

1 Introduction

Conservation translocations are increasingly used to counteract species loss (Seddon et al., 2007; IUCN/SSC, 2013) and comprise (1) reintroductions, (2) reinforcements/augmentations, (3) assisted colonizations, and (4) ecological replacements (Bodine et al., 2008; Brichieri-Colombi and Moehrenschrager, 2016). However, translocations are costly and have high failure rates due to animals experiencing low post-release survival (Berger-Tal et al., 2020). Factors known to influence translocation success include habitat quality (Paraskevopoulou et al., 2022), the number of animals released and their origins (i.e., wild- or captive-sourced; Wolf et al., 1998; Morris et al., 2021), as well as age and sex class (Miller et al., 1999; Sasmal et al., 2015). Additionally, the most recent IUCN Guidelines for Reintroductions and Other Conservation Translocations (2013) emphasize the importance of determining how behavioral and physiological attributes affect translocation success. In this paper, we focus on variation in personality and hormone responses to translocation.

Personality is a widely documented phenomenon in which consistent inter-individual differences exist across suites of correlated behaviors (Sih et al., 2004). One example of commonly correlated behaviors is the proactive-reactive syndrome. Proactive individuals are more active, aggressive, bold (i.e., risk-taking), exploratory, neophilic (i.e., fearless toward new stimuli), and/or routine-driven than reactive individuals (Koolhaas et al., 1999; Kotrschal, 2001; Sih et al., 2004). For translocated animals, a proactive strategy can improve competitive ability and access to resources in a novel environment (Sinn et al., 2014). Conversely, reactive individuals may be more risk-averse and therefore better at avoiding threats like vehicles or predators (Réale et al., 2000; Bremner-Harrison et al., 2004; Careau et al., 2008; Choi et al., 2019).

Individual differences in proactive behaviors prior to or during the translocation process have forecasted post-release success. In European minks (*Mustela lutreola*) and Tasmanian devils (*Sarcophilus harrissii*), individuals classified as proactive during pre-release novel object tests experience greater post-release survival (Sinn et al., 2014; Haage et al., 2017). Similarly, burrowing bettongs (*Bettongia lesueur*) that are less docile (i.e., more proactive; Réale et al., 2000) during handling experience greater post-release survival (West et al., 2019). On the other hand, brushtail possums (*Trichosurus vulpecula*) that are more agitated (i.e., proactive) during processing gain more body mass post-release, but have lower survival than animals that are fearful and emotionally reactive during holding (May et al., 2016).

The interplay of personality with post-release movement may represent the greatest behavioral challenge in translocations (Bremner-Harrison et al., 2004; Berger-Tal et al., 2020). Proactive animals are more inclined to disperse widely from the release site, leading to higher mortality (Swaisgood, 2010). In an urban population of San Joaquin kit foxes (*Vulpes macrotis mutica*), individuals were captured, handled, and monitored after release to evaluate their candidacy for translocation (Bremner-Harrison and Cypher, 2011). Upon release, foxes that moved farther from the site of capture in this study had lower survival than individuals that

remained closer to the site of capture. In swift foxes reintroduced to the Blackfeet Reservation, Montana, proactive individuals dispersed farther and had higher mortality post-release (Bremner-Harrison et al., 2004). The Blackfeet reintroduction only tracked 16 foxes after release and conclusions were based on a small number of confirmed mortalities ($n = 5$); nonetheless, it suggests that the link between proactive behaviors and movement could be an important component in the success of swift fox reintroductions.

Moreover, translocations comprise a series of potential acute stressors including capture, handling, transport, pre-release quarantine, and release into a novel environment (Teixeira et al., 2007; Franceschini et al., 2008). Fecal glucocorticoid metabolite (fGM) analysis provides a noninvasive measure of animals' physiological responses to translocation. For instance, several mammals show increased fGM concentrations after translocation (Goymann et al., 1999; Terio et al., 1999; Hing et al., 2017). Translocations can also have long-term additive effects leading to chronic stress (Armstrong and Seddon, 2008; Wingfield and Romero, 2010) with reduced hypothalamic-pituitary-adrenal (HPA) axis reactivity and impaired negative feedback (Dickens et al., 2009). Further, sustained high levels of glucocorticoids can adversely affect the cognitive processes (McEwen and Sapolsky, 1995; Mendl, 1999) that enable animals to acclimatize to new surroundings (Teixeira et al., 2007). Similarly, physiological stress may facilitate dispersal away from the release site (Wingfield and Ramenofsky, 1997) as animals seek a more familiar environment (Drugan et al., 1997).

Fecal GM concentrations can covary with personality traits (Clary et al., 2014) to represent a stress 'coping style' (Kotrschal, 2001). For example, proactive animals often have a lower glucocorticoid response to stressors, making them well-acclimated to stable (e.g., source) environments (Koolhaas et al., 1999; Kotrschal, 2001; Wilson et al., 2022). Contrarily, reactive animals often have a higher glucocorticoid response to stressors and are inclined to adjust their behaviors and physiology to prevailing conditions, including novel (e.g., release) environments. Reactive animals are also more likely to express immobility and vigilance in response to stressors (Koolhaas et al., 1999). While reactive individuals are considered better release candidates due to their propensity to remain close to release sites (McDougall et al., 2006), their proactive and less stress-prone counterparts may be more successful if an elevated or prolonged stress response confers significant fitness costs after release (Teixeira et al., 2007).

The swift fox is a small, omnivorous canid of regional conservation concern in North America's short- and mixed-grass prairies (Egoscue, 1979; Kunkel et al., 2003; Young et al., 2023). Past translocations (Moehrenschrager and Macdonald, 2003; Ausband and Foresman, 2007b; Sasmal and Phillips, 2016) focused primarily on the impacts of extrinsic factors on post-release success (e.g., habitat quality, predation; Waters, 2010; Butler et al., 2021). By contrast, only one swift fox translocation explored the fitness implications of personality (Bremner-Harrison et al., 2004). Although stress was cited as a possible cause of low post-release survival in another swift fox translocation (Armstrong and Seddon, 2008; Sasmal et al., 2016), studies have yet to incorporate physiological biomarkers into swift fox conservation measures

(reviewed in Waters, 2010; Montgomery et al., 2018; Riddell et al., 2021).

By leveraging a recent reintroduction to the Fort Belknap Reservation, Montana, we aimed to fill a crucial knowledge gap regarding the behavioral and endocrine correlates of swift fox post-release success (Figure 1), thereby informing future management strategies. We hypothesized that proactive behaviors and physiological stress responses would differ among foxes throughout the translocation process, and that this would translate to variability in post-release movements and survival (Supplementary Table 1). In particular, we expected foxes' behavioral responses during handling to covary with their stress physiology such that foxes with higher fGM concentrations would be more reactive during handling. Further, we predicted that more proactive foxes with lower fGM concentrations would travel greater distances and have a reduced probability of survival after release. We included release cohort, age, and sex as predictors to consider demographic variation.

2 Materials and methods

2.1 Study Area

All translocations and monitoring of the nascent swift fox population took place on the Fort Belknap Reservation (48.2000° N, 108.5340°W) and surrounding Blaine and Phillips Counties in

northcentral Montana (Figure 2). Prior to reintroduction, swift foxes were extirpated from the reservation for over 50 years due to a broader range contraction in the northern Great Plains that followed European settlement (Sovada et al., 2009). The Fort Belknap Reservation is a sovereign nation and homeland to the Aaniiih and Nakoda Tribes. The reservation was established by the U.S. government in 1888 and is bounded to the north by the Milk River (Montana Office of Public Instruction, 2009). The Fort Belknap Community's aims for the reintroduction were twofold: (1) restore a culturally significant species to their sovereign lands, and (2) fill a distributional gap of over 300 km between reintroduced northern populations and contiguous southern populations (Nelson et al., 2025).

The reintroduction area consists of short- and mixed-grass prairie, of which the predominant vegetation types are western wheatgrass (*Elymus smithii*), needle-and-thread grass (*Heterostipa comata*), Sandberg bluegrass (*Poa secunda*) and blue grama (*Bouteloua gracilis*; Charboneau et al., 2013). Shrubs and forbs include sagebrush (*Artemisia* spp.), plains prickly pear (*Opuntia polyacantha*), and greasewood (*Sarcobatus vermiculatus*). Soil composition is primarily bentonite clay, and the landscape is allocated largely to cattle grazing. Though swift foxes generally select habitats with shorter vegetation structure (e.g., short-grass prairie, prairie dog towns) for denning opportunities and predator avoidance (Kitchen et al., 1999; Thompson and Gese, 2007; Sasmal et al., 2016), they can occupy other conditions such as sagebrush steppe (Olson and Lindzey, 2002). Preliminary models indicated highly suitable habitat in and around Fort Belknap, based on

