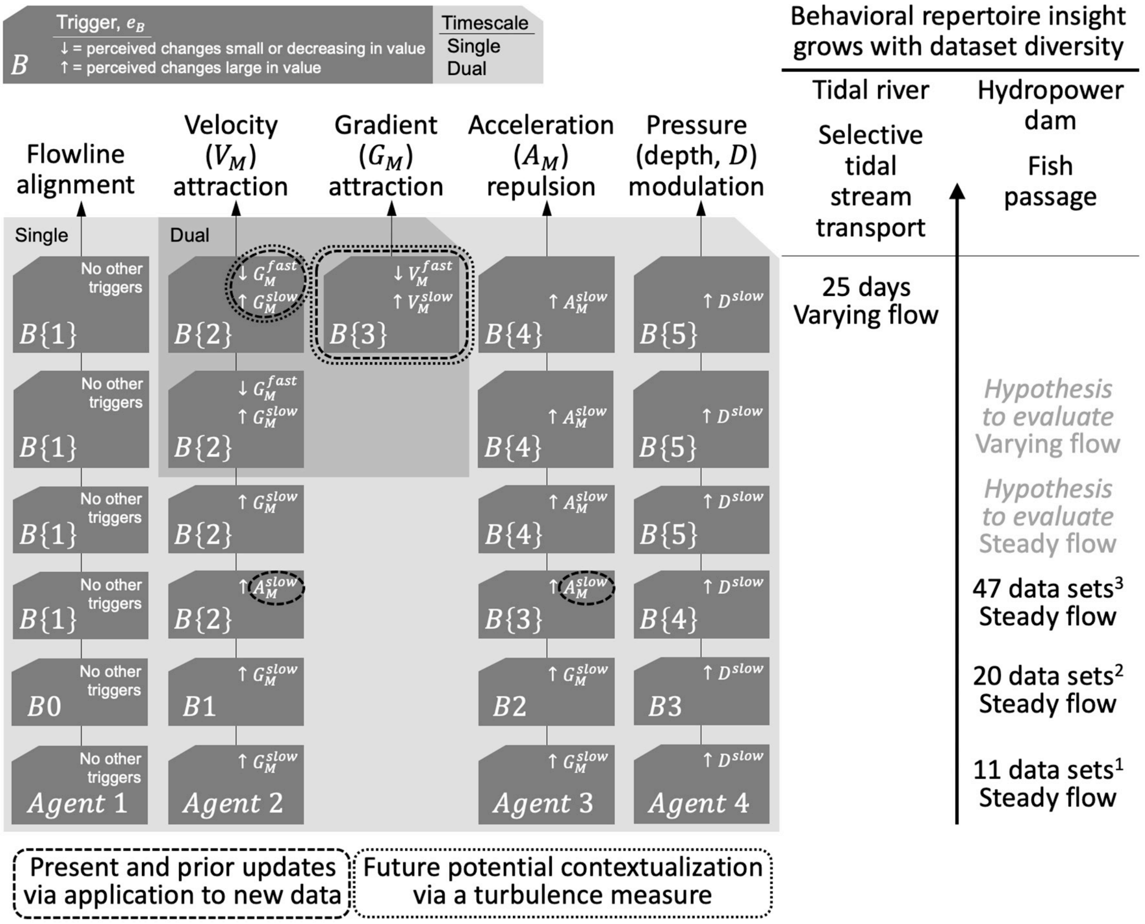


FIGURE 13
Results to date and future potential improvements from iterative near-term ecological forecasting (Dietze et al., 2018) in the context of fish passage, guidance, and movement prediction for water operations management and infrastructure design. The salmon movement behavioral repertoire developed in our tidal study is a conceptual superset of the fish hydrodynamic responses found in simpler environments represented with steady flow. Old notation from past applications: to a single dam [1]Lower Granite Dam (Goodwin, 2004), [2]multiple dams (Goodwin et al., 2006), and [3]basin-wide (Goodwin et al., 2014) where G_M and the term *strain* in prior works[1,2] are interchangeable for the data and *acclimatization* is used[1,2] instead of the terms *habituation* and *memory* used herein.

of our modeling approach, shortcomings, limitations, and future improvement opportunities.

