



## OPEN ACCESS

## EDITED BY

Jose F. Gonzalez-Maya,  
Metropolitan Autonomous University, Mexico

## REVIEWED BY

Qamar Qureshi,  
Wildlife Institute of India, India  
Tinyiko Cavin Shivambu,  
University of South Africa, South Africa

## \*CORRESPONDENCE

Andrew F. Mashintonio  
✉ mashinto@kutztown.edu

<sup>†</sup>These authors have contributed equally to this work

RECEIVED 05 June 2025

REVISED 29 October 2025

ACCEPTED 17 November 2025

PUBLISHED 01 December 2025

## CITATION

Keller SM, Mashintonio AF and Barber DR (2025) Mammals show no spatiotemporal avoidance of trails or roads in a forested raptor sanctuary. *Front. Ecol. Evol.* 13:1642044. doi: 10.3389/fevo.2025.1642044

## COPYRIGHT

© 2025 Keller, Mashintonio and Barber. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](#). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

# Mammals show no spatiotemporal avoidance of trails or roads in a forested raptor sanctuary

Shannon M. Keller<sup>1†</sup>, Andrew F. Mashintonio<sup>1\*†</sup> and David R. Barber<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Kutztown University of Pennsylvania, Kutztown, PA, United States,

<sup>2</sup>Acopian Center for Conservation Learning, Hawk Mountain Sanctuary Association, Orwigsburg, PA, United States

Disturbance from human presence can cause changes in wildlife behavior, physiology, and fitness. Wildlife in conservation areas that also serve as recreational areas for people are especially vulnerable to these disturbances. Animals may avoid human presence spatially, by moving to new locations, or temporally, by becoming more active when human activity is low. We examined spatial and temporal changes to mammal occupancy (interpreted as site use) and detection probability at Hawk Mountain Sanctuary (HMS), a raptor sanctuary that provides both wildlife conservation and hiking trails. We placed 12 camera traps at random locations throughout the sanctuary and nearby Acopian Center, capturing images from March to November 2022. We used the distances to trails and roads as covariates representing human presence, time of day (dawn, day, dusk, or night) to estimate temporal response, and distance to streams and elevation as environmental covariates that can affect site use. Fifteen mammal species were detected over 2,837 trap nights. Bobcat (*Lynx rufus*) were the only species to show potential spatial avoidance of humans by avoiding roads, while no species showed temporal avoidance. Time of day affected detection probability for most species but aligned with each species' expected diel patterns. These results suggest that mammals at HMS are not shifting their behavior to avoid trails and roads. Despite the potential for human-wildlife conflict in a multiple-use conservation area, this study demonstrates that managers can be successful at balancing recreational opportunities for people with maintenance of diverse wildlife.

## KEYWORDS

camera traps, conservation biology, detection probability, habitat, Hawk Mountain Sanctuary, occupancy, site use, wildlife management

# 1 Introduction

Wildlife habitat is increasingly being negatively affected by human activities, necessitating conservation action to prevent biodiversity loss (Ellis, 2011; Lovejoy, 2016). One approach to conserve nature is the establishment of protected areas, defined as a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley and Stolton, 2008). Protected areas vary in their goals and levels of protection, from wilderness areas that seek to minimize human disturbance to areas that allow limited natural resource extraction (Dudley and Stolton, 2008; Stamper et al., 2013; Dietz et al., 2020). In the United States, various public and privately held lands are considered protected areas, including National Parks and National Wildlife Refuges, numerous state-run parks, and wildlife sanctuaries (Mockrin et al., 2018; Dietz et al., 2020). Many of these sites allow human recreation, including hiking, camping, and swimming, among other activities (Marion et al., 2016; Pegler et al., 2024; Van Deursen et al., 2024). While resource extraction is typically prohibited in these areas, these recreational activities invariably still reduce the availability of their natural resources (Marion et al., 2016). This can have an adverse impact on wildlife, causing physiological and reproductive changes, negative shifts in abundance or occupancy, and changes in community composition (Larson et al., 2016; Chen et al., 2022). How wildlife responds to human disturbance in a protected area is an important and understudied issue, especially as the popularity of outdoor recreation in the United States and the amount of land dedicated to recreation increase (Larson et al., 2016; Nickel et al., 2020).

Animal response to human disturbance has been shown to depend on the duration and consistency of the disturbance (Gaynor et al., 2018; Nickel et al., 2020). Many mammal species view humans with fear, which can have negative effects across trophic levels through altered predator-prey relationships (Gaynor et al., 2018; Suraci et al., 2019; Nickel et al., 2020; Murphy et al., 2021). Temporal response to human disturbance varies by species and the nature of the disturbance (Lewis et al., 2021). Normally diurnal or crepuscular species may shift towards nocturnality when human presence is high (Gallo et al., 2022). For an animal that is not adapted to nighttime activity, this can disrupt foraging and predator avoidance behaviors (Gaynor et al., 2018). Carnivores are more likely to increase nocturnality in developed areas (Rivera et al., 2022). When predators become more nocturnal, prey species respond with increasing diurnal activity (Gallo et al., 2022). Gallo et al. (2022) found decreased nocturnality with increases in urbanization among raccoons (*Procyon lotor*), eastern cottontails (*Sylvilagus floridanus*), and white-tailed deer (*Odocoileus virginianus*), while Virginia opossums (*Didelphis virginiana*) increased nocturnal activity. Spatially, some ungulates have been shown to prefer areas close to people, using their presence as a “human shield” against carnivores (Shannon et al., 2014; Suraci et al., 2019; Gaynor et al., 2021). Kautz et al. (2022) showed that female white-tailed deer increased use of sites near roads during the

summer, reducing fawn predation. Elk (*Cervus canadensis*) density in Banff National Park was higher in areas where human development displaced wolves (*Canis lupus*) than in areas with less people and more wolves (Hebblewhite et al., 2005).

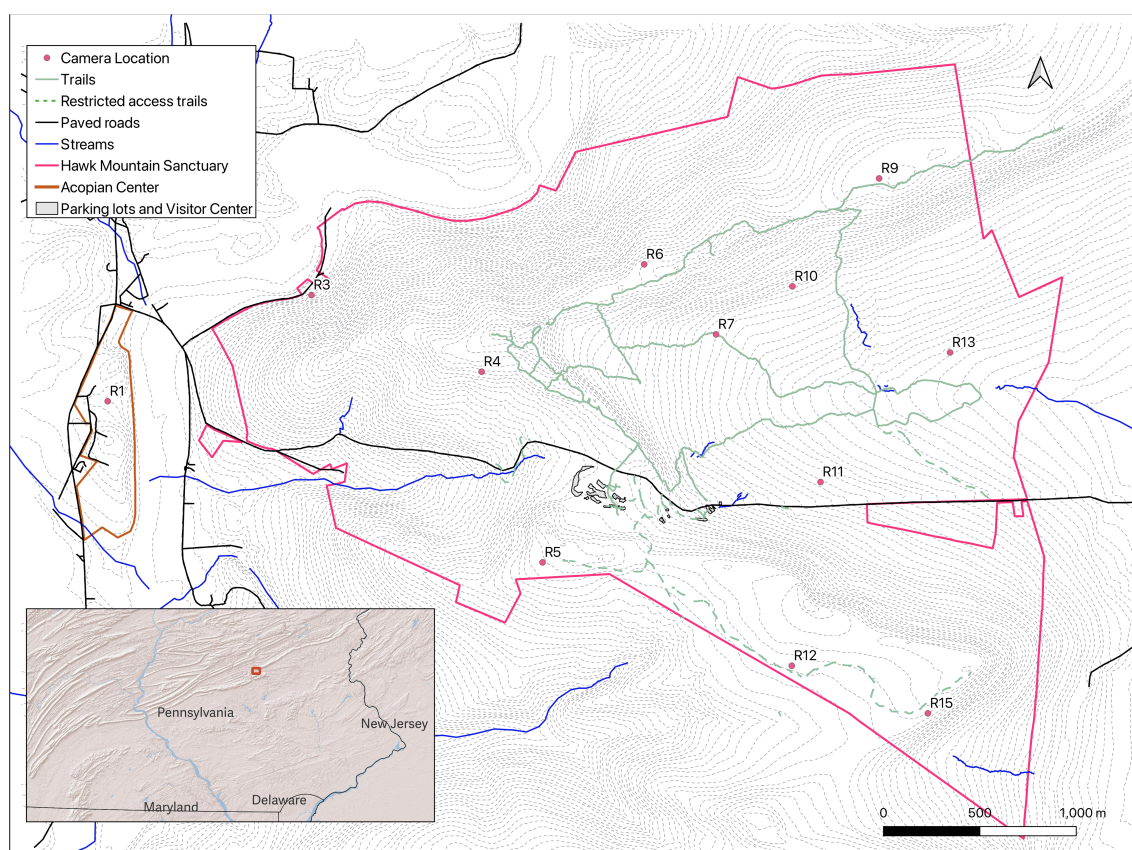
This study examines spatiotemporal responses to human presence via avoidance of roads and trails by mammals in a wildlife sanctuary that also serves as a recreational area. We do this by estimating occupancy, the proportion of sites occupied by a species (MacKenzie et al., 2002), and detection probability, the likelihood that a species will be detected at a site it occupies, of medium to large terrestrial mammals in the sanctuary. Since we cannot assume independence between sites, particularly for wide-ranging species in our study (e.g. coyotes; *Canis latrans*), we are interpreting the occupancy parameter as site use, or the probability that a site was used by the species at least once within the time period surveyed (MacKenzie and Royle, 2005). We hypothesized that sites farther from trails and roads would have higher use, and that sites closer to trails and roads would receive higher use during the night compared to the day. We also expected that other site-specific and survey-specific environmental factors, including proximity to streams, elevation, precipitation, and temperature, will have varying effects on the targeted species. This study contributes to our understanding of human-wildlife coexistence in a conservation setting, as well as demonstrates the use of time of day in occupancy modeling.