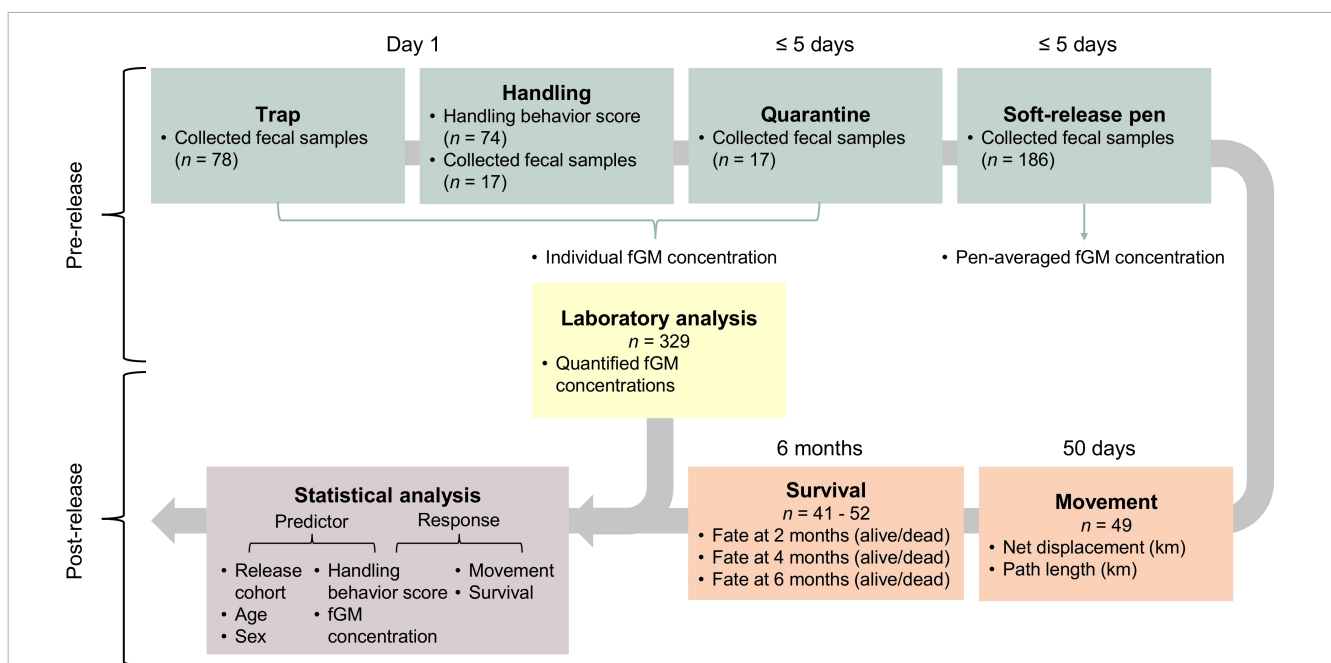


FIGURE 1

Flow diagram summarizing the translocation timeline for 76 swift foxes released on the Fort Belknap Reservation, Montana, 2021–2022, including collection and analysis of pre-release behavioral and physiological predictors as well as post-release response variables. Handling scores were generated from behavioral assessments of proactive personality, and fecal glucocorticoid metabolite (fGM) concentrations were quantified using a validated enzyme immunoassay. Postrelease response variables included foxes' movements and survival based on GPS collar data. Net displacement represented foxes' straight-line distances traveled from the soft-release pens on day 50, whereas path length measured foxes' cumulative distances traveled in the first 50 days. Note that sample sizes reflect raw numbers of individuals or samples prior to model fitting.

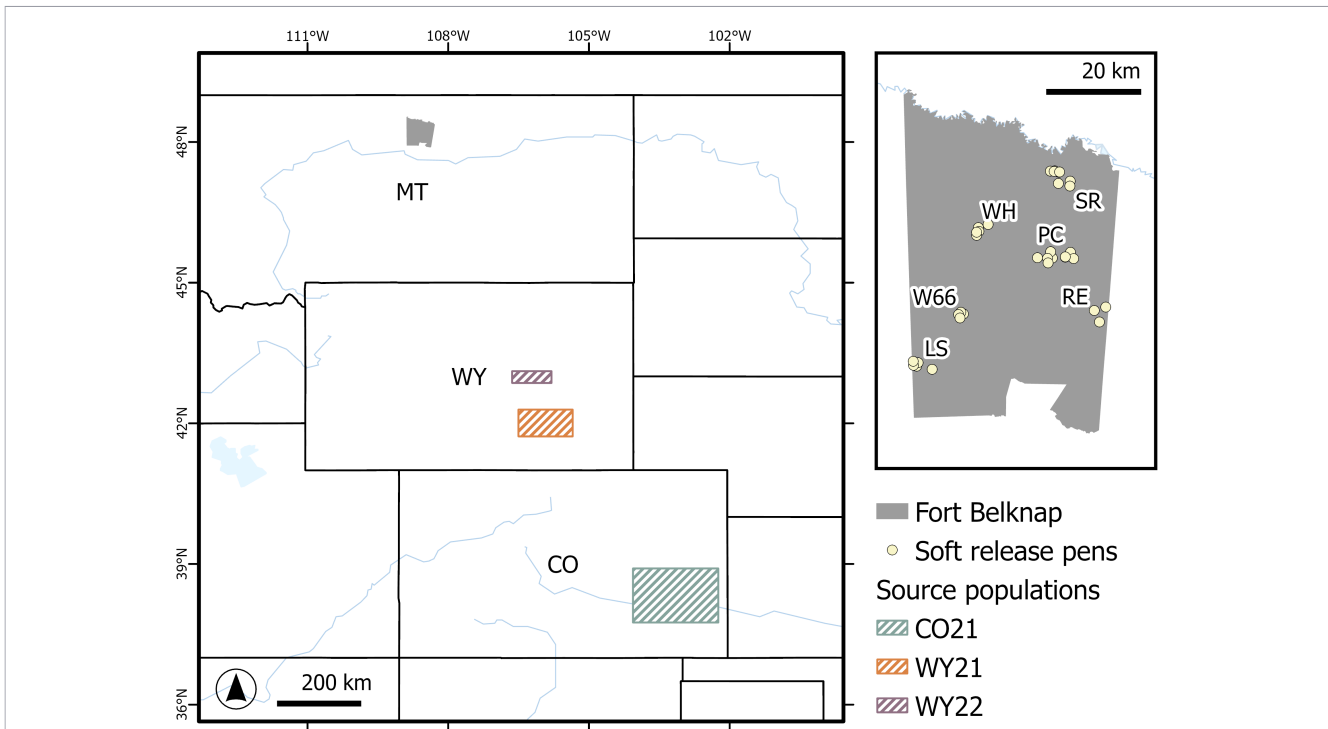


FIGURE 2 Map of the study area, including locations of swift fox source populations in Colorado and Wyoming (striped boxes) as well as soft-release pens (yellow points) on the Fort Belknap Reservation (gray polygon), Montana. Foxes from CO21, WY21, and WY22 were sourced respectively from Comanche National Grassland, Colorado in 2021; Shirley Basin, Wyoming in 2021; and Casper, Wyoming in 2022. Release areas included Lake 17 (LS), Peoples Creek (PC), Strike Reservoir (SR), and Wildhorse (WH) in 2021 as well as Route 11 (RE) and West Highway 66 (W66) in 2022. Each release area included three to five soft-release pens.

remotely sensed data and the distribution of key predator (coyote) and prey (lagomorph, rodent, orthopteran) species (Paraskevopoulou et al., 2022).

2.2 Trapping protocol

Trapping and translocations occurred between late August and early October, when juveniles disperse from their natal dens (Egoscue, 1979; Figure 1; Table 1). Standard capture, handling, husbandry, and release protocols (Moehrensclager et al., 2003; Sasmal et al., 2015) were followed for swift foxes sourced from three locations: Comanche National Grassland, Colorado (38.06430°N, 103.67704°W) in 2021; Shirley Basin, Wyoming (42.3225°N, 106.3089°W) in 2021; and Casper, Wyoming (42.8487°N, 106.2981°W) in 2022. Release cohorts are hereafter referred to as CO21, WY21, and WY22, respectively. All source populations resided in proximity to white- (*Cynomys leucurus*; WY21) or

black-tailed (*Cynomys ludovicianus*; CO21, WY22) prairie dog colonies (Nelson et al., 2025), an important habitat feature for swift foxes as a den-dependent and generalist predator (Kitchen et al., 1999; Sasmal et al., 2016).

Seventy-six foxes were captured using Tomahawk traps (Tomahawk Live Trap, Hazelhurst, WI) baited with meat scraps, sardines, and/or skunk-based attractant (Canine Call, Russ Carman Lures, New Milford, PA). Traps were set at night between 1800 and 2000 and checked the following morning between 0600 and 0800. State veterinary staff conducted health examinations and morphometric assessments. Individuals were sexed and classified as adult or juvenile based on tooth wear, body size, and reproductive condition (i.e., male testicular descent and whether a female was non-lactating, lactating, or pregnant). In swift foxes, mating typically occurs in late December, followed by parturition in March, and weaning of the pups in June (Egoscue, 1979; Poessel and Gese, 2013). Therefore, all adult females were non-lactating at

TABLE 1 Geographic locations of source populations for each release cohort, dates of translocation, number of individuals translocated, as well as age and sex ratios for swift foxes released on the Fort Belknap Reservation, Montana, 2021-2022.

Source population	Translocation date	Number of foxes	Age ratio	Sex ratio
Comanche National Grassland, CO	August, 2021	30	12A:18J	15F:15M
Shirley Basin, WY	September, 2021	18	11A:7J	9F:9M
Casper, WY	September, 2022	28	15A:13J	9F:19M
Total	-	76	38A:38J	33F:43M

the time of capture. Healthy foxes were designated for translocation and fitted with lightweight cellular GPS collars (57 g; ES-400, Cellular Tracking Technologies, Rio Grande, NJ) marked with a unique numeric code (e.g., W01) for visual identification.

After handling, individuals were held in quarantine for 1–5 d before being transported in 4x4 vehicles to Fort Belknap. During quarantine, foxes were held individually in ca. 58 x 38.6 x 30.1-cm carriers rated for animals up to 6.8 kg (Aspen Pet, Arlington, TX). Raw beef and water were provided daily. Signs of illness or injury were documented, all of which were minor and thus did not preclude animals from being released. Fecal samples were collected from the live traps ($n = 78$), during veterinary examinations ($n = 17$), as well as during quarantine ($n = 17$) and were stored individually in sealable plastic bags with silica desiccant (Dry & Dry, Brea, CA). All fecal samples were frozen and stored at -20°C until transport on dry ice to the Smithsonian's National Zoo and Conservation Biology Institute (NZCBI) for hormone extraction and assay.

2.3 Personality assessment

Published literature on kit and swift fox behavior together with expert opinion were used to select *a priori* behaviors indicative of the proactive-reactive syndrome (Supplementary Table 2; Bremner-Harrison et al., 2004; Bremner-Harrison and Cypher, 2011; Bremner-Harrison et al., 2018), including putative measures of activity, boldness, and docility (May et al., 2016). Behavioral responses of swift foxes during handling were recorded in binary- and Likert-scale formats by the same handler (Supplementary Table 2). For example, entering handling bags more readily or showing greater resistance to handlers were considered proactive behaviors, whereas passive dispositions that were prone to freezing/immobility were considered reactive (Réale et al., 2000; Quinn and Cresswell, 2005; May et al., 2016; West et al., 2019). Proactive behaviors likewise included biting or moving toward personnel; by contrast, reactive behaviors included more frequent vocalizations or attempts to flee from personnel (Bremner-Harrison et al., 2004; Bremner-Harrison and Cypher, 2011).

