



Fine-tuning coexistence: Wildlife's short-term responses to dynamic human disturbance patterns

Davide Mirante^{a,*}, Leonardo Ancillotto^{b,c}, Andrea Zampetti^a, Giuseppe Coiro^a, Gianfranco Pisa^d, Cristina Santocchi^d, Matteo Giuliani^a, Luca Santini^a

^a Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Rome, Italy

^b Institute of Terrestrial Ecosystem Research (IRET), National Research Council (CNR), via Madonna del Piano 10, Sesto Fiorentino 50019, Italy

^c National Biodiversity Future Center, Piazza Marina 61, Palermo 90133, Italy

^d Environmental Management and Education (GEA), via delle Bandite 33, Soriano nel Cimino 01038, Italy

ARTICLE INFO

Keywords:

Nature tourism
Ecotourism
Wildlife response
Human disturbance
Camera-trapping

ABSTRACT

Anthropogenic disturbance elicits adaptive responses in wildlife, generally aimed at risk-avoidance, ultimately imposing constraints on their spatial and temporal niches. Previous studies have largely focused on long-term adaptive responses to stable human pressure, but rapid adjustments in wildlife's diel and habitat use patterns in response to fine-scale variations in human presence have so far been overlooked. In this study we estimate short-term spatio-temporal deviations in local habitat use and diel activity of medium and large mammal species in response to rapid variations in human disturbance. We employed a year-long camera-trapping within a small private reserve, and recorded spatio-temporal information on all sources of anthropogenic disturbance in the area. By controlling for the average habitat use and diel activity, we explored fine-scale spatiotemporal adjustments in seven mammal species. We found evidence of spatial and/or temporal avoidance across all species, except wild boar, with variations in magnitude and direction coherent with species traits and expected levels of human-tolerance. Most species exhibited temporal avoidance of human activities, with porcupine and roe deer eliciting particularly strong responses. Notably, foxes concurrently displayed temporal avoidance and spatial attraction, likely driven by the presence of anthropogenic trophic resources. Our study underscores the role of behavioral plasticity in enabling wildlife to adjust daily habitat use and activity patterns to varying levels of human pressure across space and time. Understanding these nuanced behavioral strategies can help to promote wildlife-human coexistence and mitigating the adverse impacts of human presence on wildlife fitness.

1. Introduction

Wildlife's habitat use and diel activity patterns result from complex interactions between intrinsic (e.g., life-history, feeding necessities, resting) and extrinsic drivers (e.g., environmental constraints, temperature, inter- and intra-specific interactions), and play a crucial role in determining individuals' fitness (Halle and Stenseth, 2012). Today humans constitute a prevalent extrinsic factor (Frid and Dill, 2002; Geffroy et al., 2015), inducing strong adaptive responses in wildlife aimed at risk-avoidance, and ultimately influencing

* Correspondence to: Via Anastasio de Filis 24, Terni, TR 05100, Italy.

E-mail address: davide.mirante@uniroma1.it (D. Mirante).

<https://doi.org/10.1016/j.gecco.2024.e03053>

Received 15 March 2024; Received in revised form 20 May 2024; Accepted 19 June 2024

Available online 20 June 2024

2351-9894/© 2024 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

animal physiology and behavior both at the species and community level (Gaynor et al., 2018; Salvatori et al., 2023; Zanette et al., 2023). However, anthropogenic influence may prove beneficial for generalist species capable of exploiting human-associated food resources (Fedriani et al., 2001). Furthermore, prey species may experience reduced predation pressure in areas impacted by human activities due to the absence or reduced density of predators (i.e., human shield effect; Berger, 2007).

With the increase in human encroachment and the growing societal interest in nature-based tourism and outdoor recreational activities (Balmford et al., 2009), understanding the complex dynamics underlying the coexistence between humans and wildlife becomes essential. Many studies have investigated wildlife responses to human presence through spatio-temporal comparisons of habitat use and activity patterns across gradients of human disturbance. Human presence has been found to be a key factor in shaping habitat use and activity patterns in mammals, effectively reducing the spatial and temporal niche, consistently across taxa and guilds e. g., carnivores (Ladle et al., 2018; Corradini et al., 2021; Sévêque et al., 2022), herbivores (Richard and Côté 2016; Plante et al., 2018) and omnivores (Oberosler et al., 2017; Li et al., 2022). Constraints in habitat use and activity patterns can exert direct impacts on wildlife fitness not only by directly influencing access to trophic resources, shelter, and favorable habitats, but also by indirectly hindering niche partitioning, thereby increasing competition among coexisting species. Species' ecological and life-history traits play a crucial role in shaping wildlife tolerance to human activities as well as direction and intensity of their responses (Suraci et al., 2021). To date, studies on spatiotemporal responses of wildlife to human disturbance have predominantly focused on long-term shifts in habitat use and activity patterns attributed to stable differences in human pressure across areas or time spans. However, while human impacts tend to concentrate in specific areas and times, it can be highly dynamic and unpredictable, forcing animals to adjust the use of their spatio-temporal niche over short time frames. Such fine-tuning of individual activity remains mostly unexplored. Furthermore, studies exploring the impact of outdoor recreation on wildlife generally lack a proper quantification of human disturbance, often employing arbitrary categorical levels of disturbance (Marion et al., 2020; Sarmiento et al., 2017; Lesmerises et al., 2018). Similarly, the spatial distribution of recreational activities is rarely recorded (Olson et al., 2018). These studies provide key insights into general trends, yet detailed quantification and mapping of human activities are necessary to provide meaningful results from a managerial perspective (Larson et al., 2016). This approach is therefore critical for developing sustainable tourism practices that preserve their multiple benefits for human's health and local economies (Frumkin et al., 2017; Wolsko et al., 2019), while simultaneously protecting ecosystem processes and wildlife fitness.