## 2 Method

### 2.1 Study area

Hawk Mountain Sanctuary (HMS) is a private 2,600-acre raptor sanctuary located on the Kittatinny Ridge, the southernmost ridge in the Ridge and Valley Physiographic Province in Berks and Schuylkill Counties, Pennsylvania (Hawk Mountain Sanctuary, 2025; Figure 1). It is predominantly mixed oak forest with small areas of conifer cover, open meadow, and rock scree (Hawk Mountain Sanctuary, 2017). Elevation ranges from 152–463 m above sea level. Over the course of this study, the monthly average low temperature ranged from 3.4°C in March to 20.2°C in July, and the monthly average high temperature ranged from 13°C in March to 30.5°C in August. Average monthly precipitation ranged from 40.4 mm in August to 110.9 mm in May. The regional landscape is highly fragmented due to agricultural and ongoing development pressures in the valley bottomlands; however, the Sanctuary is within one of the largest blocks of contiguous forest (approx. 6000 ha) in southeastern Pennsylvania. The human population of the surrounding counties is approximately 573,000 people with a 12% poverty rate and \$67,000 - \$78,000 median income (DataUSA, 2025a, b).

Hawk Mountain’s mission is to conserve birds of prey worldwide by providing leadership in raptor conservation science and education, and by maintaining HMS as a model observation, research, and education facility. Since its founding in 1934, the Sanctuary property has been maintained as a relatively untouched



**FIGURE 1**  
Map of Hawk Mountain Sanctuary and the nearby Acopian Center with the locations of cameras and relevant environmental features. Inset: location of study area (red polygon) within Pennsylvania, USA.

preserve with regards to development and timber management, though it is split by a paved road. Although human influence has been minimized, the Sanctuary actively manages non-native invasive plants and white-tailed deer populations. Approximately 60,000 people visit the sanctuary each year to use the 13 km of hiking trails (Hawk Mountain Sanctuary, 2025). While the majority of trail use occurs from September through November, hiking trails are utilized throughout the year. The trails are open daily from dawn to dusk. The nearby Acopian Center is located at the base of the mountain and includes a mixture of open fields and small patches of forest, which are not open to the public. There are an additional 4.2 km of restricted access trails throughout the Sanctuary that are used by park managers and researchers to more easily access the forest interior.

## 2.2 Image collection and processing

We divided the sanctuary into grids and placed one camera at a randomly chosen location within 15 grids (Stevens and Olsen, 2004). Three cameras failed, leaving us with 12 sites for this study. Each site was at least 470 m away from any other site ( $\bar{x}$  = 807 m). Cameras (Dark Ops HD Apex motion-sensing camera, Browning, Birmingham, AL, USA) were placed in March 2022

(Figure 1). We set cameras on trees 0.2 to 0.6 m above the ground and facing north to optimize detection of the targeted species (Sunarto et al., 2013). If terrain did not allow a camera to face north, the camera faced south instead. Eleven of the sites were forested and one site was in a meadow adjacent to sanctuary buildings at the Acopian Center, which still experienced human activity from sanctuary staff and the nearby road. The delay period was set to one second, and only one image was taken with each trigger. Lures or bait were not used to avoid biasing detections (Rocha et al., 2016). We visited cameras every 3–4 months to exchange SD cards and trim surrounding vegetation.

Cameras were active from 14-Mar-2022 to 23-Nov-2022, resulting in 97,691 images across 2,837 trap-nights (Supplementary Material 1). We processed images using Camelot Open-Source Camera Trap software (Hendry and Mann, 2017). Each image was labeled according to the species or object it contained. For each species, we developed encounter histories by pooling detections into 6-day survey periods, which reduces the number of non-detections in the dataset to improve statistical power (Erb et al., 2012; Gray, 2012; Cid et al., 2013; Tobler et al., 2015). Before pooling detections, each day was first divided into four groups based on the time of day (diel period; see below); thus our encounter histories for all species included 168 survey periods, where a detection was recorded for a survey if there was at least one

capture of the species during that survey period (Supplementary Material 2).

### 2.3 Statistical analysis

We used single-species single-season occupancy models (MacKenzie et al., 2006) to estimate probability of site use during the season ( $\psi$ ) and detection probability ( $p$ ) for each identified mammal species using the PRESENCE occupancy software (Hines, 2006). Because closure is unlikely for the wide-ranging species in our study, our estimate of site use is likely larger than true occupancy (proportion of an area where a species occurs; MacKenzie and Royle, 2005). We find this acceptable because our objective was to determine whether the mammal species inhabiting our study area are avoiding trails and roads and not to explicitly estimate occupancy.

We included the distance to the nearest trail (including restricted access trails) (trail), distance to the nearest paved road (road), distance to the nearest stream (stream), and elevation (elev) as environmental covariates potentially affecting site use (Table 1). Distance to feature layers were created from maps of these features using the Proximity (raster distance) processing tool in QGIS version 3.34.3 (QGIS, 2024). The trail and road covariates served as a proxy for human presence, as direct measures were unavailable given the placement of the cameras. We included temperature (temp), precipitation (precip), and time of day (diel) as covariates potentially affecting detection probability (Table 1). Temperature and rainfall can affect both the activity level of an organism and the performance of certain camera trap models, leading to variation in detection probability (Rowcliffe et al., 2011; McIntyre et al., 2020). We used the average time of sunrise and sunset across each 6-day survey period to determine the dawn (sunrise +/- two hours) and dusk (sunset +/- two hours) time periods. Day was thus the time period between dawn and dusk, while night was the time period between dusk and the following dawn. We included the diel covariate in all models as three parameters – dawn, dusk, and night, with day being the reference period (MacKenzie et al., 2006; Gallo et al., 2022). To determine whether species were avoiding

trails or roads during periods of high human activity (i.e. day), we included interaction terms between diel and both distance to trails and distance to roads.

We obtained weather, sunrise, and sunset data from Visual Crossings Corporation (2024). We standardized all covariates except diel to have zero mean and unit standard deviation to improve numerical optimization and allow for easier comparison between coefficient estimates (Cade, 2015; Broms et al., 2016; Santon et al., 2023). We included both a linear and quadratic form of all covariates except diel and precipitation in the initial step of our model selection approach; the quadratic form was included to identify any non-linear relationships.

To construct a candidate set of models for each species, we first fit models of site use and detection probability using each covariate from Table 1 separately (Arnold, 2010; Morin et al., 2020). We compared models using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson, 2002). Top models for each parameter ( $\psi$  and  $p$ ), along with any model with  $\Delta AIC_c \leq 5$  from the respective top model, were carried forward to a second model selection step (Morin et al., 2020). If two models within  $\Delta AIC_c \leq 5$  had covariates with a high (>0.6) Pearson correlation coefficient, only one of those models was carried forward (Gilhooly et al., 2019).