2.4 Soft-release protocol

After quarantine, foxes were transported to soft-release pens at Fort Belknap where they were held for up to 5 d to acclimatize to their surroundings (Figure 2; Sasmal et al., 2015). Soft-release pens measured ca. 1.8 x 1.2 x 1.2 m and were placed atop inactive prairie dog burrows to provide a shelter. Between 3–5 soft-release pens were spaced at least 500 m apart in each of six locations. These locations were informed by previous habitat suitability models (Paraskevopoulou et al., 2022), the presence of active black-tailed prairie dog colonies, and local community experts (i.e., Fort Belknap Fish and Wildlife staff). Between 1–4 foxes were housed per pen and consisted of suspected relatives (based on the proximity of their capture locations) or male-female pairs. Foxes were provided with raw beef or bison as well as water during daily husbandry visits. Between 1–2 infrared cameras (Hyperfirer 2, Reconyx, Holmen, WI) were deployed and secured to a 40-cm

high wooden stake ca. 5 m from each pen for a separate behavior study (see Todd, 2024). Fecal samples ($n = 186$) were collected opportunistically every 1–2 d during husbandry visits at the pens but could not be definitively linked to individuals; thus, fGM concentrations from these samples were averaged at the pen level (hereafter “pen-averaged fGM concentrations”) to account for individual variation.

2.5 Post-release monitoring

The post-release dispersal patterns and survival of each fox were monitored for up to 10 months as their GPS collars transmitted data over the Verizon cellular network (Supplementary Table 3, 4). The last date of data transmission by each collar and dates of known mortalities (indicated by the collar's activity sensor) were recorded for inference on survival. To mitigate collar malfunctions, GPS locations were supplemented with detections from baited cameras, sightings shared by the Fort Belknap Community, and visual surveys in the following spring (Supplementary Figure 1; Butler et al., 2021). Foxes were visually identified via the unique numeric code (e.g., W01) printed on their collars. Two post-release movement metrics were selected for analyses: (1) an individual's net displacement or straight-line distance traveled from the soft-release pen on day 50, and (2) its path length or cumulative distance traveled in the first 50 days. Fifty days post-release was chosen as the metric of interest based on an earlier Canadian reintroduction, in which translocated swift foxes' movements resembled those of resident foxes 50 days after release (i.e., settlement phase; Moehrenschrager and Macdonald, 2003). A maximum of three GPS locations were logged per fox per night; therefore, post-release movements were regarded as minimum estimates.

2.6 Hormone extraction and analysis

Hormone extraction was performed using a method established for canids (Jones et al., 2018). First, samples were lyophilized (VirTis Ultra 35XL, SP Scientific, Warminster, PA), pulverized, and sifted. A 0.2 (± 0.02) g aliquot of well-mixed fecal powder was then weighed out and combined with 100 μL ^3H -labeled cortisol to monitor extraction efficiency. Samples were vigorously shaken for 30 min in 5 mL of 90% ethanol (Pharmco, Greenfield Global, Brookfield, CT) using a large-capacity mixer set to a motor speed of 60 (Glas-col, Terre Haute, IN), and then centrifuged for 15 min at 2500 rpm (Sorvall RC-3B Plus, Thermo Scientific, Waltham, MA). The supernatants were decanted, and the process was repeated by reconstituting fecal pellets in 5 mL of 90% ethanol, vortexing for 30 s (Maxi Mix II, Thermo Scientific, Waltham, MA), centrifuging for 15 min at 2500 rpm, and decanting the supernatants. The supernatants containing hormone extract were then pooled and dried under an air stream. The final extracts were resuspended in 1 mL of dilution buffer (Assay Buffer Concentrate X053, Arbor Assays, Ann Arbor, MI), vortexed, and stored in 12x55 mm polypropylene tubes (Sarstedt, Newton, NC) at -20°C until hormone analysis.

Extraction efficiency was monitored with a multi-purpose scintillation counter (LS6500, Beckman Coulter, Indianapolis, IN),

and calculated using the disintegrations per minute (DPM) values of samples (50 μ L plus 3 mL of scintillation cocktail; Ultima Gold, PerkinElmer, Waltham, MA) as well as the mean DPM of two blanks (3 mL of scintillation cocktail) and two totals (100 μ L 3 H-labeled cortisol plus 3 mL of scintillation cocktail). Samples with an H-number ≥ 100 were re-run with only 25 μ L of sample plus 3 or 6 mL of scintillation cocktail. The mean extraction efficiency (\pm standard deviation) of all fecal samples, including re-extractions, was $78.0\% \pm 19.2\%$ ($n = 334$).

Fecal glucocorticoid metabolite concentrations were assessed using an in-house double antibody enzyme immunoassay ($n = 329$; Fazio et al., 2020) in 96-well plates (Costar[®] 9018, Corning Life Sciences, Tewksbury, MA) pre-coated with goat anti-rabbit IgG (A009, Arbor Assays, Ann Arbor, MI). Fecal extracts were diluted in dilution buffer (neat to 1:400) to achieve 30–70% binding. Cortisol antibodies (polyclonal antibody R4866 supplied by C. J. Munro, University of California, Davis, CA; 1:70,000 working dilution) and peroxidase enzyme-conjugated tracers (hydrocortisone 3CMO, Steraloids, Newport, RI; 1:29,000 working dilution) were added to each well containing 50 μ L of a serially diluted cortisol standard (hydrocortisone, MilliporeSigma, St. Louis, MO) or fecal extract, and incubated for 1 h. Unbound components were washed away with wash solution (Wash Buffer Concentrate X007, Arbor Assays, Ann Arbor, MI) and optical density was measured at 450 nm using a FilterMax F5 multi-mode microplate reader and the Softmax Pro v. 6.5.1 software (Molecular Devices, San Jose, CA).

Samples, standards, and quality controls (hydrocortisone, MilliporeSigma, St. Louis, MO) were assayed in duplicate, and assays were validated by demonstrating parallelism between serial dilutions of pooled fecal extract ($n = 20$ samples) and the associated standard curve, as well as sufficient recovery of steroid standard added to equal volumes of pooled fecal extract ($n = 2$ samples, diluted 1:10) after removing endogenous hormone. The pooled extract demonstrated parallelism with slopes matching the standard curve ($r = 0.99$; Supplementary Figure 2), and recovery of added standard was $96.83 \pm 62.76\%$ ($y = 1.15x + 5.82$, $R^2 = 0.997$). Hormone concentrations were quantified as ng/mL, then divided by the dry weight of the extracted feces as well as the extraction efficiency to report values as ng/g dry feces. Mean intra-assay variability of duplicate samples was 2.8%. Inter-assay variabilities for two internal controls were 6.4% (high concentration) and 11.7% (low concentration).

In our study, samples from the live traps were collected within 18 h of defecation, which is a liberal estimate based on when traps were set, checked, and the duration before some foxes were processed. During handling, samples were collected immediately upon defecation. During quarantine, samples were collected within 3 d of defecation. In the soft-release pens, samples were collected within 2 d of defecation. The excretion lag time for fGM concentrations is 8–14 h in *Vulpes* species (Hovland et al., 2017; Larm et al., 2021). Based on this excretion lag time and the timing of sample collection in our study, we deduced that fGM concentrations in samples collected from the live trap and during handling reflected foxes' hormone concentration prior to or at the time of capture. Further, fGM concentrations in samples collected during quarantine likely reflected foxes' hormone responses to

capture and handling. Finally, fGM concentrations in samples collected from the soft-release pens likely represented foxes' hormone responses to translocation. For biological validation of the assay, we examined changes in fGM concentrations between the trap, handling, and quarantine stages. While fGM concentrations during handling tended to be higher than those observed in the live traps or during quarantine, differences were not significant, likely due to high variability in fGM trajectories among individuals (Supplementary Figures 3–6; Supplementary Table 5).

2.7 Statistical analyses

All statistical analyses and plotting were conducted in R v. 4.2.2 (R Core Team, 2022). Statistical significance was set at $\alpha = 0.05$.

2.7.1 Personality

For behaviors scored in binary formats during handling, proactive responses were scored as 1 and reactive responses as 0 (Supplementary Table 2). For behaviors scored in Likert-scale formats, responses were ranked in ascending order from 1 (most reactive) to 5 (most proactive). All behaviors scored in binary and Likert-scale formats were then summed and averaged to produce a handling score for each fox ($n = 74$). This allowed scores to vary along a continuum with higher values indicating a more proactive temperament (Bremner-Harrison and Cypher, 2011).

2.7.2 Fecal glucocorticoid metabolites

A single average fGM concentration was calculated for each fox across trap, handling, and quarantine (hereafter “individual fGM concentrations”) to address pseudoreplication and uneven sampling frequencies across individuals (Jones et al., 2018). Note that most individual samples were collected from the live traps ($n = 78$; 69.6%) relative to handling ($n = 17$; 15.2%) and quarantine ($n = 17$; 15.2%). This implies that most individual fGM concentrations comprised values that represented hormone excretion before or at the time of capture. Moreover, fGM concentrations from the live traps were not significantly different ($P > 0.05$) from fGM concentrations during handling and quarantine for a subset of individuals with available data (Supplementary Table 5), suggesting that none of the three stages had a disproportionate effect on individual fGM averages. Both individual and pen-averaged fGM concentrations were log₁₀-transformed prior to analysis to improve model fit (Choi et al., 2022).

We tested whether mean fGM concentrations differed between samples collected pre-transport (i.e., from trap, handling, and quarantine) and at the soft-release pens to affirm if swift foxes exhibit a physiological response to translocation like other species (e.g., Goymann et al., 1999; Terio et al., 1999; Hing et al., 2017). To do this, the mean fGM concentrations from all individuals that shared a soft-release pen were averaged so both pre-transport and pen fGM concentrations comprised means of multiple individuals. The resultant dataset consisted of a single row for each pen grouping. Wilcoxon signed rank tests for paired samples were then performed on the full dataset ($n = 31$) and when the data

were partitioned by release cohort (CO21: $n = 14$; WY21: $n = 6$; WY22: $n = 11$).