Here we investigate fine-scale spatio-temporal adjustments of wildlife in response to human activities in a small private reserve

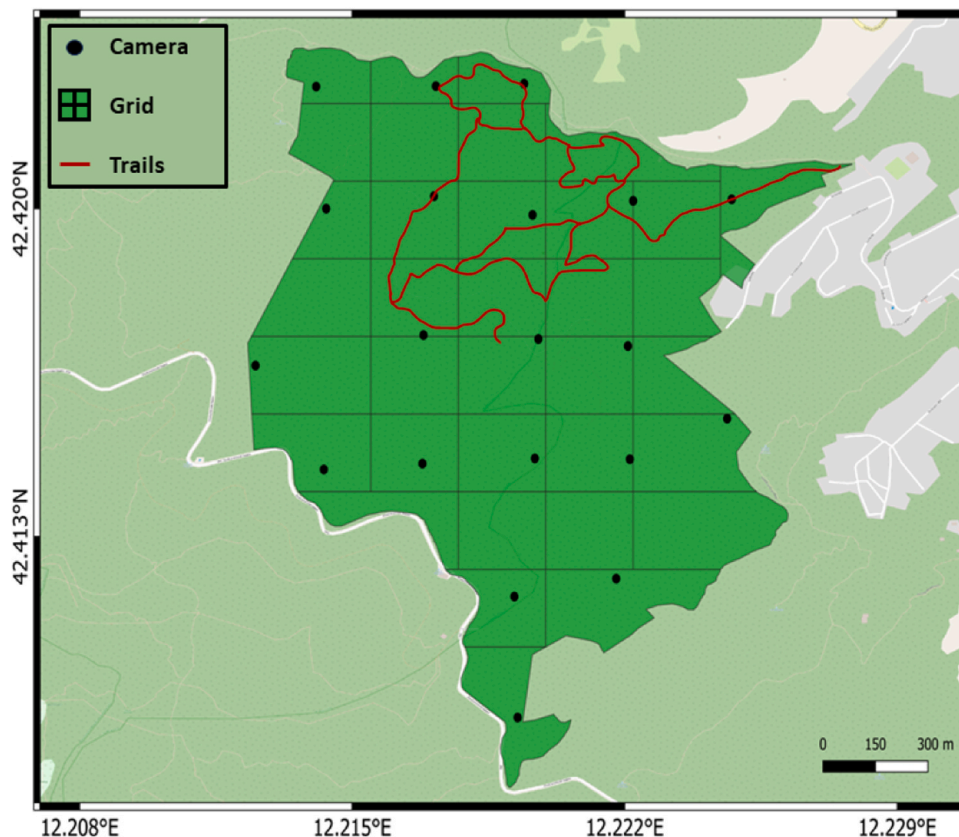


Fig. 1. Distribution of the camera traps in the private reserve “Tenuta Sant’Egidio” in Viterbo, central Italy. The 20 camera trap locations are represented by black dots, while the main hiking trails are indicated by the red lines. The overlaid grid (35 quadrants) refers to the grid used to geolocalize human activities during the study period.

dedicated to ecotourism. We conducted an intensive camera-trapping study throughout an entire year and recorded detailed spatial and temporal information on all sources of anthropogenic disturbance in the area to investigate short-term adaptive shifts in temporal and spatial patterns of the local mammalian community in response to quickly fluctuating anthropogenic pressures. Since this area receives visitors and organizes activities year-round, temporal and spatial patterns of local wildlife are likely to be adapted to human activities. Here, we focus on divergences from the stable spatial and temporal patterns observed in the area in response to spatio-temporal changes in human activities, hence focusing on rapid adjustments aimed at human avoidance. We expect most species to show evidence of human-avoidance either on the spatial or temporal axis, or both simultaneously, to minimize contact with human-related activities. We expect the magnitude of the response on either axes to be coherent with the species' ability to exploit anthropogenic resources, and coherent with the known ecology of the species. For example, we expect elusive species such as roe deer (*Capreolus capreolus*) and badgers (*Meles meles*) to exhibit comparatively stronger responses than other species (Bonnot et al., 2013; Oberosler et al., 2017), and generalist species able to thrive in human-modified environments such as foxes (*Vulpes vulpes*) and wild boars (*Sus scrofa*) (Santini et al., 2019) displaying weaker or no response on the temporal axis due to their high tolerance towards human presence, and possibly some degree of spatial attraction due to the exploitation of anthropogenic trophic resources (e.g., leftovers, wastes, pet food, etc.).