During the first step we also tested for inclusion of quadratic and interaction terms in the models. For each covariate listed above, we ran additional models that included the linear and quadratic form of the covariate, i.e.,

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$$

where  $y$  represents the parameter to be estimated ( $\psi$  or  $p$ ),  $\beta_n$  represents the coefficient estimates, and  $x_1$  represents the covariate. If this model had an  $AIC_c$  score that was at least 2 better than the model with the linear covariate and the shape of the relationship (as determined by plotting the coefficient estimates across the range of observed values of the covariate) was non-linear, we selected the quadratic form to carry to the next step, provided it was within  $\Delta AIC_c \leq 5$  of the top model (Arnold, 2010). For environmental covariates representing human presence, we ran additional models that included interaction terms with diel, i.e.:

TABLE 1 Descriptions of model covariates.

Covariate (abbreviation)	Description	Expected influence
Distance to trails (Trail)* <sup>a</sup>	The distance a site is from the nearest trail (including restricted access trails).	Site use
Distance to roads (Road)* <sup>a,b</sup>	The distance a site is from the nearest paved road.	Site use
Distance to streams (Stream)*	The distance a site is from the nearest stream.	Site use
Elevation (Elev)*	A site's elevation.	Site use
Temperature (Temp)*	Average temperature during survey period.	Detection probability
Precipitation (Precip)	Average amount of precipitation during survey period.	Detection probability
Time of day (Diel) <sup>a,b</sup>	Dawn and dusk were defined as two-hour windows around sunrise and sunset. Night was the period between dusk and dawn, while day was the period between dawn and dusk.	Detection probability

All covariates except diel were standardized.

\*Includes linear and quadratic versions to identify non-linear relationships.

<sup>a,b</sup>Covariates with the same letter were included as an additional interaction term.



$$\psi = \beta_0 + \beta_1 x_1 + \beta_2 x_1 x_2$$

where  $x_1$  represents the environmental covariate and  $x_2$  represents the diel covariate. We did not include interaction terms for models of  $p$ . If this model had an  $AIC_c$  score that was at least 2 better than the model without the interaction term, we selected the interaction form to carry to the next step, provided it was within  $\Delta AIC_c \leq 5$  of the top model (Arnold, 2010). Quadratic forms of these covariates were also tested in conjunction with interaction terms, which took the form:

$$\psi = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1 x_2 + \beta_4 x_1^2 x_2$$

Selection of a model with a quadratic interaction term followed the same rules as those described above for quadratic models without interaction terms.

In our second step, we fit models that combined the top covariates selected from the first step (including quadratic or interaction terms as appropriate) for site use and detection probability. We limited each model to only have one covariate per parameter ( $\psi$  or  $p$ ) due to the small sample size of our data ( $n = 12$  sites). All models fit during this second step were included in the full candidate set, which can be found in Supplementary Material 3. We performed MacKenzie-Bailey goodness-of-fit tests on all models in both steps (MacKenzie and Bailey, 2004) using 1000 bootstraps. For species with models that had  $\hat{c} > 1$ , we used quasi-AIC (QAIC) for model comparison (MacKenzie and Bailey, 2004).

To account for model selection uncertainty in some species, we calculated model-averaged parameter estimates using each model's output ( $AIC_c$ , Akaike weight [ $w_i$ ], and parameter estimate; Charalambous et al., 2024). The parameter estimates were weighted by the Akaike weight and then averaged across all models in the final list. Along with model-averaged estimates for detection probability and site use, we present model-averaged coefficients ( $\beta$  estimate, standard error, [85% confidence interval]) to help contextualize the results (Arnold, 2010; Wilkinson et al., 2023). Covariates that were missing from a given model were assigned an estimate of zero for averaging purposes (Symonds and Moussalli, 2011). We did not use the model-averaged coefficients to make inferences directly because of potential issues of interpretation due to different scales and collinearity among covariates (Cade, 2015). All post-model fit processing was performed using Mathematica version 13.0 (Wolfram Research, Inc., 2022).

## 3 Results

### 3.1 Species survey

We detected 15 mammal species across all sites (Figure 2). The number of detections across the 168 survey periods was highest for white-tailed deer ( $n = 605$  detections) followed by 330 detections for eastern gray squirrels (*Sciurus carolinensis*). All other species had 70 or fewer, with striped skunks (*Mephitis mephitis*) having the fewest

detections with only one. American mink (*Mustela vison*) and striped skunk were not included in further analysis because they had too few detections to accurately estimate site use, and white-tailed deer were not included because they were present at every site.

### 3.2 Detection probability

Weighted mean detection probabilities ranged from 0.0041 (SE = 0.0003, 85% CI = [0.0035, 0.0046]) for bobcat (*Lynx rufus*) to 0.1786 (0.0000, [0.1786, 0.1786]) for gray squirrel (Figure 2). Covariates from the first step in our model selection process usually included diel or temperature, but rarely both, and sometimes included precipitation (Supplementary Material 3). Higher temperature was associated with higher detection probability for black bear (*Ursus americanus*) ( $\beta_{temp} = 0.23, 0.14, [0.02, 0.44]$ ), coyote (0.30, 0.22, [-0.02, 0.62]), and ermine (*Mustela erminea*) (0.26, 0.25, [-0.09, 0.62];  $\beta_{temp}^2 = -0.03, 0.08, [-0.15, 0.08]$ ), whereas cottontail (-2.62, 0.00, [-2.62, -2.62]; -0.91, 0.00, [-0.91, -0.91]) and red fox (*Vulpes vulpes*) (-0.10, 0.11, [-0.25, 0.07]; -0.07, 0.08, [-0.18, 0.05]) had higher detection probability at low to intermediate temperature (Figure 3). There was weak support for temperature affecting detection probability of ermine and red fox and no support for temperature affecting detection probability of bobcat (-0.02, 0.04, [-0.07, 0.03]; Supplementary Material 3). Precipitation did not influence detection probability for bobcat ( $\beta_{precip} = -0.01, 0.02, [-0.05, 0.02]$ ) or coyote (-0.05, 0.08, [-0.17, 0.07]), the only species where precipitation was included in the step two models (Supplementary Material 3).

Detection probability was highest during the day for chipmunk (*Tamias striatus*) ( $\beta_{dawn} = -2.63, 0.00, [-2.63, -2.63]$ ;  $\beta_{dusk} = -2.28, 0.00, [-2.28, -2.28]$ ;  $\beta_{night} = -4.26, 0.00, [-4.26, -4.26]$ ) and gray squirrel (-1.15, 0.00, [-1.15, -1.15]; -1.20, 0.00, [-1.20, -1.20]; -50.67, 72.00, [-154.34, 53.01]; Figure 4). Southern flying squirrel (*Glaucomys volans*) (29.83, 30.12, [-13.54, 73.20]; 80.84, 35.70, [29.44, 132.24]; 83.64, 35.70, [32.24, 135.04]), porcupine (*Erethizon dorsatum*) (0.41, 0.00, [0.41, 0.41]; 0.41, 0.00, [0.41, 0.41]; 2.30, 0.00, [2.30, 2.30]), raccoon (1.40, 0.00, [1.40, 1.40]; 0.70, 0.00, [0.70, 0.70]; 2.66, 0.00, [2.66, 2.66]), and red fox (-0.08, 0.10, [-0.22, 0.06]; -0.16, 0.20, [-0.46, 0.13]; 0.13, 0.17, [-0.11, 0.38]) all had a higher detection probability at night, though there was weak support for diel affecting detection probability of red fox (Figure 4, Supplementary Material 3). No species were more likely to be detected during dawn or dusk (Figure 4). The top model(s) for bobcat and opossum had no covariates for detection probability (Supplementary Material 4).