In addition, we tested whether foxes' behaviors covaried with their physiological responses. Because the mean fGM concentrations of samples collected from trap, handling, and quarantine largely represented individuals' hormone concentration prior to or at the time of capture, those concentrations also likely preceded the personality assessments recorded during handling. Therefore, we considered individual fGM concentrations a predictor of handling scores rather than the inverse.

2.7.3 Model fitting and diagnostics

Multicollinearity among predictors was assessed prior to model fitting by examining the correlation matrix and variance inflation factors (VIF) with the packages GGally (Schloerke et al., 2021) and usdm (Naimi et al., 2014). The collinearity thresholds were set at $r = |0.7|$ and $VIF = 3$ (Zuur et al., 2010). Collinear predictors were not included in the same model, and foxes with missing data were removed prior to analyzing each model set. All continuous response variables (handling scores, fGM concentrations, and post-release movement) were positively distributed and described using base R generalized linear models (GLMs) with a gamma error distribution and log link function. Post-release survival was binary with individuals classified as 0 (dead) or 1 (alive) and described using a binomial GLM with a logit link function. Model selection was performed via maximum likelihood and Akaike information criterion corrected for small sample sizes (AICc; Akaike, 1973) using the AICcmodavg package (Mazerolle, 2023) to obtain the most parsimonious model structure for each response variable. Null models containing only an intercept term were included in each model set. For final models containing categorical predictors, *post-hoc* Tukey pairwise comparisons of marginal means were computed with the lsmeans package (Lenth, 2016) to identify which groups significantly differed.

To test whether individuals' handling scores depended on release cohort, age, sex, or fGM concentrations, GLMs were fitted with handling scores as the response variable, and cohort, age, sex, and individual fGM concentrations (both linear and quadratic terms) as fixed effects ($n = 56$ individuals; Supplementary Table 1).

To test whether individuals' fGM concentrations depended on release cohort, age, or sex, GLMs were fitted with individual fGM concentrations as the response variable, and cohort, age, and sex as fixed effects ($n = 58$; Supplementary Table 1). Mean fGM concentrations at the soft-release pens were not definitively linked to individuals; therefore, GLMs were fitted with pen-averaged fGM concentrations as the response variable, and release cohort, release site (i.e., to consider variation in site-related stressors), and the number of days foxes were held in quarantine as fixed effects ($n = 66$; Supplementary Table 1).

To test whether individuals' post-release movements depended on release cohort, age, sex, handling scores, or fGM concentrations, GLMs were fitted with net displacement or path lengths as the response variable, and cohort, age, sex, handling scores, and

individual fGM concentrations as fixed effects ($n = 38$; Supplementary Table 1).

Survival was analyzed at 2-, 4-, and 6-months post-release after excluding foxes whose survival status could not be definitively determined (Supplementary Table 3, 4). To test whether individuals' post-release survival depended on release cohort, age, sex, handling scores, or fGM concentrations, GLMs were fitted with survival status at 2- ($n = 42$), 4- ($n = 40$), or 6-months ($n = 33$) post-release as the response variable, and cohort, age, sex, handling scores, and individual fGM concentrations as fixed effects (Supplementary Table 1).

For all final GLMs, influential cases were examined with base R functions using a Cook's distance threshold of three times the mean Cook's distance (Cook, 1977), and models were compared before and after their removal. Multicollinearity among predictors was reassessed using the variance inflation factor from the car package (Fox and Weisberg, 2019), with the collinearity threshold set at $VIF = 3$ (Zuur et al., 2010). No issues were found. The ggResidpanel package (Goode and Rey, 2019) and a custom function were used to inspect residual distributions for the gamma and binomial GLMs, respectively. Plots were generated with the packages ggeffects (Lüdtke, 2018), ggplot2 (Wickham, 2016), grid, gridExtra (Auguie, 2017), and reshape2 (Wickham, 2007).

3 Results

3.1 Determinants of personality

Handling scores were best explained by an interaction between individuals' age and sex plus fGM concentrations (quadratic effect; Table 2). This model accounted for 37% of the variability in handling scores (Supplementary Table 6). Fecal GM concentrations had a significant nonlinear relationship with handling scores (-0.567 ± 0.165 , $P = 0.001$), such that foxes with the lowest and highest fGM concentrations had lower handling scores (Figure 3). Age (0.167 ± 0.07 , $P = 0.02$), sex (0.156 ± 0.067 , $P = 0.024$), and their interaction (-0.375 ± 0.09 , $P < 0.001$) likewise had significant effects on handling scores. Tukey pairwise comparisons showed that handling scores were significantly different between juvenile females ($\bar{x} = 1.782$, $s = 0.305$) and juvenile males ($\bar{x} = 1.432$, $s = 0.313$; mean difference on log link scale: 0.218 ± 0.061 , $P = 0.004$), as well as between adult males ($\bar{x} = 1.731$, $s = 0.230$) and juvenile males (mean difference on log link scale: 0.208 ± 0.059 , $P = 0.005$; Supplementary Table 7). Handling scores did not differ in any other pairwise comparisons ($P > 0.05$).

3.2 Determinants of fecal glucocorticoid metabolites

Paired t-tests of fox groups that shared a soft-release pen indicated significant declines in mean fGM concentrations from pre-transport to pen both across ($V = 480$, $P < 0.001$) and within (CO21: $V = 98$, $P = 0.002$; WY21: $V = 21$, $P = 0.031$; WY22: $V = 65$, $P = 0.002$) release cohorts (Figure 4; Table 3).

TABLE 2 Model selection results of gamma and binomial GLMs for handling behavior scores, fecal glucocorticoid metabolite (fGM) concentrations, post-release movement, and survival of swift foxes.

Response variable	Model structure	<i>k</i>	AICc	ΔAICc	<i>w_i</i>	<i>LL</i>
Behavior						
Handling score	~ age * sex + log ₁₀ (cortisol) ²	7	17.67	0.00	0.95	-0.67
fGM concentrations						
Individual fGM concentrations	~ release cohort * age	7	96.53	0.00	0.72	-40.15
Pen-averaged fGM concentrations	~ release cohort	4	32.49	0.00	1.00	-11.92
Movement						
Net displacement (day 50)	~ release cohort	4	320.98	0.00	0.24	-155.89
	~ release cohort * handling score	7	321.85	0.86	0.16	-152.06
Path length (day 50)	~ release cohort * age	7	487.83	0.00	0.27	-235.05
	~ release cohort + age	5	488.54	0.70	0.19	-238.33
	~ age + sex + log ₁₀ (cortisol)	5	489.86	2.03	0.10	-238.99
Survival						
2 months	~ age + handling score ²	4	49.32	0.00	0.54	-20.12
4 months	~ age	2	50.64	0.00	0.36	-23.16
	~ age + log ₁₀ (cortisol)	3	52.52	1.88	0.14	-22.92
6 months	~ age	2	46.35	0.00	0.24	-20.97
	~ age + handling score ²	4	47.67	1.32	0.13	-19.12
	~ age + sex	3	47.84	1.49	0.12	-20.51
	~ 1	1	47.85	1.50	0.12	-22.86

Apart from path length (day 50), only candidate models within two ΔAICc are shown.

k, number of parameters; AICc, AICc value for each model; ΔAICc, difference in AICc value relative to top model; *w_i*, Akaike weight; *LL*, log-likelihood.

Mean individual fGM concentrations were best explained by an interaction between individuals' release cohort and age, with the model accounting for 27% of the variability in fGM concentrations (Figure 5; Table 2; Supplementary Table 6). Tukey pairwise comparisons (Supplementary Table 7) showed that CO21 juveniles ($\bar{x} = 3.343, s = 0.365$) had significantly higher fGM concentrations than WY21 ($\bar{x} = 2.526, s = 0.437$; mean difference on log link scale: $0.281 \pm 0.085, P = 0.02$) and WY22 ($\bar{x} = 2.711, s = 0.426$; mean difference on log link scale: $0.210 \pm 0.069, P = 0.041$) juveniles. Additionally, adults ($\bar{x} = 3.450, s = 0.587$) had significantly higher fGM concentrations than juveniles in the WY21 cohort (mean difference on log link scale: $0.312 \pm 0.096, P = 0.023$). No other pairwise comparisons yielded significant results ($P > 0.05$).

Mean fGM concentrations at the soft-release pens were best explained by release cohort (35%; Figure 6; Table 2; Supplementary Table 6). Tukey pairwise comparisons (Supplementary Table 7) showed that WY22 ($\bar{x} = 2.224, s = 0.321$) foxes had lower mean fGM concentrations at the soft-release pens than CO21 ($\bar{x} = 2.708, s = 0.275$; mean difference on log link scale: $0.197 \pm 0.033, P < 0.001$) and WY21 ($\bar{x} = 2.546, s = 0.254$; mean difference on log link scale: $0.135 \pm 0.039, P = 0.003$) foxes. Pen-averaged fGM concentrations did not differ between the CO21 and WY21 cohorts (mean difference on log link scale: $0.062 \pm 0.037, P = 0.230$).

3.3 Post-release Movement

Post-release net displacement was best explained by release cohort, though the model only accounted for 16% of the variability

in net displacement (Table 2; Supplementary Table 6). WY21 ($\bar{x} = 50.004, s = 53.323$) foxes moved significantly greater net distances from the soft-release pens in the first 50 days than WY22 foxes ($\bar{x} = 14.354, s = 14.853$; mean difference on log link scale: $1.248 \pm 0.398, P = 0.01$; Supplementary Table 7). Net displacement did not differ between CO21 ($\bar{x} = 20.451, s = 14.859$) foxes and the WY21 (mean difference on log link scale: $-0.894 \pm 0.393, P = 0.073$) or WY22 (mean difference on log link scale: $0.354 \pm 0.346, P = 0.568$) cohorts. Though handling scores did not improve the model's AICc score, there was a significant interaction with handling scores in the WY21 cohort that increased the model's explanatory power to 29% ($5.028 \pm 1.130, P < 0.001$; Figure 7; Table 2; Supplementary Table 6). Whereas CO21 and WY22 foxes with higher handling scores traveled slightly smaller net distances from the release pens, WY21 foxes with higher handling scores traveled significantly greater net distances. Refitting the model without influential cases revealed that these cohort-related differences were driven by two adult males in the WY21 cohort that traveled net distances > 100 km from the soft-release pens (Supplementary Table 8, 9).