2. Materials and methods

2.1. Study area

We conducted our camera-trap survey within the boundaries of Tenuta Sant'Egidio, a private reserve of 130 ha located on Mount Cimino (1053 m a.s.l.) in Viterbo, central Italy (42°25'10.0" N, 12°12'36.0" E, Fig. 1). The western half of the reserve surface area falls within the Site of Community Importance 'Monte Cimino versante Nord' (IT6010022). The eastern border of the reserve, conversely, faces the peri-urban development of the nearby country town (Soriano nel Cimino). The study area ranges between 470 and 750 m of altitude and is characterized by a homogeneous deciduous woodland habitat dominated by chestnut (*Castanea sativa*), with sporadic beech (*Fagus sylvatica*) formations occurring in the upper altitudinal limit. The reserve area is characterized by the presence of caves and rocky outcrops but does not harbor any known stable body of water. The area hosts common species of the Italian mammal community such as wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), european badger (*Meles meles*), crested porcupine (*Hystrix cristata*), red fox (*Vulpes vulpes*) and beech marten (*Martes foina*), as well as species of high conservation interest, such as apennine wolf (*Canis lupus italicus*), pine marten (*Martes martes*) and european wildcat (*Felis silvestris*). These species are characterized by different behaviors and habitat preferences, including species with nocturnal (e.g., badger, porcupine), crepuscular (i.e., wild boar, fox, apennine wolf) and cathemeral (i.e., roe deer) behaviors, belonging to diverse dietary guilds such as omnivore (e.g., wild boar), herbivore (e.g., porcupine, roe deer), and displaying varying degree of adaptability to human disturbance and habitat specialization (e.g., wild boar vs pine marten). The reserve provides naturalistic education tours for school classes, and several activities for tourists such as hiking or short courses, and more occasionally hosts survival camps. The northeastern part of the area is characterized by multiple hiking trails, and most of the touristic and educational activities are held there, hence it experiences a consistent influx of tourists throughout the year. The remaining part of the area instead, while not formally restricted, is accessible to tourists only sporadically and for specific activities (such as survival courses or campsites for school classes). Notably, the area is partly fenced, and all activities within the reserve borders are guided and overseen by the reserve staff.

2.2. Data collection

Our survey began the second week of June 2022 and continued for one year, ending the first week of July 2023. We installed twenty camera-traps Browning Patriot at the vertices of a rectangular, random-origin systematic grid with a resolution of 250 × 300 m (Fig. S1). All cameras were positioned in close proximity to the designated location, typically between 1 and 10 m except for two cameras for which the sampled point was inaccessible. In these cases, cameras were placed at the closest available point within the borders of their grid quadrant (approximately 100–130 m afar from the original spot, Fig. 1). Cameras have been installed on the nearest tree available in the designated location, at a height of 60–80 centimeters, facing North to avoid over-exposure in pictures, with the field of view starting approximately at 150 centimeters from the camera. We recorded the coordinates of each camera with a GPS unit (Garmin Etrex 32x).

Camera-traps were configured with a trigger delay of 0.15 seconds, capturing a "burst" of three pictures for each trigger, and with 1 second of delay between successive triggers. We conducted maintenance to replace batteries and memory cards of each camera trap approximately every 30 days. We did not use any bait to attract wildlife.

For each location we collected trees' diameters at breast height (DBH) and shrub coverage by traversing two linear transects, arranged in a cross centered on the camera trap location, measuring 10 m of length and 3 m of width. DBH has been measured for all trees inside the transect at 1.40 m of height. Shrubs length has been measured parallel to the direction of the transect, and shrub coverage has been calculated as the percentage of the total length of the transect covered by shrubs. Daily temperature and precipitation data were collected from the "Stazione di Soriano nel Cimino" weather station, located approximately 500 m from the study area (42°25'16.0" N, 12°13'54.0" E°).

Throughout the year, the reserve staff documented each human activity in the study area, including the activity of camera-trapping operators, on a previously agreed-upon sheet, reporting the following details: start time, end time, location, number of participants, type of activity (e.g., hiking, education, maintenance, etc.), and additional notes when deemed necessary. To geolocalise human

activities, we partitioned the study area into 35 quadrants by over-imposing a second independent regular grid with a resolution of 180 m (Fig. 1). This resolution was chosen in agreement with the staff to achieve the highest possible spatial resolution while still allowing the staff to record the information with ease in the sheet. For the same purpose, in collaboration with the staff, the grid was further adjusted to align the quadrants with meaningful borders, roads and other recognizable landscape features (Fig. 1).

2.3. Data processing

The pictures collected were manually annotated at the species level and compiled into a dataset using the R package *camtrapR* (Niedballa et al., 2016), while human disturbance information was manually digitized by the authors. For our analyses, we produced a separated dataset for each species. For every hour and each camera of each week, the dataset included the following information: detection/non-detection of the target species, hour, camera coordinates and ID. Subsequently, we calculated the number of people at each camera trapping site as the mean within a 100 m buffer around the camera trap. The buffer sizes were defined to cover most of the study area while avoiding overlap within the buffers of different camera sites. However, to test the sensitivity of our results to this parameter, we repeated the analysis using half (50 m) and twice (200 m) the buffer size. To reduce zero detections to improve model convergence, we aggregated both human disturbance and wildlife occurrence data at a weekly time resolution. This aggregation probably reduces the variance captured by the model, however this simplification is justified by the much higher variance observed across weeks of the years than within weeks (see Table S2 and Fig. S2).