### 3.3 Site use estimation

Raccoon had the highest estimate of overall site use at 0.938 (SE = 0.013, 85% CI = [0.919, 0.956]) while cottontail had the lowest at 0.167 (0.000, [0.067, 0.167]; Figure 2). The top site use models (within  $\Delta AIC_c \leq 2$ ) for four species – chipmunk, opossum, porcupine, and raccoon – did not include any environmental covariates. Black

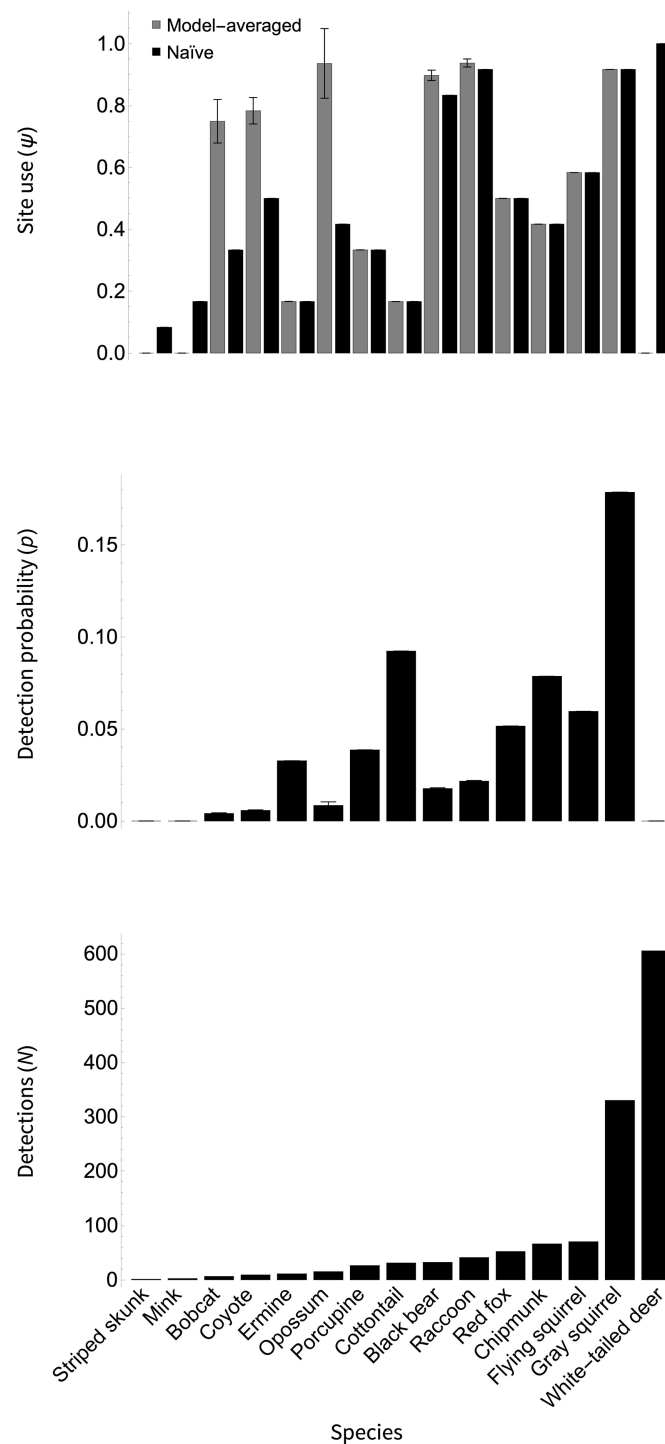


FIGURE 2

Distribution of the number of detections over 168 survey periods, weighted model-averaged overall detection probabilities ( $p$ ), and naïve and weighted model-averaged overall site use ( $\psi$ ) for all target species identified. Error bars represent standard error of weighted model averages.

bear ( $\beta_{\text{trail}} = -34.97, 23.97, [-69.48, -0.46]$ ) had highest site use near trails (Figure 3), while ermine ( $-100246.00, 59056.80, [-185288.00, -15204.60]$ ;  $\beta_{\text{trail}}^2 = -56939.20, 33627.30, [-105363.00, -8515.81]$ ) had highest site use away from trails. Bobcat avoided sites near roads ( $\beta_{\text{road}} = 158.32, 83.24, [38.45, 278.18]$ ), whereas cottontail ( $-1.27, 1.29, [-3.13, 0.58]$ ) and gray squirrel ( $-49.03, 96.41, [-187.86, 89.79]$ )

preferred sites near roads (Figure 3). There was weak support for distance to roads affecting site use of chipmunk ( $-0.00, 0.54, [-0.78, 0.77]$ ;  $0.00, 0.77, [-1.10, 1.11]$ ) or porcupine ( $-0.09, 1.58, [-2.36, 2.19]$ ) or for distance to roads affecting site use of raccoon ( $-0.06, 1.03, [-1.55, 1.42]$ ) or red fox ( $-0.19, 0.26, [-0.57, 0.19]$ ;