Post-release path lengths were best explained by an interaction between release cohort and age, with the model accounting for 46% of the variability in path lengths (Table 2; Supplementary Table 6). CO21 ($\bar{x} = 479.471, s = 199.299$) and WY21 ($\bar{x} = 513.019, s = 294.095$) adults traveled greater cumulative distances in the first 50 days than adults ($\bar{x} = 163.874, s = 139.877$; mean difference on log link scale: $1.074 \pm 0.318, P = 0.022$; $1.141 \pm 0.318, P = 0.013$) and juveniles ($\bar{x} = 169.539, s = 49.564$; mean difference on log link scale:

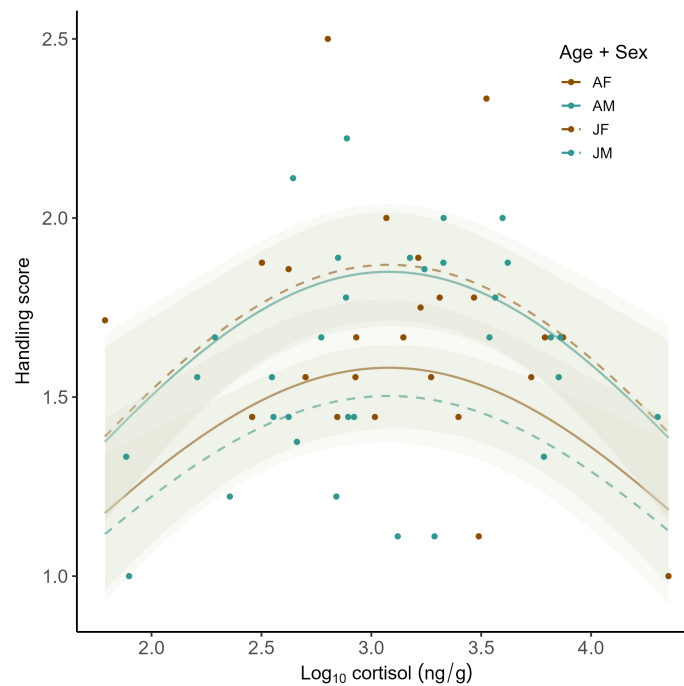


FIGURE 3

Behavior scores during handling and mean individual fecal glucocorticoid metabolite (fGM) concentrations of swift foxes, with data coded by age (solid line: adult; dotted line: juvenile) and sex (brown: female; blue: male). Effects are predicted by the top gamma GLM explaining the variability of handling score as a function of an age-sex interaction plus fGM concentrations (quadratic effect; explained deviance = 0.37, $n = 56$). Fecal GM concentrations had a significant nonlinear effect on handling scores ($P = 0.001$). Foxes with the lowest and highest fGM concentrations had lower handling scores. Additionally, there was a significant effect of age ($P = 0.020$), sex ($P = 0.024$), and their interaction ($P < 0.001$). *Post-hoc* Tukey tests showed that juvenile females ($P = 0.004$) and adult males ($P = 0.005$) had higher handling scores than juvenile males. Lines represent predicted patterns with 95% confidence intervals on top of the raw values.

1.040 ± 0.340 , $P = 0.047$; 1.107 ± 0.340 , $P = 0.03$) from the WY22 cohort (Supplementary Table 7). Further, WY21 adults traveled greater cumulative distances than CO21 juveniles ($\bar{x} = 189.696$, $s = 117.240$; mean difference on log link scale: 0.995 ± 0.311 , $P = 0.033$). No other pairwise comparisons yielded significant results ($P > 0.05$). Though the model was slightly greater than two $\Delta AICc$ from the best-fitting model, age, sex, and fGM concentrations had an additive effect that explained 35% of the variability in path lengths (Figure 8; Table 2; Supplementary Table 6). While sex (0.396 ± 0.192 , $P = 0.047$) and fGM concentrations (0.533 ± 0.179 , $P = 0.005$) significantly influenced path lengths, age improved the model but did not have a significant effect (-0.357 ± 0.198 , $P = 0.08$). Foxes with higher fGM concentrations traveled greater cumulative distances post-release and males traveled farther than females.

3.4 Post-release Survival

Of the 76 foxes released from the pens during this study, mortalities included in the binomial GLMs ranged from 13 individuals within 2-months to 16 individuals within 6-months post-release (Supplementary Table 4). Aside from two confirmed vehicle mortalities, most deceased individuals could not be recovered and for those that were, carcasses were sufficiently decomposed as to preclude definitive assessments of cause of death.

Of the 42 foxes included in the model at 2-months post-release, 29 were alive and 13 were dead (Supplementary Table 3, 4). Survival probability at 2-months post-release was best explained by handling

scores (quadratic effect) plus age, with the model accounting for 23% of the variability in survival probability (Figure 9; Table 2; Supplementary Table 6). Handling scores had a significant nonlinear effect on survival probability (10.609 ± 5.274 , $P = 0.044$) such that foxes with the lowest and highest handling scores were more likely to survive to 2 months post-release. Age likewise had a significant effect (-1.809 ± 0.830 , $P = 0.029$), with adults (Alive = 18, Dead = 4) having a higher probability of survival than juveniles (Alive = 11, Dead = 9). However, violations of residual assumptions were found, corroborating the model's poor fit and low explanatory power (Supplementary Table 6). Including additional predictors or more complex terms (e.g., interactions) was avoided due to the low effective sample size (Harrell, 2015).

Of the 40 foxes included in the model at 4-months post-release, 25 were alive and 15 were dead (Supplementary Table 3, 4). Survival probability at 4-months post-release was best explained by age, though the model only accounted for 13% of the variability in survival probability (Table 2; Supplementary Table 6). Age had a significant effect on survival probability (-1.765 ± 0.724 , $P = 0.015$) such that adults (Alive = 17, Dead = 4) were more likely to survive to 4 months post-release than juveniles (Alive = 8, Dead = 11).

Finally, of the 33 foxes included in the model at 6-months post-release, 17 were alive and 16 were dead (Supplementary Table 3, 4). Survival probability at 6-months post-release was also best explained by age (Table 2). However, this model only accounted for 8% of the variability in survival probability (Supplementary Table 6). Though adults (Alive = 11, Dead = 5) still had a higher

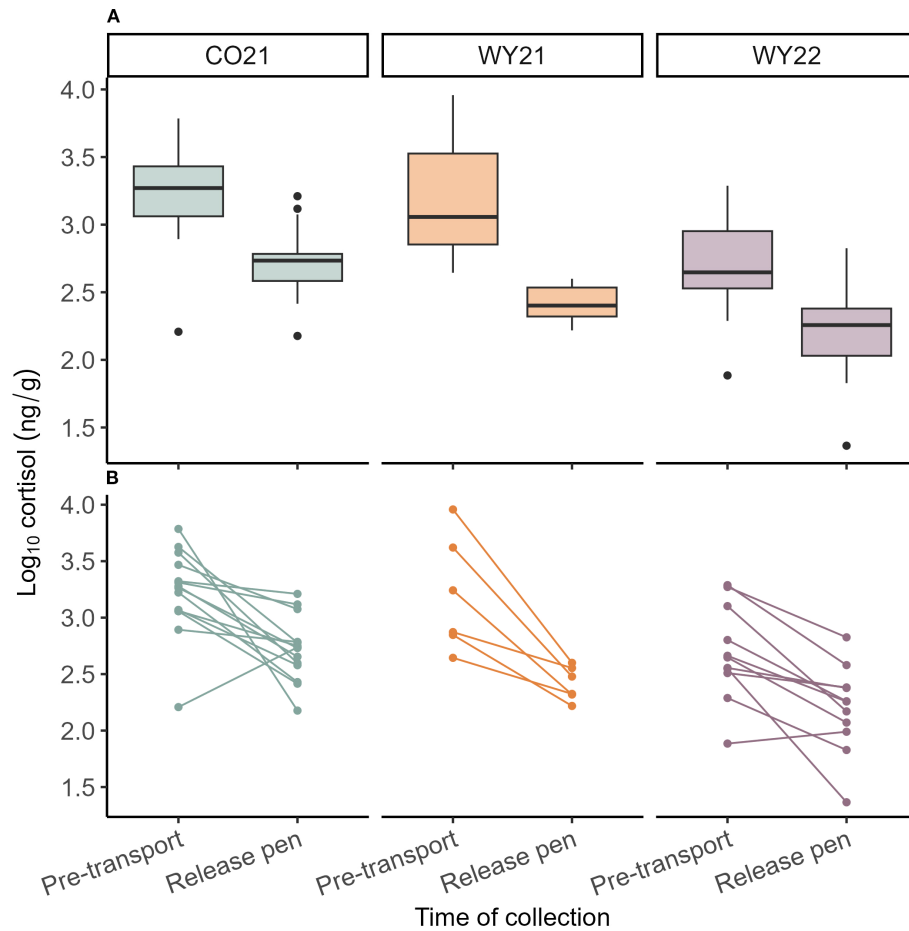


FIGURE 4

Mean fecal glucocorticoid metabolite (fGM) concentrations of samples collected pretransport and at the soft-release pen. Data are faceted and colored by release cohort. Foxes from CO21, WY21, and WY22 were sourced respectively from Comanche National Grassland, Colorado in 2021; Shirley Basin, Wyoming in 2021; and Casper, Wyoming in 2022. Pen samples were not definitively linked to individuals and therefore averaged across the 1–4 conspecifics that were held per pen. Accordingly, values represent an average of means that comprised groups of individuals sharing a pen. The group means from each cohort are consolidated in the top panel (A), and each pen group’s trajectories are shown in the lower panel (B). Paired t-tests indicated significant declines in mean fGM concentrations from pre-transport to soft-release pen across ($P < 0.001, n = 31$) and within (CO21: $P = 0.002, n = 14$; WY21: $P = 0.031, n = 6$; WY22: $P = 0.002, n = 11$) cohorts.

TABLE 3 Summary of paired t-tests comparing mean fecal glucocorticoid metabolite (fGM) concentrations pre-transport and at the soft-release pen. Wilcoxon signed rank tests were performed for the full dataset and when the data were partitioned by release cohort.