To discriminate between spatial and temporal adjustments, we generated two variables of disturbance, one reflecting the temporal distribution of human disturbance over the 24 h, and one reflecting the spatial distribution of human disturbance within the reserve. Aggregating human presence data over the 24 h (hereby named NPerSite) quantifies the average number of individuals visiting each specific site throughout the week (Fig. 2a). A negative or positive response to this variable suggests, respectively, a spatial avoidance or attraction to human impact. In contrast, aggregating human presence data across all sites per hour provides a measure of human pressure over time (hereby named NPerTime), which quantifies the average number of individuals visiting the area during specific hours of the day, throughout a week (Fig. 2b). A positive or negative response to this variable suggests temporal avoidance or attraction to humans. We subsetted all species dataset to only consider the observations in the portion of the day when touristic activities are held in the study area (between 6 a.m. and 10 p.m.). NPerSite, NPerTime, hour of detection and week were \log_{10} -transformed to meet normality, and all variables along with camera coordinates were standardized ($\mu=0$, $sd=1$) to constrain the two covariates in similar ranges and hence improve model convergence and facilitate the comparison of model's coefficients.

2.4. Model fitting

To assess the potential influence of human presence on wildlife use of space and time, we employed a mixed-effect Generalized Additive Model (GAMM) with a Binomial family distribution using Bayesian inference. We modeled species detection/non-detection as a function of time (hour of the day), longitude and latitude coordinates of the camera traps, week, site covariates (trees diameter at

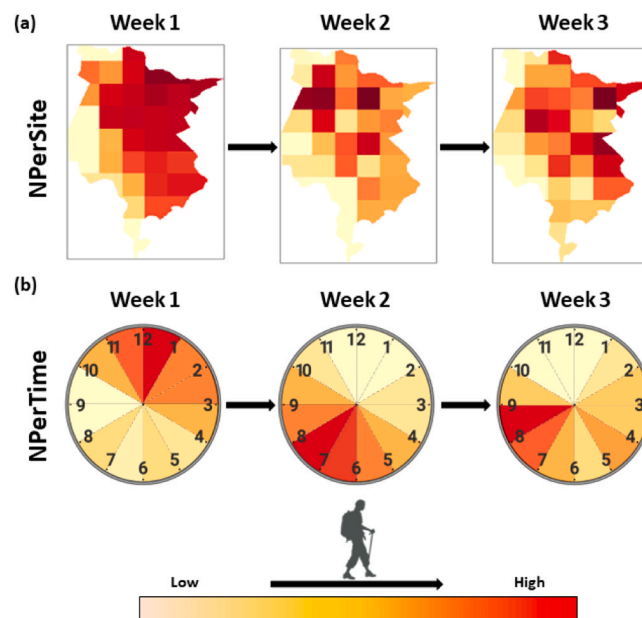


Fig. 2. Illustrative image of the two measures of spatial and temporal human disturbance employed in our analysis. NPerSite (a), above, quantifies the average number of individuals visiting each specific site throughout the week, across all hours of the day. NPerTime (b), below, quantifies the average number of individuals visiting the entire area during specific hours of the day throughout the week.

breast height and shrub coverage), precipitations, temperature, NPerTime and NperSite as follows:

$$\text{Detections} \sim \text{NPerSite} + \text{NPerTime} + \text{Dbh} + \text{Rain} + \text{Temperature} + \text{Shrub_cover} + \text{s(x,y)} + \text{s(Hour)} + \text{s(Week)} + (1|\text{Camera})$$

Week, time, spatial coordinates were modeled with thin-plate spline smooths, while environmental covariates were modeled as linear effects, and are meant to control for the typical distribution of activity over time and space. NPerTime and NPerSite are meant to capture the residual variation that remains unexplained by environmental covariates, time and spatial coordinates and that suggest spatio-temporal human attraction or avoidance.

Due to the prevalence of 0 s (non-detections) in the model, we weighted detections and non-detections by the inverse of their frequency in the sample, so that despite the sample imbalance they weighted equally in the model. Further, we included random effects for camera ID to address the non-independence of multiple observations obtained from the same camera. We fitted one model per species.

To prevent overfitting and facilitate the convergence of our models, we applied weakly informative prior distributions. Specifically, we utilized a normal distribution $N(0, 0.5^2)$ for NPerTime and NPerSite slope coefficients, to constrain the estimation of large effect sizes for our predictors, unless substantiated by a robust signal in our data (Lemoine, 2019). For each model we ran 5 MCMC chains with 5000 iterations each, using the first 2000 iterations as warmups, resulting in 15.000 effective posteriors per model. Chain convergence was explored through traceplots and with the R-hat diagnostic. Following Dormann et al. (2013), we established a collinearity threshold $r > |0.7|$ for our variables. No correlation exceeded this threshold, so all predictor variables were retained (Fig. S3).