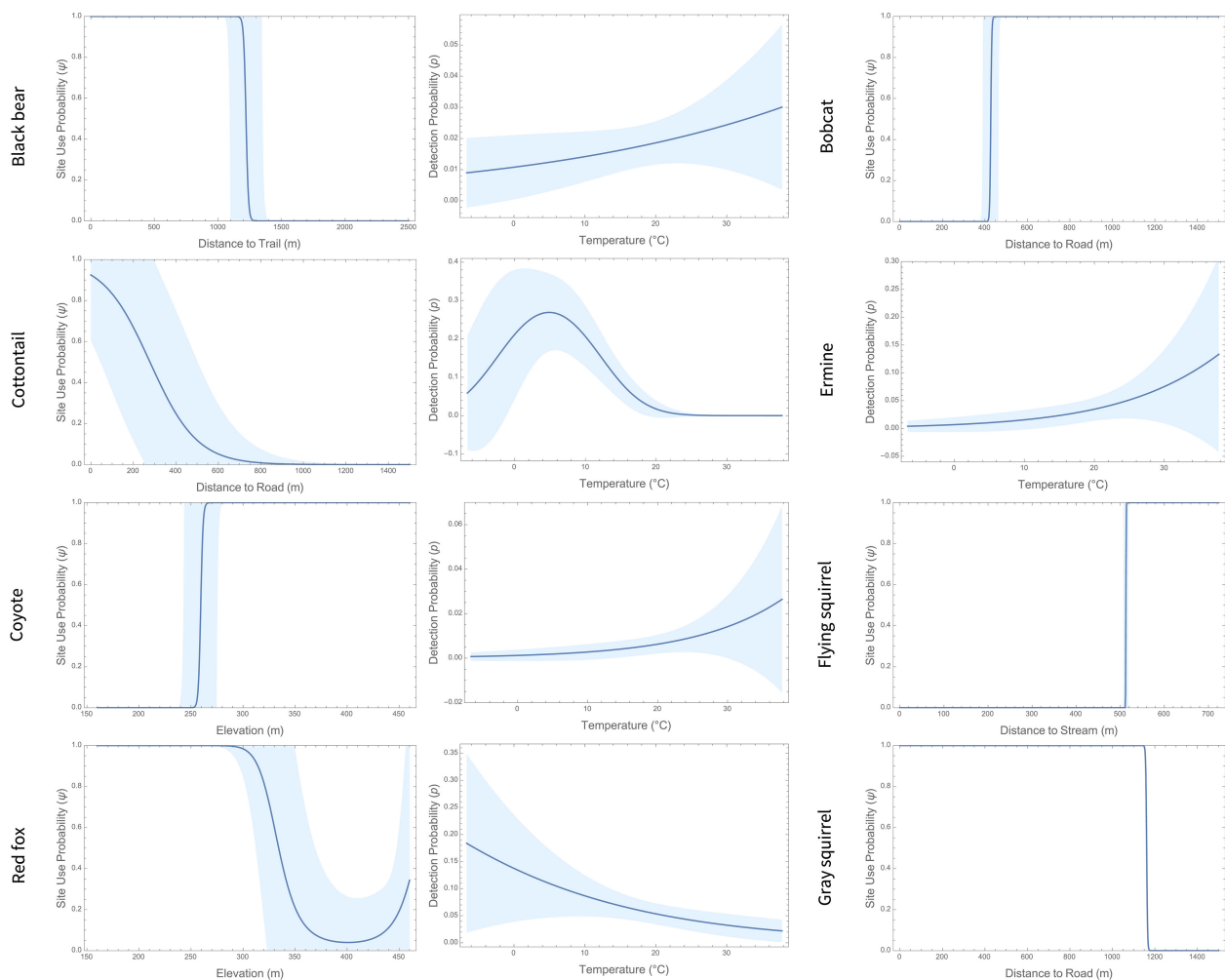


FIGURE 3

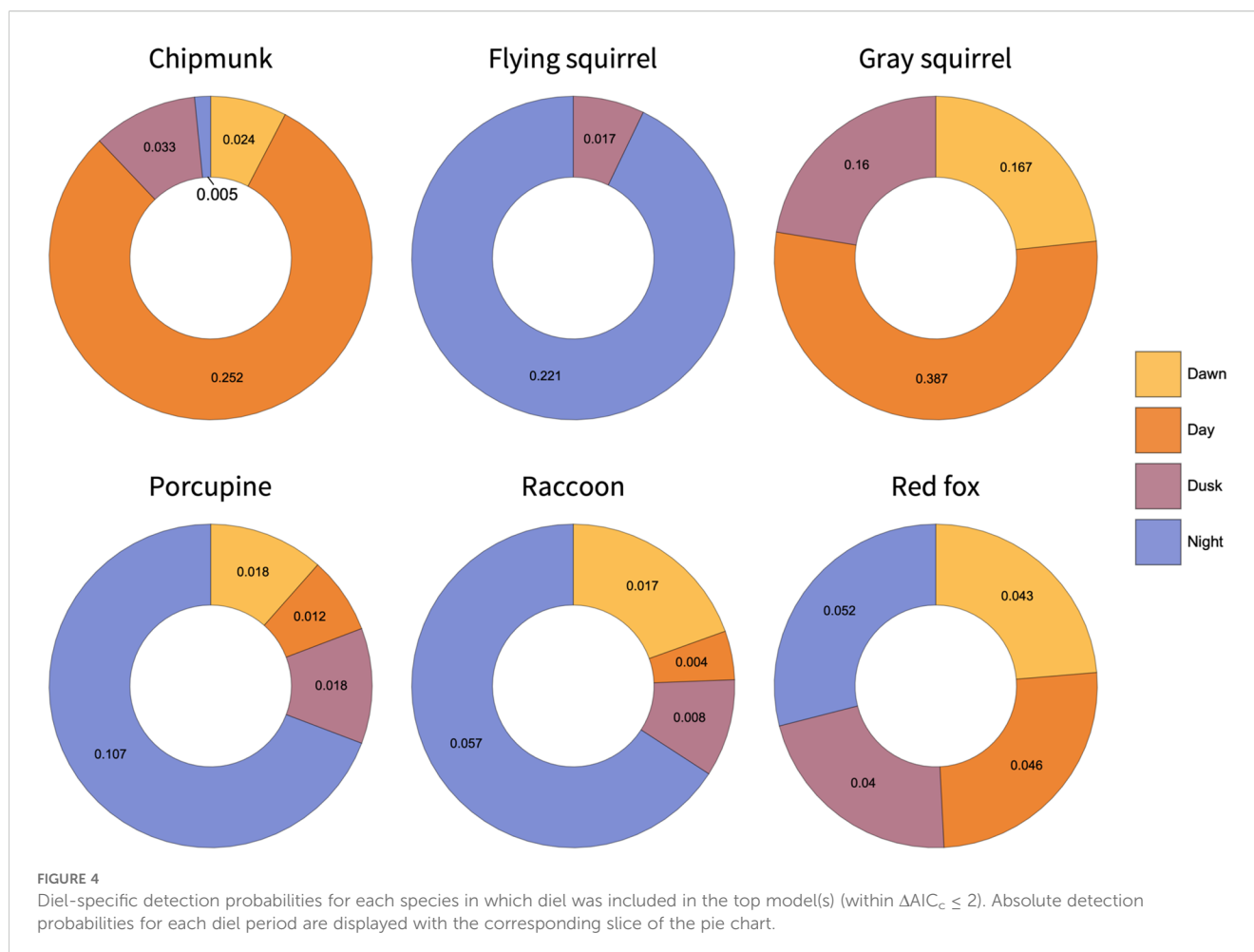
Predicted  $\psi$  and  $p$  across each covariate for each species except diel, which was composed of three separate parameters. Only covariates included in the top model(s) (within  $\Delta AIC_c \leq 2$ ) for each species are shown. For chipmunk, opossum, porcupine, and raccoon, the only important covariate was diel (or none).

Supplementary Material 3). Interactions between diel and roads and diel and trails were not important for any species.

Flying squirrel avoided sites near streams ( $\beta_{\text{stream}} = 739.89, 517.28, [-4.99, 1484.76]$ ), while coyote preferred sites at higher elevation ( $\beta_{\text{elev}} = 49.04, 22.67, [16.39, 81.68]$ ) and red fox preferred sites at lower elevation ( $-4.16, 2.87, [-8.30, -0.03]$ ;  $\beta_{\text{elev}}^2 = 3.70, 2.55, [0.02, 7.38]$ ; Figure 3). There was no support for distance to streams affecting site use of bobcat ( $-12.52, 18.77, [-39.54, 14.51]$ ), chipmunk ( $0.02, 0.47, [-0.66, 0.69]$ ), cottontail ( $-136.21, 433.04, [-759.79, 487.37]$ ;  $\beta_{\text{stream}}^2 = -190.06, 604.24, [-1060.16, 680.04]$ ), gray squirrel ( $1.17, 73.30, [-104.38, 106.71]$ ;  $0.79, 49.72, [-70.80, 72.39]$ ), porcupine ( $-0.00, 0.07, [-0.10, 0.09]$ ), or raccoon ( $-5.15, 42.85, [-66.86, 56.56]$ ), nor was there support for elevation affecting site use of bobcat ( $42.82, 63.83, [-49.10, 134.74]$ ), cottontail ( $-0.16, 0.39, [-0.72, 0.39]$ ), gray squirrel ( $-0.05, 2.86, [-4.17, 4.08]$ ;  $0.08, 4.86, [-6.93, 7.08]$ ), or raccoon ( $-0.08, 1.35, [-2.03, 1.86]$ ; Supplementary Material 3).

## 4 Discussion

This study provides evidence that most mammals at HMS are not altering their spatiotemporal behavior in response to the presence of humans, represented here by the interaction between time of day and the proximity to trails and roads. Kays et al. (2017) also found that most forest-dwelling terrestrial mammals were minimally impacted by recreational hiking in protected forests across the eastern United States. It may be that there is optimal habitat near the trails and roads of HMS that is worth the potential risk of encountering humans. It is also possible that mammals at HMS are negatively affected by human presence through other mechanisms, such as stress or increased energetic costs to find resources, which were not captured by our models (Larson et al., 2016; Gaynor et al., 2018). Our results may also be impacted by the uneven distribution of human visitors on trails both spatially and temporally; the majority of visitors utilize the main trail leading from the visitor's center to numerous lookout points from



September through November. The effect of humans on wildlife may vary seasonally, particularly since many behaviors of these species can be affected by time of year (Elbroch and Rinehart, 2011; Kupferman et al., 2021; Hubbard et al., 2022; Mayer et al., 2023; Belamaric et al., 2024; Minns et al., 2024). Furthermore, even if mammals are avoiding this portion of the trail, this represents a small fraction of the total trails available within the sanctuary. Our setup ( $n = 12$  sites) may have also lacked the statistical power to detect an effect of the interaction terms, given the complexity of those models (Goldstein et al., 2024). While twelve sites were enough to provide adequate coverage of the Sanctuary, a more intensive sampling strategy during the busiest months for visitation may reveal a stronger effect of human presence.

With our data spanning spring through fall, the closure assumption may be violated if species are moving in and out of sites between sampling periods (MacKenzie and Royle, 2005). While we reinterpreted the occupancy parameter as site use to account for this, non-closure can still lead to biased estimates when detection probability is low (Rota et al., 2009). Dynamic or multi-season occupancy models that can account for immigration into and emigration out of sites across time have been suggested as a solution to the violation of the closure assumption when using single-season models (Valente et al., 2017). However, for mobile animals with large ranges, the closure assumption may never be met, as it is always possible an individual crosses a site boundary

between sampling periods (Valente et al., 2024). We therefore acknowledge that our estimates of site use are likely higher than they would be under a shorter sampling period and instead focus on the effects of environmental variables on these estimates.