Mean of pretransport fGM concentrations	Mean of pen fGM concentrations	Pseudo median	V	95% CI	P
All cohorts					
3.028	2.472	0.542	480	0.389 – 0.711	< 0.001***
CO21					
3.224	2.717	0.507	98	0.250 – 0.756	0.002**
WY21					
3.197	2.416	0.776	21	0.318 – 1.358	0.031*
WY22					
2.687	2.191	0.492	65	0.236 – 0.754	0.002**

Mean values represent an average of means that comprised groups of 1–4 individual swift foxes that shared a soft-release pen.

CO21 = Comanche National Grassland, Colorado, 2021.

WY21 = Shirley Basin, Wyoming, 2021.

WY22 = Casper, Wyoming, 2022.

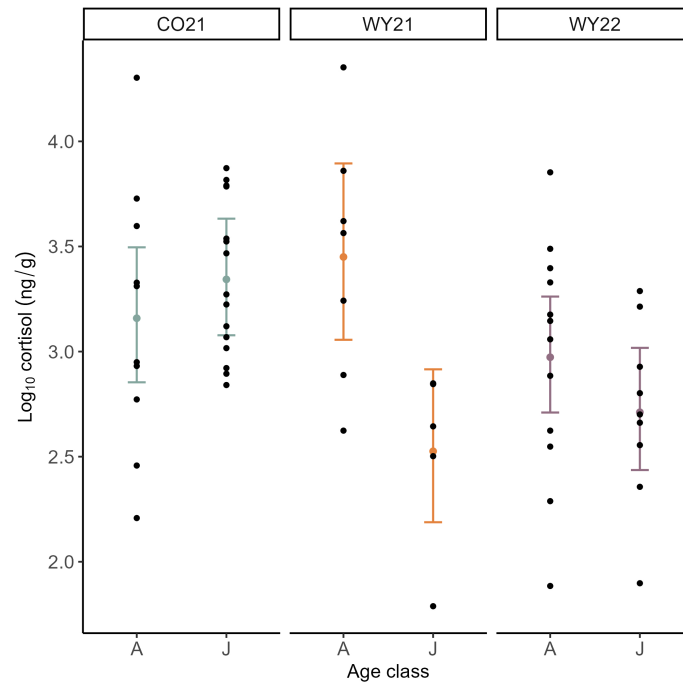


FIGURE 5

Mean individual fecal glucocorticoid metabolite (fGM) concentrations of adult and juvenile swift foxes, with facets and colors by release cohort. Foxes from CO21, WY21, and WY22 were sourced respectively from Comanche National Grassland, Colorado in 2021; Shirley Basin, Wyoming in 2021; and Casper, Wyoming in 2022. Effects are predicted by the top gamma GLM explaining the variability of individual fGM concentrations as a function of the interaction between release cohort and age (explained deviance = 0.27, $n = 58$). CO21 juveniles had significantly higher fGM concentrations than WY21 ($P = 0.020$) and WY22 ($P = 0.041$) juveniles. Additionally, adults had significantly higher fGM concentrations than juveniles in the WY21 cohort ($P = 0.023$). Error bars represent predicted patterns with 95% confidence intervals on top of the raw values.

probability of survival than juveniles (Alive = 6, Dead = 11), the effect was no longer significant (1.395 ± 0.741 , $P = 0.06$).

4 Discussion

The present study investigated whether personality and physiological stress responses differed among individuals during a reintroduction program for the swift fox, a canid of regional conservation concern in North America's grasslands. Further, we analyzed whether such differences forecasted post-release fitness while accounting for demographic variables. Our models showed that individuals' fGM concentrations, age, and sex were associated with their behavioral responses to handling (i.e., handling scores). We also found that fGM concentrations were associated with increased cumulative distances travelled and handling scores were related to short-term survival.

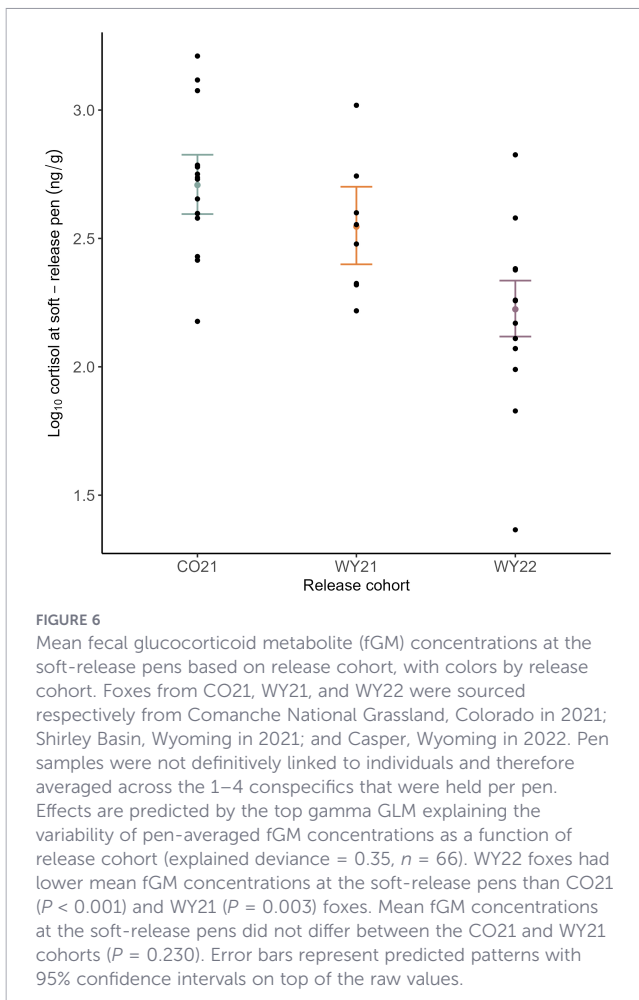
4.1 Determinants of personality

Swift fox handling scores were best explained by an interaction between individuals' age and sex plus their fGM concentrations. We expected males to be more proactive than females given their greater propensity to disperse from natal sites or after the loss of a mate (Kamler et al., 2004), life history events that could favor aggressive, bold, and/or exploratory behaviors (Cote et al., 2010). Our results were more nuanced, indicating that both juvenile

females and adult males had higher handling scores (i.e., were more proactive) than juvenile males.

Previous studies in *Vulpes* demonstrate that age- and sex-related patterns in proactive behaviors vary based on species, animal origins, and sampling method. For example, free-living male San Joaquin kit foxes are more proactive during handling than females irrespective of age class (Bremner-Harrison and Cypher, 2011). In captive-raised swift foxes reintroduced to the Blackfoot Reservation, proactive behaviors observed during a novel-object test did not vary between the sexes, but adults were consistently more proactive than juveniles (Bremner-Harrison et al., 2004). Free-living adult male and female arctic foxes (*Vulpes lagopus*) respond similarly to approaching humans while juvenile responses to being trapped vary between consecutive trapping events (Choi et al., 2019). In the present study, we did not predict an effect of age on proactive behaviors. However, given male-biased dispersal in free-living swift foxes, males may be more vulnerable to novel or threatening stimuli than comparatively philopatric females. Consequently, there could be a stronger selection pressure for reactive dispositions in naïve juvenile males (Bremner-Harrison et al., 2004; Lea and Blumstein, 2011). As males age and become more experienced, they might exhibit less fearful reactions to stressors, which could explain the more proactive behaviors we observed in the adults in this study.

We also expected a negative relationship between proactive behaviors (i.e., being more active, bold, and/or less docile) and fGM concentrations based on the literature on coping styles (Koolhaas et al., 1999). Our results were partially consistent with this, as



individuals with the highest fGM concentrations had lower handling scores (i.e., were more reactive). However, individuals with the lowest fGM concentrations also had lower handling scores. By comparison, farmed silver foxes (*Vulpes vulpes*) exhibit a positive relationship (Hovland et al., 2017) and farmed arctic foxes display a negative relationship (Larm et al., 2021) between fGM concentrations prior to handling and pro-active behaviors. Hovland et al. (2017) postulated that glucocorticoids could modulate the behavioral preparedness of individuals in responding to future stressors as part of the proactive-reactive coping strategy (Koolhaas et al., 1999; Kotrschal, 2001). In our study, foxes with moderate fGM concentrations had higher handling scores. Foxes with the lowest and highest fGM concentrations may have been more reactive during handling due to a modest adrenal response, or to the freezing/immobility characteristic of high-glucocorticoid individuals.

Finally, we recognize there may have been a bias toward proactive foxes in our study population because proactive individuals are known to enter traps more readily than reactive individuals in some species (e.g., Réale et al., 2000; Carter et al., 2012; Santicchia et al., 2021). Personnel also varied considerably during trapping and quarantine; however, we were unable to train all personnel to score foxes' behaviors consistently before translocations occurred due to logistical constraints. Therefore, we assumed that interobserver biases influenced behavioral

observations during trapping and quarantine, so we did not assess the repeatability (i.e., consistency) of foxes' behavioral responses between stages of the translocation process (Sinn et al., 2014; May et al., 2016; Haage et al., 2017).

4.2 Determinants of fecal glucocorticoid metabolites

Our results indicated that swift fox mean fGM concentrations declined from pre-transport to soft-release pen for most groups that shared a pen. Other studies have reported similar declines throughout translocation (Dickens et al., 2010; Lèche et al., 2016) or lack of a temporal effect (Heiken et al., 2016). One possible explanation for the decline in fGM concentrations over time is that social interactions attenuated the stress of translocation and captivity (Creel et al., 2013), as nearly all foxes were transferred to pens in groups of two to four individuals. Swift foxes are socially monogamous and form pair bonds, though trios of related individuals (Kitchen et al., 2006; Poessel and Gese, 2013) and same-sex dyads (Olson and Lindzey, 2002) have been reported. The presence of conspecifics, especially relatives, can reduce stress and/or improve post-release fitness in translocated animals (Sachser et al., 1998; Shier, 2006). In some cases, our camera traps documented individuals digging out of their pens and subsequently locating and digging into the pens of conspecifics, which were likely relatives based on the proximity of their capture locations. These social cues may have encouraged physiological acclimatization to the release site (Lèche et al., 2016).