5.2. Fish swim paths

Simulated salmon paths emerge from behaviors that depend on past experience, resulting in movement trajectories that differ among individuals experiencing the same momentary condition. In our approach, two hypothetical fish experiencing the same condition at a moment in time will exhibit different behaviors and, therefore, movement paths because their past histories are not identical.

While examples can be found in our study in which two simulated salmon — or a simulated and tagged fish — trace nearly the same path (e.g., **Figures 8**, **9**), more generally, pairs of individuals (modeled versus modeled; modeled versus tagged) do not have identical trajectories that coincide both spatially and temporally. Thus, our study highlights a surprising but useful paradox: that is, one-to-one paired synchrony between simulated and tagged salmon paths, while desirable, is not a requisite for satisfactory hindcasting and future prediction of route passage/entrainment. Upon inspection, there are several reasons for the paradox.

One reason for the paradox is that movement dynamics near the junction are more important for determining entrainment than behavior elsewhere within the river reach. Therefore, paths do not have to coincide perfectly both spatially and temporally throughout the entire reach. The most important factors for the correspondence between modeled and tagged fish passage/entrainment proportions in our tidal study are that each of the sample populations (i) volitionally control much of their displacement and fate within the river channel, in contrast to passive particles, and (ii) make decisions similarly-enough in similar-enough proportions across a broad range of conditions. Location holding is one way that a tagged salmon may sample river hydrodynamics analogous to a simulated salmon, but at a later time after milling in a region for a while. Another reason for the paradox is that the sample sizes, while somewhat relatively small once parsed to our simulation windows

(**Figure 3** upper left), are sufficient to average out a variety of characteristics both in salmon movement and in experienced water flow patterns as evidenced by the sensitivity analysis (**Figure 12**).

5.2.1. Movement mode heatmaps

We use heatmaps to compare swim path patterns and movement modes across our samples of virtual and real fish. The relatively concentrated simulated salmon swim paths along the river thalweg (**Figure 8**), compared to tagged fish (**Figure 3**), can likely be improved by distributing the modeled fish further throughout (across) the river's width by increasing the presently-negligible stochasticity in swim orientation. Increasing swim orientation stochasticity, however, will come at the expense of slowing down their speed-over-ground that is already slower than tagged fish. Speed-over-ground could be increased by implementing faster swim velocities (e.g., larger fish), but bigger individuals will bias the decision-support tool away from resembling the smaller-sized salmon important to water operations management. A distribution of small-to-large salmon fork lengths is likely a desired next step, but not part of the study herein.

Another possibility for reducing the discrepancy between simulated and tagged salmon path concentrations is modifying how the sensitivity of perceived changes in G_M and V_M are handled. Presently, G_M and V_M perceived changes are handled via threshold values that do not change with time. Perhaps the threshold values, instead, depend on previous hydrodynamic experience, which would add yet another layer of contextuality to behavior.

Further, the G_M trigger and attraction behavior may themselves be contextualized via multimodal signal integration (Gil-Guevara et al., 2022) with a turbulence measure (**Figure 13**). While our development efforts with year 2009 data reveal that *TKE* is sometimes not present in areas where salmon repeatedly re-orient (**Figure 6** and **Supplementary Figures 1**, **3**, **5**), perhaps the less pronounced *TKE* values have value in eliciting less concentrated paths when used in combination with our existing hydrodynamic triggers (**Table 5**). A challenge within the above endeavor is to realize a more distributed concentration of simulated salmon swim paths across the river's width without incurring a concomitant increase in boundary interactions.

Other observed discrepancies between simulated and tagged salmon evident from the heatmaps (**Figure 3** vs. **Figure 8**) include more tagged salmon exhibiting reach milling and riverbank tendencies, although this is a natural byproduct of our focus on zig-zagging behavior. Interestingly, heatmaps reveal similarities between tagged and simulation salmon milling near the bridge despite the piers (and associated hydrodynamics) being absent from the year 2009 flow field renderings.