We summarized the posterior distribution of our coefficients by reporting the mean along with 95 % credible intervals. Further, for each coefficient we report the probability of direction (PD), an index of confidence in the effect that strongly correlates to the frequentist p-value (Makowski et al., 2019). The PD varies between 50 % and 100 % and describes the probability of the parameter being different from zero. We report our results by expressing the coefficient (β), the PD, and as the percentage change in species detection odds ratio (% change = $(1 - \exp(\beta)) * 100$). From the posterior distribution we also predicted species' utilization of space and time conditional on absence of human disturbance, to visualize species baseline spatial and temporal patterns in the study area.

We conducted all analyses in R v. 4.3.0 (R Core Team 2020). We fitted all models using the package *brms* v.2.20.4 (Bürkner, 2021), and used *tidybayes* 3.0.6 (Wickham, 2014) and *ggplot2* v. 3.4.2 (Wickham et al., 2016) for data visualization.

3. Results

Detection events were recorded for the following species: wild boar (*S. scrofa*), roe deer (*C. capreolus*), European badger (*M. meles*), crested porcupine (*H. cristata*), red fox (*V. vulpes*), beech marten (*M. foina*), pine marten (*M. martes*), Apennine wolf (*C. lupus italicus*) and European wild cat (*F. silvestris*). However, Apennine wolves and European wildcats were rarely detected ($n=36$ and $n=2$, respectively), and unambiguous classification of wildcat from feral cats was not possible. Consequently, we excluded these two species from our analyses due to the limited sample size. Furthermore, since the beech and the pine marten are hardly distinguishable from camera-trap pictures, we grouped them at the genus level (*Martes* spp.). Full details of the sample size for species included in our analyses can be found in Supplementary Materials (Table S1).

The R-hat values of all parameters in our models were ≤ 1.01 , indicating good model convergence (Table S3). Visual inspection of traceplots further supported the achievement of convergence of all MCMC chains (Fig. S4-S9).

Most species consistently displayed lower probabilities of occurrence in the north-eastern section of the area, which is most frequently used for touristic and educational activities. In contrast, *Martes* spp. showed a uniform usage of the area (Fig. S10). Baseline

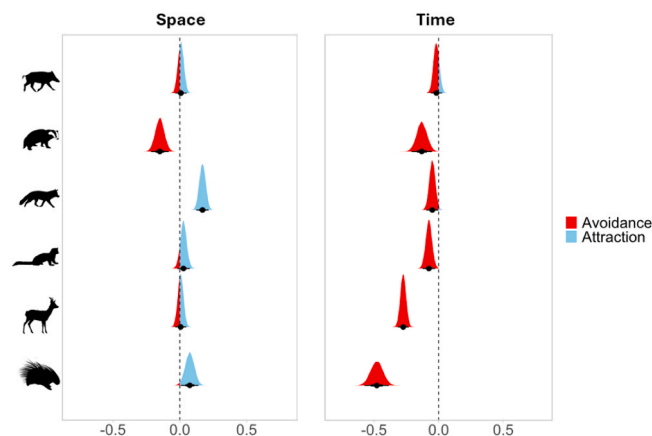


Fig. 3. Posterior distributions of the estimated slope coefficient, in logit, for NPerSite (left) and NPerTime (right) for all the modeled species. Negative estimates indicate spatial or temporal avoidance, positive estimates suggest spatial or temporal attraction. Error bars represent 95 % confidence intervals of the estimate. Silhouettes downloaded from phylopic (www.phylopic.org).

temporal patterns of species occurrence probability indicated higher activity in crepuscular hours for all species. Badgers and porcupines exhibited a particularly steep decline in the probability of occurrence during the central hours of the day, while roe deer displayed several peaks of activity throughout the day (Fig. S11).

We found NPerSite (spatial disturbance) to have a negative association to the probability of occurrence in badgers, with a 13.9 % reduction in the odds of detection for every unit increase of the predictor (mean estimate (β) = -0.15 , CI95 = $-0.21 - -0.08$, PD = 100 %, Table S3, Fig. 3). Conversely, fox occurrence was positively related to NPerSite, showing a 18.5 % higher relative probability of detection per unit increase in the predictor (β = 0.17 , CI95 = $0.12 - 0.22$, PD = 100 %, Table S3, Fig. 3). Porcupine occurrence also exhibit a weakly positive relationship with NPerSite with a 7.25 % higher odds of detection per predictor increase (β = 0.07 , CI95 = $0.01 - 0.14$, PD = 98.66 %, Table S3, Fig. 3). We found no clear effect of NPerSite and probability of occurrence in roe deer (β = 0.01 , CI95 = $-0.03 - 0.05$, PD = 62.12 %, Table S3, Fig. 3), wild boars (β = 0.01 , CI95 = $-0.03 - 0.05$, PD = 65.10 %, Table S3, Fig. 3) or *Martes spp.* (β = 0.03 , CI95 = $-0.02 - 0.08$, PD = 87.83 %, Table S3, Fig. 3).