For most species in our study, model-averaged site use estimates were similar to naïve occupancy when detection probability was at least 0.01, suggesting limited bias from violation of the closure assumption. Three species (bobcat, coyote, opossum) with estimates of detection probability lower than 0.01 had the largest increases in estimated site use compared to naïve occupancy. For these highly elusive species, models of site use may be too unreliable to provide accurate inference (Pautrel et al., 2023). Instead, we treat these species descriptively. Occupied sites for bobcat were generally far from the nearest road, matching model output. They were also mostly higher elevation and closer to trails, which was not captured by our models. Despite very few detections, coyote was detected at half of our study sites; these sites were all generally higher-elevation, again matching model output. Opossum was also detected at mostly higher-elevation sites that were far from streams, but neither of these relationships were captured by our models. And despite having a higher detection probability and a less-biased site use estimate, ermine was only detected at two sites (Supplementary Material 2), making it difficult to make projections of site use across various distances to trails.



Large animals may utilize trails as an easy method of moving through habitat or as an opportunity to forage for anthropogenic food sources (Lewis et al., 2021). This has led to a lack of response to human disturbance from black bears (Lewis et al., 2021), though here we document a positive response to trails by black bears. Alternatively, ermines may show an avoidance of trails given their preference for sites farther from trails. While weasel species in North America are generally understudied (Cheeseman et al., 2024), two weasel species in Maine were found to prefer disturbed forest stands, indicating tolerance of human disturbance at larger spatial scales (Evans and Mortelliti, 2022). Road effects vary by species size and behavior (Fahrig and Rytwinski, 2009). Mid-sized mammals with low population densities and large ranges are negatively impacted by roads while small mammals that are fast enough to avoid car traffic may benefit from roads as a food source (Fahrig and Rytwinski, 2009). Here, we saw that bobcats avoided sites near roads while gray squirrels and cottontails preferred them; no other species' site use was affected by the presence of roads.

While our study did not find a temporal shift in the use of trails or roads, time of day itself had a strong effect on detection probability for many species, matching expected behavior (Elbroch and Rinehart, 2011). Black bears are known to increase their nocturnal activity during the hunting season prior to hibernation (Hubbard et al., 2022), but our study period ended just prior to hunting season in Pennsylvania. Coyotes also shift towards more nocturnal activity when human presence is high (Rivera et al., 2022). Here, coyotes were regularly detected during both day and night, suggesting the impact of humans is low. Ermine have been shown to alter their diel behavior to match the nocturnal behavior of their prey and to avoid competitors that are active at other times (Kupferman et al., 2021). Red foxes, though often nocturnal (Elbroch and Rinehart, 2011), have been found to increase daytime activity when vegetation was available (Gallo et al., 2022). HMS offers large areas of cover, likely contributing to the combination of nocturnal and diurnal activity we observed. Despite similarities in habitat use and diet (Carver et al., 2011), both opossums and raccoons were more active nocturnally at HMS, matching the findings of previous studies (Kaufmann, 1982; Ryser, 1995; Gardner and Sunquist, 2003; Gehrt, 2003).

Flying squirrels were the only species with apparent avoidance of streams. Our sites far from streams may have had more large trees than sites proximal to streams. Flying squirrels prefer tall, large-diameter trees for den cavities and gliding (Elbroch and Rinehart, 2011; Howard et al., 2020). They may also avoid areas with dense understory, which is present around most of the streams at HMS. Although coyotes and red foxes responded to elevation, our sites did not represent the full elevational range of HMS, so we cannot draw any firm conclusions about the relationship between site use and elevation. The apparent preference for sites at differing elevations may also be due to other unmeasured environmental variables such as forest cover and vegetation density, which are also important components of habitat that can affect mammal site use and detection (Boron et al., 2019). For example, available vegetative

cover may lessen the effects that human presence has on predator species like black bear, coyote, bobcat, and red fox (Nickel et al., 2020).

We considered the distance from trails and roads as proxies for human presence. Roads are a severe threat to many species because they can cause increased mortality, altered behavior, and fragmented habitat (Fahrig and Rytwinski, 2009; D'Amico et al., 2016). Human activities on both roads and trails can cause noise and disturbances that affect behavior, leading to both a spatial and temporal avoidance of roads and trails (Fahrig and Rytwinski, 2009; Rogala et al., 2011; Westekemper et al., 2018; Soultan et al., 2021). We did not incorporate frequency of trail use by humans into our models, as most of our cameras were off-trail and did not have any human sightings. The inclusion of this parameter can be useful, since increases in park visitation and trail density can affect detection and site use (Marion et al., 2024; Boone et al., 2025). Human detections can also be useful for conducting an activity pattern analysis to measure temporal overlap between humans and wildlife and to identify potential avoidance behavior (Ma et al., 2025). Although the majority of trail use at HMS is concentrated between the visitor center and the North Lookout (near camera R4), most trails enjoy near-daily use by humans (personal observation). It is unknown whether the intensity of use by humans along these other trails is large enough to have a measurable effect on site use, but even light traffic can have a negative impact on habitat quality (Marion et al., 2016).

Conservation areas are important for wildlife, but many also provide recreational opportunities for humans. Managers of these areas must strike a balance between habitat protection and accessibility, which has become more challenging as human use of these areas has increased in recent years. The potential for negative impacts on wildlife is high, necessitating continual monitoring of populations to detect and measure any changes in key population metrics. Our method to detect both spatial and temporal changes in site use can be utilized by managers of conservation areas to determine the impact of human visitors on wildlife. More specifically, incorporating interactions between features of the landscape and time of day can identify whether organisms are shifting their use of sites to avoid human presence. Many organisms utilize trails to travel more quickly across the landscape. Varying the landscapes through which trails, roads, and other park infrastructure are built can ensure that sufficient space and suitable habitat are available for a mammal community with a spectrum of behavior and habitat needs. Our results demonstrate the success that managers can have at balancing recreational opportunities for people and maintenance of diverse wildlife populations within a protected area.

## Data availability statement

The data presented in the study are deposited in the Zenodo repository, accession number 14759470.

## Ethics statement

This animal study was approved by the Kutztown University Institutional Review Board. This study was conducted in accordance with local legislation and institutional requirements.

## Author contributions

SK: Conceptualization, Data curation, Formal Analysis, Investigation, Software, Validation, Writing – original draft, Writing – review & editing. AM: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. DB: Data curation, Resources, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research and/or publication of this article. This work was supported by a Kutztown University Research Committee Grant.

## Acknowledgments

This is Hawk Mountain Sanctuary contribution to conservation science number 406.

## References

- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* 74, 1175–1178. doi: 10.1111/j.1937-2817.2010.tb01236.x
- Belamaric, P. N., Appel, C. L., and Bean, W. T. (2024). A new search behaviour: porcupines scout for winter habitat during summer. *Anim. Behav.* 212, 137–148. doi: 10.1016/j.anbehav.2024.03.007
- Boone, H. M., Romanski, M., Kellner, K., Kays, R., Potvin, L., Roloff, G., et al. (2025). Recreational trail use alters mammal diel and space use during and after COVID-19 restrictions in a U.S. national park. *Glob. Ecol. Conserv.* 57, e03363. doi: 10.1016/j.gecco.2024.e03363
- Boron, V., Deere, N. J., Xofis, P., Link, A., Quiñones-Guerrero, A., Payan, E., et al. (2019). Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biol. Conserv.* 232, 108–116. doi: 10.1016/j.biocon.2019.01.030
- Broms, K. M., Hooten, M. B., and Fitzpatrick, R. M. (2016). Model selection and assessment for multi-species occupancy models. *Ecology* 97, 1759–1770. doi: 10.1890/154-1471.1
- Burnham, K. P., and Anderson, D. R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach* (New York: Springer-Verlag).
- Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology* 96, 2370–2382. doi: 10.1890/14-1639.1
- Carver, B. D., Kennedy, M. L., Houston, A. E., and Franklin, S. B. (2011). Assessment of temporal partitioning in foraging patterns of syntopic Virginia opossums and raccoons. *J. Mammal.* 92, 134–139. doi: 10.1644/10-MAMM-A-066.1
- Charalambous, C., Musil, P., Legoguelin, M., Musilová, Z., and Hořák, D. (2024). Temporal variation in habitat quality shapes the distribution-abundance relationship in waterbirds at landscape scale. *Ecosphere* 15, e70088. doi: 10.1002/ecs2.70088
- Cheeseman, A. E., Jachowski, D. S., and Kays, R. (2024). From past habitats to present threats: tracing North American weasel distributions through a century of climate and land use change. *Landsc. Ecol.* 39, 104. doi: 10.1007/s10980-024-01902-3
- Chen, C., Brodie, J. F., Kays, R., Davies, T. J., Liu, R., Fisher, J. T., et al. (2022). Global camera trap synthesis highlights the importance of protected areas in maintaining mammal diversity. *Conserv. Lett.* 15, e12865. doi: 10.1111/conl.12865
- Cid, B., Oliveria-Santos, L. G. R., and Mourão, G. (2013). Seasonal habitat use of agoutis (*Dasyprocta azarae*) is driven by the palm *Attalea phalerata* in Brazilian pantanal. *Biotropica* 45, 380–385. doi: 10.1111/btp.12012
- D'Amico, M., Périquet, S., Román, J., and Revilla, E. (2016). Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *J. Appl. Ecol.* 53, 181–190. doi: 10.1111/1365-2664.12572
- DataUSA (2025a). *Berks County, PA* (DataUSA.io). <https://datausa.io/profile/geo/berks-county-pa>. (Accessed July 7, 2025).
- DataUSA (2025b). *Schuylkill County, PA* (DataUSA.io). <https://datausa.io/profile/geo/schuylkill-county-pa>. (Accessed July 7, 2025).
- Dietz, M. S., Belote, R. T., Gage, J., and Hahn, B. A. (2020). An assessment of vulnerable wildlife, their habitats, and protected areas in the contiguous United States. *Biol. Conserv.* 248, 108646. doi: 10.1016/j.biocon.2020.108646
- Dudley, N., and Stolton, S. (2008) *Defining protected areas: an international conference in Almeria, Spain*, Gland, Switzerland: IUCN. 220.