5.2.2. Synchronizing modeled and tagged fish swim paths

A better end-state of the model would preserve the existing entrainment fidelity while gaining full synchronization between real and simulated fish trajectories (path plus timing), which requires reproducing the emergence of different movement modes in the same proportions. Manual classification was best able to handle anomalies in the real-world fish data for this present study, but future work should focus on automated methods that can assist the development and parameterization of more realistic reproductions of tagged fish movement modes and individual trajectories.

A solid next step would be a quantitatively rigorous movement mode classification (Romine et al., 2014; Vilk et al., 2022) combined with trajectory similarity measures such as the Fréchet distance or dynamic time warping (Magdy et al., 2015; Cleasby et al., 2019; Su et al., 2020; Tao et al., 2021) for gauging the one-to-one correspondence between pairs of simulated and tagged salmon swim paths. Larger (longer) river spatial domains and temporal windows would facilitate the analysis of movement mode emergence, allowing us to better understand whether modes are more closely correlated with specific individuals, a particular sequence of environmental experiences, or a mix of factors.

Existing travel time discrepancies between simulated and real fish may be improved through the previously mentioned tactic of releasing modeled salmon with a distribution of sizes (fork lengths). Larger fish swim faster if the assumed *body lengths per second* remains unchanged, although it is also possible to modify the assumptions of *drift*, *cruise*, and *burst* swimming $BL\ s^{-1}$ for our identically-sized 120 mm salmon. With the model as is, we discuss three possible explanations for the slower transit time of the simulated salmon example in ebb flow (**Figure 8** and **Supplementary Figures 1**, **2**): swimming depth, rheotaxis, and RANS flow field modeling, all of which relate to hydrodynamic model fidelity that we discuss in the next section.

5.2.3. Hydrodynamic model fidelity

Rivers have more heterogeneity than we can fully measure or model (**Figure 4**), and the issue is relevant to fish movement analysis as evident in the comparison of real and simulated travel times in **Figure 8** and **Supplementary Figures 1**, **2** during ebb flow. Our fish behavior simulations using 2-D *xy*-plane horizontal slices use the hydrodynamics extracted from just under the water surface where river flow is typically fastest (**Supplementary Figure 2**). In 2-D, simulated individuals cannot move along the river bottom where water speed is slower and sometimes approaches zero. Given that 2-D simulated fish transit times (**Supplementary Figure 2** particle: 46 *min*; salmon: 1 *h* 1 *min*) are similar to the results from 3-D (**Figure 8** and **Supplementary Figure 1** particle: 46 *min*; salmon: 1 *h* 3 *min*), we can conclude that vertical heterogeneity in river flow contributes negligibly to the travel time of these specific individuals over the duration they journey the reach in this flow condition.

Notice that the tagged fish transits the stretch in 41 *min* while the passive particle takes 46 *min*. The result appears at first inconsistent with our finding that simulated salmon must orient against the flow, which slows ELAM fish relative to a passive particle. Orienting the simulated 120 mm sized salmon more with the flow (negative rheotaxis), however, increases the zig-zag period (wavelength) that reduces similarity between simulated and tagged fish swim paths.

Another possible explanation for the longer simulated salmon transit time resides in the notion that RANS modeling represents an average flow field condition of the river (**Figure 4**). RANS flow field modeling can miss high-velocity regions or cores (Constantinescu et al., 2011b). We surmise that real-world flow field heterogeneity provides tagged salmon opportunities in the real world to exploit regions of faster-than-RANS water that is unavailable to simulated fish and may at least partially explain the slower transit times of the modeled fish in ebb flow (**Figure 8** and **Supplementary Figures 1**, **2**).