We found evidence of strong temporal avoidance for porcupines (β = -0.48 , CI95 = $-0.57 - -0.39$, PD = 100 %, Table S3, Fig. 3) and roe deer (β = -0.27 , CI95 = $-0.32 - -0.23$, PD = 100 %, Table S3, Fig. 3), showing respectively a 38.12 % and 23.66 % decrease in their odds of occurrence for each increase in NperTime (temporal disturbance). Concerning mesocarnivores, we found a clear negative association between NperTime and probability of occurrence for badgers (β = -0.15 , CI95 = $-0.21 - -0.08$, PD = 100 %, Table S3, Fig. 3), fox (β = -0.05 , CI95 = $-0.10 - -0.00$, PD = 98.24 %, Table S3, Fig. 3) and *Martes spp.* (β = -0.08 , CI95 = $-0.12 - -0.03$, PD = 99.93 %, Table S3, Fig. 3). Finally, we found no evidence of an association between NperTime and relative probability of occurrence for wild boars (β = -0.02 , CI95 = $-0.06 - 0.03$), PD = 76.79 %, Table S3, Fig. 3).

Our sensitivity test to the buffer size showed only minor fluctuations in the magnitude of the effect sizes for all species except for the porcupine, and confidence intervals (CI95) of the coefficients obtained from the sensitivity analysis overlap with those of the original analysis (Fig. S12). Porcupines showed no substantial variations in their spatial response with a buffer size of 50 m, but stronger spatial attraction with a buffer size of 200 m (β = 0.27 , CI95 = $0.20 - 0.34$, PD = 100 %, Fig. S12).

Finally, wild boar, fox, porcupine and *Martes spp.* detections displayed a similar positive relationship with precipitations, while roe deer and badger showed a negative association (Table S3). Concurrently, wild boar, roe deer, badger and porcupine detection probability was negatively influenced by increases in temperature, while the fox was positively influenced. Instead, temperature showed no effect on *Martes spp.* detection probability (Table S3). None of the species exhibited any relationship with trees' diameter at breast height and shrub coverage (Table S3).

4. Discussion

Our study provides a robust framework to investigate short-term responses to varying anthropogenic disturbance in wildlife, and highlights the diverse adaptive strategies of different species to coexist with humans in our study area. The baseline temporal and spatial patterns of all species reveal a tendency toward a well-established long-term spatial and/or temporal avoidance, with the north-eastern section of the study area, frequently experiencing touristic activities, and central hours of the day, in which human activity is more pervasive and intense, being overall avoided by local species even in absence of human disturbance.

We found all local species, with the exception of wild boar, to exhibit additional short-term human-avoidant behaviors on the temporal or the spatial axis at increasing human presence, with herbivorous species (roe deers and porcupines) evoking comparatively stronger responses than mesocarnivores (martens, badgers and foxes) on the temporal axis. Badger was the only species exhibiting evidence of short-term spatial avoidance of human activities. Notably two species (foxes and wild boars) exhibited diverse patterns indicative of human-tolerance: wild boar displaying no human-avoidant response on either axis, and fox concurrently exhibiting both spatial attraction and temporal avoidance towards human activities.

Temporal avoidance emerged as the prevailing fine-tuning strategy within the local mammalian community, with the majority of species exhibiting some degree of temporal avoidance of human activities, coherently with long-term and large scale trends previously reported in the literature (Patten and Burger, 2018; 2024). This outcome could be attributed to the overall scarce predation, poaching, or hunting pressure within the borders of our study area, which makes temporal avoidance to yield far greater benefits than spatial avoidance, as it minimizes the chance of encounters with humans without limiting access to favorable habitats, and without a substantial increase in predation risk. The strong temporal avoidance shown by local herbivores is coherent with previously reported long-term shifts and aligns with our expectations. An increase in nocturnal activity due to lethal (i.e., hunting or poaching) and non-lethal human activities has been previously reported for both roe deer (Bonnot et al., 2013, 2020) and porcupine (Lovari et al., 2017). Nevertheless, both species did not exhibit spatial avoidance toward human activities, contrarily to long-term responses previously reported in literature (Bonnot et al., 2013; Lovari et al., 2017; Mori, 2017). However, as mentioned, human presence is not associated with concrete risks in our study area (e.g. hunting or persecution), hence these species may not perceive the need to avoid areas engaged in human activities once those have ceased. The very weak but unexpected spatial attraction toward human activities observed for porcupine is a phenomenon whose underlying causes are not clear. This phenomenon could be driven by trophic sources beyond the study area boundaries, as private vegetable gardens, or sporadic opportunistic feeding on trophic sources situated at the entrance of the study area, such as tourists' leftovers. These sources could drive increases in porcupine activity in the northwestern part of the area, during hours unaffected by human activity. Martens exhibited temporal avoidance of human activities, but no spatial responses. While pine and beech marten are indeed sympatric in the study area and are commonly aggregated at the genus level in camera-trap studies due to the inherent difficulty in distinguishing the two species in photos, the two species display different levels of tolerance towards human activities, with beech marten being more tolerant to cultivated and urbanized areas compared to pine marten (Fonda et al., 2021). The differential susceptibility to human disturbance of the two species makes inferences on the effects quantified

by our models challenging, as we are likely measuring an “averaged” effect of two distinct and possibly divergent responses. However, given that partial segregations on temporal and spatial niches are essential for the two marten species to live in sympatry and limit interspecific competition, evidences of overall constraints imposed by human presence on either axis, as in this study, could suggest an induced increase in competition and may deserve further exploration.