## 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.

## Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1642044/full#supplementary-material>

- Elbroch, M., and Rinehart, K. (2011). *Peterson reference guide to behavior of North American mammals* (New York: Houghton Mifflin Harcourt Publishing Company).
- Ellis, E. C. (2011). Anthropogenic transformation of the terrestrial biosphere. *Phil. Trans. R. Soc. A* 369, 1010–1035. doi: 10.1098/rsta.2010.0331
- Erb, P. L., McShea, W. J., and Guralnick, R. P. (2012). Anthropogenic influences on macro-level mammal occupancy in the Appalachian Trail Corridor. *PLoS One* 7, e42574. doi: 10.1371/journal.pone.0042574
- Evans, B. E., and Mortelliti, A. (2022). Disturbance and occupancy patterns of American ermine (*Mustela richardsonii*) and long-tailed weasel (*Neogale frenata*): results from a large-scale natural experiment in Maine, United States. *Mammalogy* 103, 1338–1349. doi: 10.1093/jmammal/gyac079
- Fahrig, L., and Rytewski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecol. Soc.* 14, 21. Available online at: <https://www.jstor.org/stable/26268057> (Accessed July 1, 2025).
- Gallo, T., Fidino, M., Gerber, B., Ahlers, A. A., Angstrom, J. L., Amaya, M., et al. (2022). Mammals adjust diel activity across gradients of urbanization. *eLife* 11, e74756. doi: 10.7554/eLife.74756
- Gardner, A. L., and Sunquist, M. E. (2003). “Opossum,” in *Wild mammals of North America: biology, management, and conservation*, 2nd ed. Eds. G. A. Feldhamer, B. C. Thompson and J. A. Chapman (Johns Hopkins University Press, Baltimore, MD), 3–29.
- Gaynor, K. M., Hohnowski, C. E., Carter, N. H., and Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* 360, 1231–1235. doi: 10.1126/science.aar7121
- Gaynor, K. M., McInturf, A., and Brashares, J. S. (2021). Contrasting patterns of risk from humans and non-human predators shape temporal activity of prey. *J. Anim. Ecol.* 91, 46–60. doi: 10.1111/1365-2656.13621
- Gehrt, S. D. (2003). “Raccoons and allies,” in *Wild mammals of North America: biology, management, and conservation*, 2nd ed. Eds. G. A. Feldhamer, B. C. Thompson and J. A. Chapman (Johns Hopkins University Press, Baltimore, MD), 611–634.
- Gilhooly, P. S., Nielsen, S. E., Whittington, J., and St. Clair, C. C. (2019). Wildlife mortality on roads and railways following highway mitigation. *Ecosphere* 10, e02597. doi: 10.1002/ecs2.2597
- Gray, T. N. E. (2012). Studying large mammals with imperfect detection: status and habitat preferences of wild cattle and large carnivores in Eastern Cambodia. *Biotropica* 44, 531–536. doi: 10.1111/j.1744-7429.2011.00846.x
- Goldstein, B. R., Keller, A. G., Calhoun, K. L., Barker, K. J., Montealegre-Mora, F., Serota, M. W., Van Scoyoc, A., et al. (2024). How do ecologists estimate occupancy in practice? *Ecography*, e07402. doi: 10.1111/ecog.07402
- Hawk Mountain Sanctuary (2017). *Forest Management Plan* (Kempton, PA, USA: Hawk Mountain Sanctuary Association).
- Hawk Mountain Sanctuary (2025). *Who we are* (Kempton (PA: Hawk Mountain Sanctuary). Available online at: <https://www.hawkmountain.org/about/who-we-are> (Accessed May 9, 2025).
- Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., et al. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144. doi: 10.7939/R3CR5NF2D
- Hendry, H., and Mann, C. (2017). Camelot – intuitive software for camera trap data management. *BioRxiv*. doi: 10.1101/203216
- Hines, J. E. (2006). PRESENCE2 – software to estimate patch occupancy and related parameters. Version 2.13.39 (USGS-PWRC). Available online at: <http://www.mbr-pwrc.usgs.gov/software/presence.html> (Accessed June 6, 2022).
- Howard, J. M., Loos, J. E., and Essner, R. L. (2020). Movement and microhabitat selection in the southern flying squirrel (*Glaucomys volans*) in southwestern Illinois. *Northeast. Nat.* 27, 35–47. doi: 10.1656/045.027.0104
- Hubbard, T., Cove, M. V., and Lafferty, D. J. R. (2022). Human recreation impacts seasonal activity and occupancy of American black bears (*Ursus americanus*) across the anthropogenic-wildland interface. *Sci. Rep.* 12, 12201. doi: 10.1038/s41598-022-15665-x
- Kaufmann, J. H. (1982). “Raccoon and allies,” in *Wild mammals of North America: biology, management, and economics*. Eds. J. A. Chapman and G. A. Feldhamer (Johns Hopkins University Press, Baltimore, MD), 567–585.
- Kautz, T. M., Fowler, N. L., Petroelje, T. R., Duquette, J. F., Beyer, D. E. Jr., and Belant, J. L. (2022). Compensatory human and predator risk trade-offs in neonatal white-tailed deer. *Glob. Ecol. Conserv.* 36, e02089. doi: 10.1016/j.gecco.2022.e02089
- Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., et al. (2017). Does hunting or hiking affect wildlife communities in protected areas? *J. Appl. Ecol.* 54, 242–252. doi: 10.1111/1365-2664.12700
- Kupferman, C. A., Crupi, A. P., Waits, L. P., and Gilbert, S. L. (2021). Spatial and temporal partitioning of mustelids in Southeast Alaska. *Ecosphere* 12, e03827. doi: 10.1002/ecs2.3827
- Larson, C. L., Reed, S. E., Merenlender, A. M., and Crooks, K. R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS One* 11, e0167259. doi: 10.1371/journal.pone.0167259
- Lewis, J. S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A. R., VandeWoude, S., et al. (2021). Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. *Ecosphere* 12, e03487. doi: 10.1002/ecs2.3487
- Lovejoy, T. E. (2016). Conservation biology: the importance of wilderness. *Curr. Biol.* 26, R1235–R1237. doi: 10.1016/j.cub.2016.10.038
- Ma, Y., Wang, X., Liu, B., Zhou, R., Ju, D., Ji, X., et al. (2025). Analysis of the effects of prey, competitors, and human activity on the spatiotemporal distribution of the wolverine (*Gulo gulo*) in a boreal region of Heilongjiang Province, China. *Biology* 14, 1165. doi: 10.3390/biology14091165
- MacKenzie, D. I., and Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *J. Agric. Biol. Environ. Stat.* 9, 300–318. doi: 10.1198/108571104X3361
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255. doi: 10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence* (Massachusetts: Elsevier/Academic Press).
- MacKenzie, D. I., and Royle, A. (2005). Designing occupancy studies: general advice and allocating survey effort. *J. Appl. Ecol.* 42, 1105–1114. doi: 10.1111/j.1365-2664.2005.01098.x
- Marion, S., Curveira Santos, G., Herdman, E., Hubbs, A., Kearney, S. P., and Burton, A. C. (2024). Mammal responses to human recreation depend on landscape context. *PLoS One* 19, e0300870. doi: 10.1371/journal.pone.0300870
- Marion, J. L., Leung, Y., Eagleston, H., and Burroughs, K. (2016). A review and synthesis of recreation ecology research findings on visitor impacts to wilderness and protected natural areas. *J. For.* 114, 352–362. doi: 10.5849/jof.15-498
- Mayer, A. E., Gano, L. S., Brown, C., and Gerber, B. D. (2023). Diel activity structures the occurrence of a mammal community in a human-dominated landscape. *Ecol. Evol.* 13, e10684. doi: 10.1002/ecs3.10684
- McIntyre, T., Majelant, T. L., Slip, D. J., and Harcourt, R. G. (2020). Quantifying imperfect camera-trap detection probabilities: implications for density modeling. *Wildl. Res.* 47, 177–185. doi: 10.1071/WR19040
- Minns, R., Persad, R., Menelon, L., Newar, S. L., O'Brien, P. P., Stead, S. M., et al. (2024). Seasonal nest use of sympatric North American flying squirrels. *Wildl. Res.* 51, WR23041. doi: 10.1071/WR23041
- Mockrin, M. H., Stewart, S. I., Matonis, M. S., Johnson, K. M., Hammer, R. B., and Radeloff, V. C. (2018). Sprawling and diverse: the changing US population and implications for public lands in the 21<sup>st</sup> century. *J. Environ. Manage.* 215, 153–165. doi: 10.1016/j.jenvman.2018.03.053
- Morin, D. J., Yackulic, C. B., Diffendorfer, J. E., Lesmeister, D. B., Nielsen, C. K., Reid, J., et al. (2020). Is your *ad hoc* model selection strategy affecting your multimodel inference? *Ecosphere* 11, e02997. doi: 10.1002/ecs2.2997
- Murphy, A., Diefenbach, D. R., Terment, M., Lovallo, M., and Miller, D. (2021). Threading the needle: how humans influence predator-prey spatiotemporal interactions in a multiple-predator system. *J. Anim. Ecol.* 90, 2377–2390. doi: 10.1111/1365-2656.13548
- Nickel, B. A., Suraci, J. P., Allen, M. L., and Wilms, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biol. Conserv.* 241, 108383. doi: 10.1016/j.biocon.2019.108383
- Pautrel, L., Moulherat, S., Gimenez, O., and Etienne, M. (2023). Analysing biodiversity observation data collected in continuous time: should we use discrete- or continuous-time occupancy models? *Methods Ecol. Evol.* 15, 935–950. doi: 10.1111/2041-210X.14314
- Pegler, G. F., de Lemos, C. C., and Ranieri, V. E. L. (2024). Exploring the application of environmental impact assessment to tourism and recreation in protected areas: a systematic literature review. *Environ. Dev. Sustain* 1–23. doi: 10.1007/s10668-024-04532-6
- QGIS Developmental Team (2024). *QGIS Geographic Information System* (Open Source Geospatial Foundation Project). Available online at: <http://qgis.osgeo.org> (Accessed July 1, 2022).
- Rivera, K., Fidino, M., Farris, Z. J., Magle, S. B., Murphy, A., and Gerber, B. D. (2022). Rethinking habitat occupancy modeling and the role of diel activity in an anthropogenic world. *Am. Nat.* 200, 556–570. doi: 10.1086/720714
- Rocha, D. G., Ramalho, E. E., and Magnusson, W. E. (2016). Baiting for carnivores might negatively affect capture rates of prey species in camera-trap studies. *J. Zool.* 300, 205–212. doi: 10.1111/jzo.12372
- Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., and Musiani, M. (2011). Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecol. Soc.* 16, 16. doi: 10.5751/ES-04251-160316
- Rota, C. T., Fletcher, R. J. Jr., Dorazio, R. M., and Betts, M. G. (2009). Occupancy estimation and the closure assumption. *J. Appl. Ecol.* 46, 1173–1181. doi: 10.1111/j.1365-2664.2009.01734.x
- Rowcliffe, J. M., Carbone, C., Jansen, P. A., Kays, R., and Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods Ecol. Evol.* 2, 464–476. doi: 10.1111/j.2041-210X.2011.00094.x
- Ryser, J. (1995). Activity, movement and home range of Virginia opossums (*Didelphis virginiana*) in Florida. *Bull. Fla. Mus. Nat. Hist.* 38, 177–194. doi: 10.5878/flmnh.zaig8034
- Santon, M., Korner-Niervelt, F., Michiels, N. K., and Anthes, N. (2023). A versatile workflow for linear modeling in R. *Front. Ecol. Evol.* 11. doi: 10.3389/fevo.2023.1065273
- Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., and Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One* 9, e94630. doi: 10.1371/journal.pone.0094630