Stress responses are likewise grounded in individual perceptions of controllability and predictability (Koolhaas et al., 2011). Therefore, it is likely that less human disturbance at the pens coupled with access to burrows for concealment reduced fGM concentrations in this study. Swift foxes are one of the most fossorial canids in North America (Egoscue, 1979) and rely heavily on dens to avoid predators (Kitchen et al., 1999). Burrows enabled individuals in our soft-release pens to “control” a threatening situation (e.g., approaching researchers) by hiding belowground (Drugan et al., 1997). Ultimately, pen-collected scats could not be linked to individuals because we did not directly observe scat deposition or use genetic tools to verify individual identities. Thus, our inferences are limited by the fact that mean differences were only analyzed at the group level and at only two points in the translocation process, so we probably missed subtler variation among individuals. Comparisons of group means between the pre-transport and soft-release pen conditions were also complicated by the possibility that some individuals contributed more fecal samples than others in the pens, thereby skewing the pen-averaged fGM concentrations.

We found that individual fGM concentrations were best explained by an interaction between release cohort and age. Adults had significantly higher fGM concentrations than juveniles in the WY21 cohort; however, this pattern was likely overestimated due to the small sample size ($n = 12$ individuals). Additionally, Colorado juveniles had significantly higher fGM concentrations than Wyoming juveniles. Because individual fGM concentrations reflected foxes' physiological states before transport to the soft-

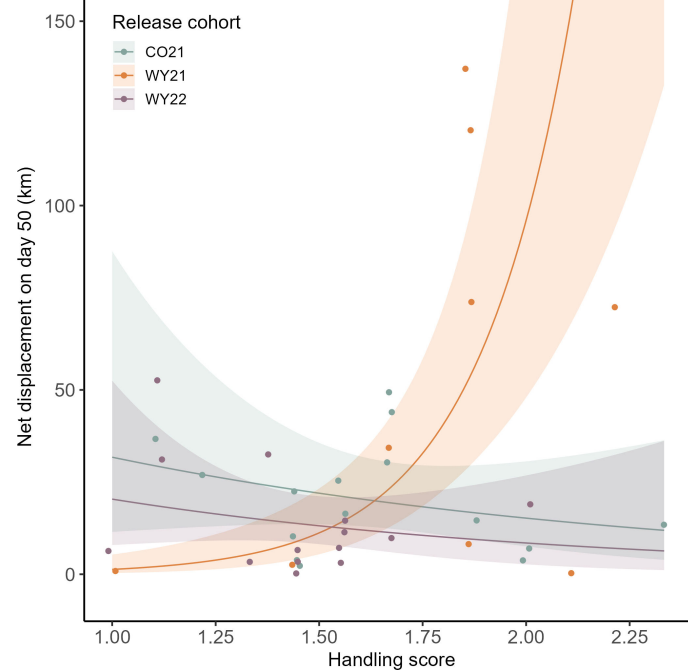


FIGURE 7

Post-release net displacement (i.e., straight-line distances traveled) based on behavior scores during handling, with colors by release cohort. Foxes from CO21, WY21, and WY22 were sourced respectively from Comanche National Grassland, Colorado in 2021; Shirley Basin, Wyoming in 2021; and Casper, Wyoming in 2022. Though handling scores did not improve the top model, there was a significant interaction with handling scores in the WY21 cohort ($P < 0.001$, explained deviance = 0.29, $n = 38$). WY21 foxes with higher handling scores traveled significantly greater net distances. Lines represent predicted patterns with 95% confidence intervals on top of the raw values.

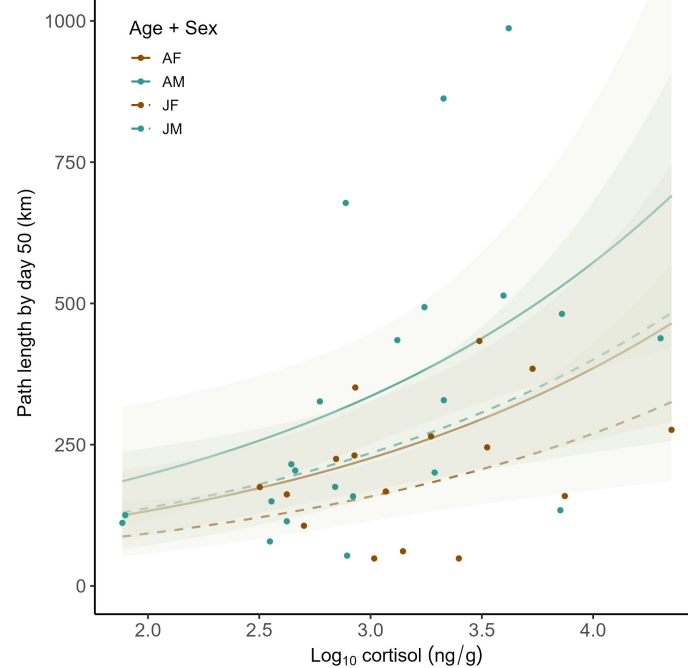


FIGURE 8

Post-release path lengths (i.e., cumulative distances traveled) in relation to mean individual fecal glucocorticoid metabolite (fGM) concentrations. Data are coded by age and sex. Foxes from CO21, WY21, and WY22 were sourced respectively from Comanche National Grassland, Colorado in 2021; Shirley Basin, Wyoming in 2021; and Casper, Wyoming in 2022. Though the model was slightly greater than two $\Delta AICc$ from the top model, age, sex, and fGM concentrations had an additive effect on path lengths (explained deviance = 0.35, $n = 38$). Sex ($P = 0.047$) and fGM concentrations ($P = 0.005$) significantly influenced path lengths. Age improved the model but did not have a significant effect ($P = 0.080$). Foxes with higher fGM concentrations traveled greater cumulative distances post-release and males traveled farther than females. Lines represent predicted patterns with 95% confidence intervals on top of the raw values.

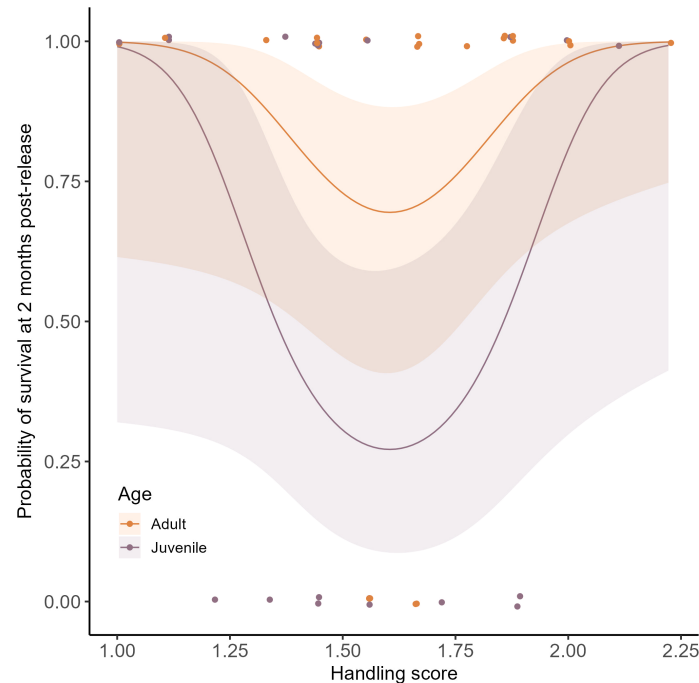


FIGURE 9

Probability of survival at 2-months post-release based on behavior scores during handling and age. Data are colored by age. Effects at 2-months post-release are predicted by the top binomial GLM explaining the variability of survival probability as a function of handling scores (quadratic effect) plus age. Handling scores had a significant nonlinear effect on survival probability ($P = 0.044$, $n = 42$) such that foxes with the lowest and highest handling scores had a higher probability of survival. Age also had a significant effect ($P = 0.029$) with adults having had a higher probability of survival than juveniles. Lines represent predicted patterns with 95% confidence intervals on top of the raw values.

release pens, elevated concentrations in the CO21 cohort could not be attributed to their longer transport time (Parker et al., 2012). Further, we observed high densities of orthopterans—a staple late-summer prey item for swift foxes (Kitchen et al., 1999)—while trapping in Colorado, which suggests food availability did not disproportionately affect juveniles from that cohort.

A more plausible site-level difference is in predation pressure. The presence of natural predators can positively associate with fGM concentrations (reviewed in Busch and Hayward, 2009; Zbyryt et al., 2018), with greater effects in juveniles due to their high predation rates (Lea and Blumstein, 2011; Hill et al., 2019). Accordingly, elevated fGM concentrations in young, naïve foxes in Colorado may mediate cautionary behaviors in response to predation pressure (see Rödel et al., 2015; Zbyryt et al., 2018). Intraguild predation from coyotes (*Canis latrans*) is a salient threat for swift foxes, particularly juveniles, across the species' range (Andersen et al., 2003; Harrison, 2003; Ausband and Foresman, 2007a). In Comanche National Grassland, environmental variables (i.e., precipitation, vegetation height) interact with predation risk to influence juvenile swift fox survival during dispersal (Gese and Thompson, 2014). In our study, we observed higher vegetation structure—a positive correlate of coyote abundance (Thompson and Gese, 2007)—in Colorado than the Wyoming sites. This may have driven differences in age-specific stress responses to predation risk between the sites (Lea and Blumstein, 2011).

We also found that WY22 foxes had significantly lower mean fGM concentrations at the soft-release pens than both the CO21 and WY21 cohorts, suggesting that pen conditions differed between years. The 2021 cohorts faced more persistent human disturbance in the pens, as we maintained camera traps and collected scats daily for the entire acclimation period. In 2022, we deployed cameras for only 24 hours due to logistical constraints and collected scats every other day. Due to the lower sample collection frequency, scats collected in 2022 were often older upon collection, allowing more time for bacterial enzymes to metabolize the excreted hormone (Palme, 2019; Osburn et al., 2025). Following defecation, fGM concentrations can remain stable for up to 24 hours in carnivores, after which the temporal dynamics of hormone degradation vary depending on the species (Osburn et al., 2025). At the time of collection, we assigned fecal samples a qualitative condition score ranging from “very fresh” to “old” as a proxy for age (see Todd, 2024). In a subset of samples collected at the soft-release pens, comparisons of fGM concentrations based on condition showed that old samples tended to have lower fGM concentrations than fresh samples; however, pairwise differences were not significant.