Fox also exhibited a similar magnitude of temporal avoidance of human activities but, notably, they simultaneously exhibited strong spatial association with human activities. This pattern aligns with the anticipated tolerance of fox towards human presence and supports the hypothesis that fox may actively avoid direct human contact but exploit human-derived trophic resources once the disturbance ceases. For foxes this pattern is expected and is likely to be driven by trophic sources within the study area, as raids on wastes and pet food by foxes and wild boar has been sporadically reported from the reserve staff.

Notably, badger was the only species showing evidence of both temporal and spatial avoidance in response to human activities. Human presence has been previously shown to sensibly reduce badgers’ activity levels (Lovell et al., 2022) to the extent that human voices alone have been shown to be sufficient for badger to exert strong anti-predatory behaviors (Clinchy et al., 2016). The higher degree of “shyness” of badger in response to human disturbance compared to other generalist species (Oberosler et al., 2017) could justify the pronounced avoidance exhibited on both axes.

Finally, wild boar showed no evidence of temporal or spatial avoidance toward human presence, confirming a remarkable tolerance towards humans by this species. Wild boar, given sufficient vegetational cover, has been shown to well tolerate not only non-lethal human disturbance (Fradin and Chamailé-Jammes, 2023), but even tolerate to some degree hunting activities (Keuling et al., 2008). Since our study area is forested and no hunting activity takes place within its boundaries, the reported pattern aligns with our expectation.

5. Conclusions

Our study provides insights on species’ behavioral plasticity in fine-tuning their spatial and temporal niche in response to weekly changes in human disturbance. Our results highlight different adaptive strategies by local species to ensure their coexistence with humans. Temporal avoidance emerged as the predominant short-term strategy, adopted by most species to minimize the chance of interactions with humans, with herbivores exhibiting notably stronger responses compared to mesocarnivores and omnivores on the temporal axis. Wild boars and foxes displayed distinctive patterns reflecting their degree of human tolerance. Wild boars displayed no response towards human activities, whereas foxes exhibited temporal avoidance of humans while simultaneously showing preferential use of areas frequented by them, presumably to exploit anthropogenic trophic resources. Taken together, these findings suggest that recreational activities do not further limit local wild species’ ability to reach resources in the short-term, but can impose constraints on their activity budget, which is continuously fine-tuned over time. This not only may reduce animals’ flexibility to adapt to environmental changes, but may impose a sustained stress on individuals, which may lead to a wide array of noxious effects, such as higher vigilance time, reduced foraging time, and heightened physiological responses (Ancillotto et al., 2019; Wilson et al., 2020; Pérez-Ortega and Hendry 2023).

Although our study has been conducted within a confined reserve area with a relatively low degree of anthropogenic disturbance, hence clearly limiting the generalizability of the local wildlife responses reported, it offers valuable guidance for future research by presenting an analytic framework to explore this kind of short-term plasticity in wildlife, and encourages subsequent studies to use precise quantification and geo-localization of human disturbance in studies trying to assess the impact of human activities on wildlife. Moreover, our study further underscores that even seemingly innocuous human presence alone has the potential to cause detectable shifts in wildlife’s spatial and temporal patterns, placing constraints on their ecological niches and potentially exerting detrimental effects. We thus emphasize the importance of understanding nuanced short-term avoidance strategies, as they could advance our understanding of behavioral adaptations that permit human-wildlife coexistence and clarify the still fundamentally unclear impact of human presence on wildlife (Larson et al., 2016; Bateman and Fleming, 2017).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgments

D. M. acknowledges the Italian Ministry of Education, University and Research, Programma Operativo Nazionale (CUP B85F21005360001) for funding their research activities. LA and LS were funded by the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU; Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B83C22002930006, Project title “National Biodiversity Future Center - NBFC”. All the authors would like to thank the GEA association and its president,

Azzurra Benedetti Gaglio, for supporting the research activity. We also would like to thank the Staff of Tenuta Sant'Egidio for their precious field support and collaboration for data collection.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03053](https://doi.org/10.1016/j.gecco.2024.e03053).