- Soultan, A., Attum, O., and Lahue, W. (2021). The relationship between landscape features and domestic species on the occupancy of native mammals in urban forests. *Urban Ecosyst.* 24, 1117–1128. doi: 10.1007/s11252-021-01100-y
- Stamper, T. J., Hicke, J. A., Jennings, M., and Aycrigg, J. (2013). Spatial and temporal patterns of changes in protected areas across the Southwestern United States. *Biodivers. Conserv.* 22, 343–356. doi: 10.1007/s10531-012-0403-2
- Stevens, D. L., and Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *J. Am. Stat. Assoc.* 99, 262–278. doi: 10.1198/016214504000000250
- Sunarto, S., Sollmann, R., Mohamed, A., and Kelly, M. J. (2013). Camera trapping for the study and conservation of tropical carnivores. *Raffles. Bull. Zool.* 28, 21–42. Available online at: <http://zoobank.org/urn:lsid:zoobank.org:pub:804A6DC9-A92A-41AE-A820-F3DA48614761> (Accessed July 1, 2025).
- Suraci, J. P., Clinchy, M., Zanette, L. Y., and Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.* 22, 1578–1586. doi: 10.1111/ele.13344
- Symonds, M. R. E., and Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioral ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21. doi: 10.1007/s00265-010-1037-6
- Tobler, M. W., Hartley, A. Z., Carrillo-Percestequi, S. E., and Powell, G. V. N. (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *J. Appl. Ecol.* 52, 413–421. doi: 10.1111/1365-2664.12399
- Valente, J. J., Hutchinson, R. A., and Betts, M. G. (2017). Distinguishing distribution dynamics from temporary emigration using dynamic occupancy models. *Methods Ecol. Evol.* 8, 1707–1716. doi: 10.1111/2041-210X.12840
- Valente, J. J., Jirinec, V., and Leu, M. (2024). Thinking beyond the closure assumption: designing surveys for estimating biological truth with occupancy models. *Methods Ecol. Evol.* 15, 2289–2300. doi: 10.1111/2041-210X.14439
- Van Deursen, J., Creany, N., Smith, B., Freimund, W., Avgar, T., and Monz, C. A. (2024). Recreation specialization: Resource selection functions as a predictive tool for protected area recreation management. *Appl. Geogr.* 167, 103267. doi: 10.1016/j.apgeog.2024.103276
- Visual Crossing Corporation (2024). *Visual Crossing Weather*, (2022). Available online at: <https://www.visualcrossing.com/> (Accessed July 1, 2022).
- Westekemper, K., Reinecke, H., Signer, J., Meißner, M., Herzog, S., and Balkenhol, N. (2018). Stay on trails – effects of human recreation on the spatiotemporal behavior of red deer *Cervus elaphus* in a German national park. *Wildl. Biol.* 2018, wlb.00403. doi: 10.2981/wlb.00403
- Wilkinson, Z. A., Kramer, H. A., Jones, G. M., Zulla, C. J., McGinn, K., Barry, J. M., et al. (2023). Tall, heterogenous forests improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California. *Ornithol. Appl.* 125, duac048. doi: 10.1093/ornithapp/duac048
- Wolfram Research, Inc (2022). *Mathematica, Version 13.1* (Champaign, IL, USA: Wolfram Research, Inc.).