In addition to differences in the frequency of sample collection, our camera traps confirmed encounters between releasees and previously translocated and/or wild-born swift foxes. Because WY22 foxes were translocated in the third consecutive year of the reintroduction program, the increased conspecific cues on the

landscape could have ameliorated translocation stress (Parker et al., 2012; Richardson and Ewen, 2016).

4.3 Post-release movement

A recent review demonstrates that hyperdispersal (i.e., extreme long-distance movements of a subset of individuals after translocation) from the release site occurs in nearly 40% of canid translocations and is associated with program failures (Bilby and Moseby, 2024), reinforcing the need to identify correlates of post-release movements. In the present study, release cohort best explained post-release net displacement in swift foxes, but the proportion of variability it explained was low. A concurrent study, which includes the swift foxes in this study, reported no significant effects of release cohort on settlement patterns in the first 100 days (Nelson et al., 2025).

Similar to a study on Tasmanian devils (Sinn et al., 2014), we found no association between fGM concentrations and net displacement. Proactive behaviors during handling also do not predict distances traveled from capture locations in San Joaquin kit foxes (Bremner-Harrison and Cypher, 2011). However, while handling scores did not improve our final model, there was a significant interaction with handling scores in the WY21 cohort that induced a twofold increase in explanatory power. WY21 foxes with higher handling scores traveled significantly greater net distances from the release pens. Notably, the effects of cohort were driven by two adult males in the WY21 cohort that traveled over 100 net kilometers from their release pens (Supplementary Table 8, 9). It was unclear why the WY21 foxes dispersed greater and more variable net distances than other cohorts, but proactive behaviors may have played a role. Moreover, the CO21 cohort was translocated to the same areas only a month prior; thus, WY21 foxes may have had to travel greater net distances to locate vacant habitat and/or avoid territorial interactions, as seen in translocated white rhinoceroses (*Ceratotherium simum*; Støen et al., 2009).

While not the top model, we found some support for fGM concentrations contributing an additive effect on path lengths. Specifically, foxes with higher fGM concentrations around the time of capture traveled greater cumulative distances post-release. The model also indicated that males traveled greater cumulative distances than females, corroborating previous observations of sex-biased dispersal in swift foxes (Moehrenschrager and Macdonald, 2003; Kamler et al., 2004) and other *Vulpes* species (Koopman et al., 2000; Kamler and Macdonald, 2014). We do not discount that the interaction of release cohort and age better explained the data, but it is possible that foxes with higher fGM concentrations around the time of capture were inclined to escape the novelty of the release site by traveling greater cumulative distances after release (Drugan et al., 1997). On the other hand, some foxes traveled large cumulative distances but remained relatively close to the release site (i.e., small net displacement). In this case, higher fGM concentrations might have signaled a greater capacity to cope with future stressors (Kozłowski et al., 2020), for instance, by mobilizing energetic reserves toward key life history events (Nelson, 2005) including the transient stage of post-release dispersal (Maag et al., 2019; Almasi et al., 2021).

Given the quadratic relationship between fGM concentrations and handling scores (Figure 3), the most compelling explanation is that foxes with moderate fGM concentrations and more proactive behaviors were disposed to greater activity and exploration after release (Koolhaas et al., 1999), culminating in larger path lengths. Studies have reported a positive relationship between proactive behaviors and total distances traveled in kit and swift foxes (Bremner-Harrison et al., 2004, 2013). Our exploratory analyses corroborated this pattern, but only in males, suggesting that swift fox stress responses could modulate the effect of proactive behaviors on post-release movements, at least in the primary dispersing sex.

4.4 Post-release survival

Mortalities are often greatest immediately after release (Swaisgood, 2010). The first two months are likely most critical for swift foxes, as translocated individuals exhibit more erratic and extensive movements than resident individuals until at least 50 days post-release (Moehrenschrager and Macdonald, 2003; Sasmal et al., 2015). Owing to associations between proactive behaviors, movement, and survival (Bremner-Harrison et al., 2004), the first 50 days may be the period when proactive behaviors exert the greatest influence on post-release fitness. Interestingly, our findings suggested that foxes with the lowest and highest handling scores were more likely to survive in the first 60 days than those with “intermediate” scores on the proactive-reactive continuum. Proactive behaviors can have adverse (May et al., 2016) or beneficial (Sinn et al., 2014; Haage et al., 2017) effects on post-release survival. In previous studies of kit and swift foxes, deceased individuals tended to be more proactive (Bremner-Harrison et al., 2004; Bremner-Harrison and Cypher, 2011). By contrast, our results provided evidence of disruptive selection for proactive and reactive personalities in the first 60 days post-release (Kotrschal, 2001), implying that the effect of personality on post-release fitness is not strictly linear in swift foxes.

Individual fGM concentrations around the time of capture were not a strong determinant of swift fox survival probability at 2-, 4-, or 6-months post-release, akin to a study on Tasmanian devils (Sinn et al., 2014). Foxes' hormone concentrations in the soft-release pens might have been a stronger predictor of survival given that they represented physiological responses to translocation. However, we did not test this relationship because we could not associate fecal samples from the pens with specific individuals. Although fGM concentrations were not directly associated with post-release survival in this study, they may have modulated handling scores which were related to survival; thus, the effects of stress physiology on post-release fitness could be more nuanced.

Considering their low explanatory power (8-23%), our survival models were likely missing variables that would better explain the data. The greater survival probability of adults in this study counters swift fox reintroductions in Canada and South Dakota, where adults and juveniles sourced from Colorado and/or Wyoming had comparable survival (Moehrenschrager and Macdonald, 2003; Schroeder, 2007), or juveniles had greater survival (Sasmal et al., 2015) after autumn releases. Though we did not test interactions due to sample size constraints, there may have been an interaction

between handling scores and age. In arctic foxes for example, more investigative and less passive (i.e., proactive) juveniles have greater survival (Choi et al., 2019). Given the demonstrable effects of post-release movement on kit and swift fox survival (Moehrenschrager and Macdonald, 2003; Bremner-Harrison et al., 2004; Bremner-Harrison and Cypher, 2011), it is possible that distances traveled impacted survival directly rather than through a behavioral or physiological mediator. Additional insights may be revealed through concurrent research on swift fox movements and population dynamics across additional years of this translocation effort (Nelson et al., unpublished data).

4.5 Conclusion

Translocations are a risky enterprise with low success rates. The present study adds to a burgeoning literature on the contributions of individual characteristics to translocation outcomes, which can guide more holistic management strategies for species of conservation concern. By investigating relationships among personality, biomarkers of stress, post-release movement, and survival, we provide the first comprehensive assessment of how the behavior and stress physiology of release candidates relate to swift fox conservation measures.

To our knowledge, this study is also the first to biologically validate a hormone assay for swift foxes. However, more work is needed to clarify whether our assay indeed provides the most appropriate measure of fGMs in swift foxes. We suggest that High-Performance Liquid Chromatography (HPLC) be used to confirm the primary fGMs excreted in swift foxes. Despite the inconsistent timing between defecation and sample collection in our study, the fGM concentrations that we measured appeared relatively stable for several days (Todd, 2024). The lack of statistical differences observed may be attributable in part to swifter desiccation in the natural, semi-arid environment of our study sites (Nhleko et al., 2022; Osburn et al., 2025). Even so, we advise future studies to conduct fecal sampling at more consistent and precise time intervals to identify where significant changes in fGM concentrations might occur post-defecation for swift foxes, and to prevent sampling delays from confounding the results (Osburn et al., 2025).

Additionally, covariance among behavioral and physiological traits may lead to complex, non-linear, or indirect effects on post-release response variables that are exacerbated by the challenges of high-resolution post-release monitoring (Bilby and Moseby, 2024). In this study, our inferences regarding foxes' post-release movements and survival were limited by the resolution of our collar data. Still, our models indicated that swift foxes' fGM concentrations were associated with behavioral variation during handling that may have forecasted short-term survival after release. Covariance between individual fGM concentrations and proactive behaviors (e.g., activity, exploration) also probably explained the positive relationship between fGM concentrations and post-release cumulative distances traveled. Given that (1) proactive behaviors were positively associated with cumulative distances traveled in males exclusively and (2) adult males were more proactive than juvenile males, we posit that fGM concentrations play a stronger

mediary role in the post-release dispersal strategies of male than female swift foxes.

The nonlinear relationship between proactive behaviors and short-term survival ultimately suggests that release cohorts comprising an array of individual temperaments may best cope with the novelty of the release site through behaviorally mediated resource partitioning and risk avoidance (Kotrschal, 2001). These advantages may be most perceptible in the earlier stages (e.g., initial releases and establishment phase) of a reintroduction—such as the first 50 days post-release in swift foxes (Moehrenschrager and Macdonald, 2003)—rather than when the population expands (i.e., growth phase) and eventually saturates the landscape (i.e., regulation phase; Sarrazin, 2007; Wilson et al., 2022).

Taken together, we urge future translocation studies to explore covariance patterns among behavioral and physiological traits. Similarly, future swift fox translocations should evaluate whether behaviors and fGM concentrations observed at other stages of translocation (e.g., during the quarantine or soft-release periods) are even stronger correlates of post-release fitness, provided that behavioral assessments minimize interobserver bias and that fecal samples can be linked to individuals. To better understand the post-release fitness implications of intrinsic attributes like personality and stress physiology, practitioners should model how these attributes interact with extrinsic, community-level covariates (e.g., predator and prey species, environmental factors, anthropogenic indices) to predict survival (Wolf and Weissing, 2012; see Paraskevopoulou et al., 2022). While there is no panacea for improving translocation outcomes, we echo the recommendation of others (Bremner-Harrison and Cypher, 2011; May et al., 2016) that capturing behavioral and physiological diversity among release candidates—in addition to genetic and demographic variation—will likely best enhance the adaptive capacity of reintroduced populations.

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 approved by Smithsonian Institution Animal Care and Use Committee (SI-20-09 and SI-23-039). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

KRT: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Visualization, Writing – original

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcosc.2026.1746027/full#supplementary-material>

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