5.2.4. Behavioral choice/decision model fidelity

Mathematical models of decision choice, and the dynamics that underlie them, are an active area of research not only in ecology and ethology but other fields as well, especially the field of economics, and have been for more than a half-century (**Table 1**). There are many different choice/decision models to choose from. The scale of our study and the assumptions we invoke do not make our study or findings the best platform to advocate for one theoretical approach (theory, model) over another. Others may find in work at the same scale (but different environmental context) or at different scales (the laboratory) that there are advantages/disadvantages to a particular theoretical approach which differ from our experience here. In this study, using sensory evidence accumulators at our available scale, we find that for the rise and fall of competing behaviors in the hierarchical repertoire to generate the type of fast response dynamics we observe in tagged fish in particular areas (e.g., near the riverbank) that we need the contribution of inhibition in our decision model. In our approach, inhibition facilitates a better transition between behaviors $B\{2, 3\}$ by keeping their sensory accumulators, e_B (Equations 4–7), in a more stable harmony compared to the same formulation without inhibition. Without inhibition, we find that $B\{2, 3\}$ responses in some contexts are simply too slow to resolve themselves when needed because the impending behavior must catch-up and overtake the accumulated evidence of another behavior's e_B and by the time the former outraces the latter the simulated fish encounters a boundary, is captured, or is entrained, for instance.

5.3. Fish passage/entrainment

Synchronizing real and simulated worlds in order to compare salmon passage/entrainment proportions is not straightforward. Tagged salmon may occupy the river reach domain prior to our simulation window and/or remain in the area afterward (**Figure 8**), which limits the number of tagged salmon that we can leverage in short windows. Analyzing the entire 2008–2009 and 2014 field seasons (**Figure 2**) with larger spatial domains extending upriver and downriver would allow us to piece apart further nuances of salmon movement modes, as previously mentioned, as well as incorporate more of the available fish field data. ELAM applications that far exceed previous limitations are becoming viable with hardware improvements (Rodi, 2017) and the ability to work with trillion-cell hydrodynamic solutions on a common computer (Imlay et al., 2018).

5.3.1. Release distribution

Decoupling the cognitive algorithm ensemble from a realistic entry of fish into the river reach domain results in simulated individuals that cannot sample the environment perfectly in line with tagged salmon. We can use alternative release distributions to assess the model's prediction performance in the context of an unknown future, but in which post-construction monitoring may provide data on how real fish responded to the management action. We measure model accuracy using *RMSE* based on multi-day contiguous windows (**Figures 11**, **12**). Daily passage/entrainment numbers are inherently more variable due to the fewer available numbers of tagged salmon (**Table 2**) and simulated fish that make up the proportions. There is value in integrating field and model passage/entrainment data over multiple days.

5.4. Guiding fish swim paths with surface booms and engineered hydrodynamics

Fish guidance is a major focus of water operations management and engineering in many rivers worldwide. Fish guidance has been attributed to turbulence plumes (Coutant, 1998, 2001; Zielinski et al., 2021) and also to velocity V_M attraction triggered by a stimulus (Goodwin et al., 2006, 2014). The V_M attraction hypothesis of fish guidance assumes the two hypotheses are compatible as turbulence is correlated in many settings with G_M and A_M identified as trigger proxies (**Figure 13**).

Analyses of fish guidance along surface booms using 3-D hydrodynamic modeling that led to the V_M attraction hypothesis have yielded different triggers, and the exact trigger remains unclear. Initial studies using the V_M hypothesis attributed the trigger to G_M only for later analysis to suggest A_M (**Figure 13**). Our study here advances past contradictions toward a consistent explanation worth evaluating further; that is, G_M and A_M play different roles near guidance structures. Here, we find that G_M triggers V_M attraction along booms which corroborates some findings in laboratory experiments (Swanson et al., 2020). Acceleration A_M on the other hand acts to repulse salmon.

A topic for future research is whether G_M attraction (triggered by V_M) acts in combination with V_M attraction (triggered by G_M) to elicit salmon guidance along infrastructure and, if so, the relative contribution of G_M attraction. Also worthy of further investigation, as mentioned previously, is how turbulence may act in combination with G_M and V_M as a trigger. Regarding acceleration, our findings add to the body of evidence that A_M can repulse fish (Haro et al., 1998; Kemp et al., 2005; Enders et al., 2009a, 2012; Vowles et al., 2014).

5.5. Other behavioral stimuli — temperature, dissolved gases, sound, and bubbles

Many of the concepts and theory that we leverage do not originate from studies on fish or hydrodynamics. Therefore, our approach may be extendable in aquatic systems to other environmental variables (**Table 1**). Insonified bubble curtains with light stimuli were deployed at the Sacramento River junction with Georgiana Slough in years 2011 and 2012 (California Department of Water Resources, 2012, 2013; Perry et al., 2014) and remain a future management option in the Bay-Delta to improve system-wide salmon survival.

5.6. Engineering best practices for predicting fish response to water operations

To facilitate iterative near-term ecological forecasting (Dietze et al., 2018) that can support water operations infrastructure engineering and management, we need best practices. We can begin developing engineering best practices for using fish movement simulations to inform civil infrastructure design and water operations management in the context of future environmental conditions that cannot be fully known in advance. While fish in the future observed during post-action monitoring are likely to experience hydrodynamics that differ in some ways from the assumptions in management design, there are several ways to maximize the utility of fish movement prediction given inherent and unavoidable limitations.

The first way to maximize the utility of fish movement prediction in design is to simulate their response to alternative designs, with each engineering concept evaluated across numerous future environmental conditions. Best practice would be to simulate across, or bracket, the likely future environmental conditions. Unfortunately, the drawback of the first method is the large number of simulations that can quickly outrace available resources.

The second method compares future design alternatives only in the context of the same conditions as past observations. The benefit of the second method is that past observations can inform some of the model's initial conditions, e.g., fish entry patterns, and simulated future outcomes can be benchmarked relative to historical data in the null case of zero changes. The downside of the second method is the limitation of the design analysis to only past observed conditions that may not be relevant to the future.

The third method compares the performance of alternative design concepts relative to one another, with no relation back to past observed historical patterns. The benefit of the third method is that the analysis of future designs can use environmental conditions that differ from the past and fewer contexts (simulations) are needed for a trend to emerge that may identify a particular design as most robust across diverse environmental states. The downside of the third approach is that at least two design alternatives are needed to make a minimal, relative comparison.

5.7. Real-time fish prediction with theory-informed machine learning

Emerging new forms of automation can help address existing ELAM model shortcomings. Easier and faster implementation of the ELAM is needed to scale-up our approach for informing water operations management and design. We are working to encode our cognitive approach, such as multiplex signal disentanglement via multi-timescale perceptions, into a reduced-order form using theory-informed neural networks. The potential is motivated by the recent revolution of *physics-informed neural networks* (Karniadakis et al., 2021), reinforcement learning (Reddy et al., 2018; Ullman, 2019; Gunnarson et al., 2021; Li L. et al., 2021; Zhu Y. et al., 2021), and emerging concepts for improving machine learning by constraining them with psychological theory (Bhatia and He, 2021; Peterson et al., 2021). A reduced-order form of the ensemble algorithms in our approach may work better for the tight schedules that are common in engineering design projects. Machine learning has the potential to improve cognitive modeling by circumventing complicated assumptions about perception, attention, and memory that burden many existing methods (Bhatia and He, 2021; Peterson et al., 2021).

At the same time, hydrodynamic RANS, DES, and LES models will only grow in capability. As 3-D modeling of rivers becomes more sophisticated, cognitive-based approaches to mechanistic and machine learning based fish prediction may find particular value in new, *in situ* measurement technologies such as Infrared Quantitative Image Velocimetry or IR-QIV (Schweitzer and Cowen, 2021). River-wide, centimeter-scale IR-QIV hydrodynamic measurements can not only inform hydrodynamic modeling but also, paired with biologgers measuring fish orientation and swim speed, provide the real-time data streams needed to inform on-the-fly ELAM theory-informed machine learning. On-the-fly ELAM theory-informed machine learning has potential to provide real-time fish prediction of behavioral response, whether seconds or days in advance, greatly reducing the present time it takes to implement an ELAM prediction analysis.

5.8. Ethohydraulics with environmental modeling to improve waterways engineering

Recursively applying near-term predictions of fish movement followed by later comparison with observed data improves ecological research relevance to society by informing sustainable decision-making (Johnson et al., 2020) and accelerating the pace of scientific discovery (Dietze et al., 2018). Our present approach to behavior modeling is an outcome of iterative, trial-and-error work (**Figure 13**) to account for fish cognition in the interpretation and near-future prediction of their movement near water operations infrastructure. In the grand scheme of needed decision-support tools, our approach is a scaffold upon which future improvement is encouraged. There are many avenues for future improvement and research. For instance, the model does not presently account for foraging or seasonal influences on feeding behavior. Also, the environment can modify the cognitive dynamics of a species (Austin and Dunlap, 2023), so the potential exists that salmon decision-making is changing whilst we're interpreting their movement behaviors from past years.

In civil and environmental engineering, a practical difficulty is the effort needed to develop 3-D representations of a river compared to less-realistic 2-D renderings (Robinson et al., 2019), especially when predicting future hydrologic conditions. Simulated salmon swim paths in 2-D are not as realistic yet sufficient to predict passage/entrainment as well as some specific trajectory patterns. In our study, the 2-D hydrodynamic features are sometimes less concentrated in the river thalweg resulting in simulated fish trajectories with wider cross-sectional excursions. Nonetheless, our findings suggest that a cognitive approach to mechanistic fish movement behavior modeling does not always require the maximum possible resolution in river hydrodynamics.

By juxtaposing the findings from multiple studies, we can deduce further hypotheses for future evaluation to build a more holistic understanding of salmon movement behavior as well as for other downstream-migrating species (**Figure 13**). The potential appears to exist for a single parameterization capable of predicting near-future, out-of-sample juvenile Pacific salmonids across diverse reservoir, dam, and tidal environments – and in different river basins – sufficient for water operations management and engineering design. Further, we speculate the repertoire (**Table 5**, **Figure 13**) is relevant to other species with a goal to move downriver and that inverted forms of the stimuli-responses may describe aspects of upstream-moving fish (McElroy et al., 2012; Zielinski et al., 2018, 2021; Zeng, 2022; Kerr et al., 2023; Luis and Pasternack, 2023).

Here, we demonstrate how prior experiences and the temporal sequencing of stimuli are central to understanding salmon movement behavior in rivers. Practically, our findings show that it is possible to construct an abstracted form of animal cognition for a mechanistic behavior model that can operate at the scale of real-world waterways infrastructure, a critical step toward making quantitative near-term predictions of fish movement a reality for improving water resources planning, management, and engineering design.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author.

Author contributions

RG, YL, DS, JM, RT, and RR designed the research. RG performed the research, analyzed the data, and wrote the manuscript. RG, YL, DT, and DS contributed new analysis tools. All authors contributed to the article and approved the submitted version.

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Conflict of interest

DT was employed by Tecplot, Inc.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.703946/full#supplementary-material

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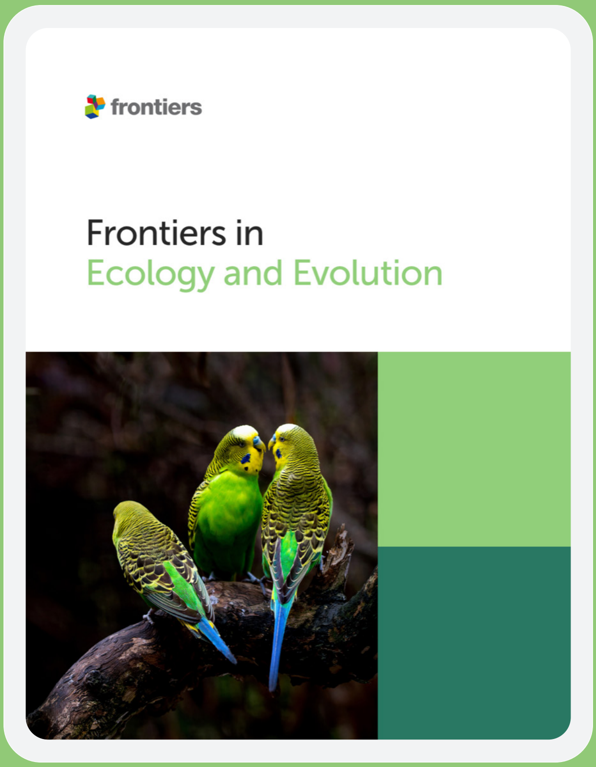
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