References

- Ancillotto, L., Venturi, G., Russo, D., 2019. Presence of humans and domestic cats affects bat behaviour in an urban nursery of greater horseshoe bats (*Rhinolophus ferrumequinum*). *Behav. Process.* 164, 4–9.
- Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M., Manica, A., 2009. A global perspective on trends in nature-based tourism. *PLoS Biol.* 7 (6), e1000144.
- Bateman, P.W., Fleming, P.A., 2017. Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biol. Conserv.* 211, 10–19.
- Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* 3 (6), 620–623.
- Bonnot, N.C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J.E., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., et al., 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. *J. Anim. Ecol.* 89 (1), 132–145.
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., Hewison, A.J.M., 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *Eur. J. Wildl. Res.* 59 (2), 185–193.
- Bürkner, P.-C., 2021. Bayesian Item Response Modeling in R with brms and Stan. *J. Stat. Softw.* 100 (5), 1–54.
- Burton, A.C., Beirne, C., Gaynor, K.M., Kays, R., 2024. Mammal responses to global changes in human activity vary by trophic group and landscape. *Nat. Ecol. Evol.*
- Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., Macdonald, D.W., 2016. Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. *Behav. Ecol.* 27 (6), 1826–1832.
- Corradini, A., Randles, M., Pedrotti, L., Van Loon, E., Passoni, G., Oberosler, V., Rovero, F., Tattoni, C., Ciolli, M., Cagnacci, F., 2021. Effects of cumulated outdoor activity on wildlife habitat use. *Biol. Conserv.* 253, 108818.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24 (3), 325–331.
- Fonda, F., Chiatante, G., Meriggi, A., Mustoni, A., Armanini, M., Mosini, A., Spada, A., Lombardini, M., Righetti, D., Granata, M., et al., 2021. Spatial distribution of the pine marten (*Martes martes*) and stone marten (*Martes foina*) in the Italian Alps. *Mamm. Biol.* 101 (3), 345–356.
- Fradin, G., Chamailé-Jammes, S., 2023. Hogs sleep like logs: Wild boars reduce the risk of anthropic disturbance by adjusting where they rest. *Ecol. Evol.* 13 (7), e10336.
- Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6 (1), 11.
- Frumkin, H., Bratman, G.N., Breslow, S.J., Cochran, B., Kahn Jr, P.H., Lawler, J.J., Levin, P.S., Tandon, P.S., Varanasi, U., Wolf, K.L., Wood, S.A., 2017. Nature contact and human health: a research agenda. *Environ. Health Perspect.* 125 (7), 075001.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360 (6394), 1232–1235.
- Geffroy, B., Samia DSM, Bessa, E., Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* 30 (12), 755–765.
- Halle, S., Stenseth, N.C., 2012. Activity Patterns in Small Mammals: An Ecological Approach. *Ecological Studies*. Springer, Berlin and New York.
- Keuling, O., Stier, N., Roth, M., 2008. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *Eur. J. Wildl. Res.* 54 (4), 729–737.
- Ladle, A., Steenweg, R., Shepherd, B., Boyce, M.S., 2018. The role of human outdoor recreation in shaping patterns of grizzly bear-black bear co-occurrence. *PLOS ONE* 13 (2), e0191730.
- Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. *PLOS ONE* 11 (12), e0167259.
- Lemoine, N.P., 2019. Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* 128 (7), 912–928.
- Lesmerises, F., Johnson, C.J., St-Laurent, M.-H., 2018. Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. *Anim. Behav.* 140, 39–47.
- Li, X., Hu, W., Bleisch, W.V., Li, Q., Wang, H., Lu, W., Sun, J., Zhang, F., Ti, B., Jiang, X., 2022. Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance. *Conserv. Biol.* 36 (3), e13839.
- Lovari, S., Corsini, M.T., Guazzini, B., Romeo, G., Mori, E., 2017. Suburban ecology of the crested porcupine in a heavily poached area: A global approach. *Eur. J. Wildl. Res.* 63 (1), 10.
- Lovell, C., Li, S., Turner, J., Carbone, C., 2022. The effect of habitat and human disturbance on the spatiotemporal activity of two urban carnivores: The results of an intensive camera trap study. *Ecol. Evol.* 12 (3), e8746.
- Makowski, D., Ben-Shachar, M., Lüdtke, D., 2019. bayestestR: describing effects and their uncertainty, existence and significance within the bayesian framework. *J. Open Source Softw.* 4 (40), 1541.
- Marion, S., Davies, A., Demšar, U., Irvine, R.J., Stephens, P.A., Long, J., 2020. A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. *Glob. Ecol. Conserv.* 22, e00917.
- Mori, E., 2017. Porcupines in the landscape of fear: Effect of hunting with dogs on the behaviour of a non-target species. *Mammal. Res.* 62 (3), 251–258.
- Niedballa, J., Sollmann, R., Courtiol, A., Wilting, A., 2016. camtrapR: An R package for efficient camera trap data management. *Methods Ecol. Evol.* 7 (12), 1457–1462.
- Oberosler, V., Groff, C., Iemma, A., Pedrini, P., Rovero, F., 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mamm. Biol.* 87, 50–61.
- Olson, L.E., Squires, J.R., Roberts, E.K., Ivan, J.S., Hebblewhite, M., 2018. Sharing the same slope: Behavioral responses of a threatened mesocarnivore to motorized and nonmotorized winter recreation. *Ecol. Evol.* 8 (16), 8555–8572.
- Patten, M., Burger, J., 2018. Reserves as double-edged sword: Avoidance behavior in an urban-adjacent wildland. *Biol. Conserv.* 218, 233–239.
- Plante, S., Dussault, C., Richard, J.H., Côté, S.D., 2018. Human disturbance effects and cumulative habitat loss in endangered migratory caribou. *Biol. Conserv.* 224, 129–143.
- Richard, J.H., Côté, S.D., 2016. Space use analyses suggest avoidance of a ski area by mountain goats: Avoidance of a Ski Area by Mountain Goats. *J. Wildl. Manag.* 80 (3), 387–395.
- Salvatori, M., Oberosler, V., Rinaldi, M., Franceschini, A., Truschi, S., Pedrini, P., Rovero, F., 2023. Crowded mountains: Long-term effects of human outdoor recreation on a community of wild mammals monitored with systematic camera trapping. *Ambio* 52 (6), 1085–1097.

- Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., Ancillotto, L., 2019. One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.* 22, 365–376.
- Sarmento, W.M., Berger, J., 2017. Human visitation limits the utility of protected areas as ecological baselines. *Biol. Conserv.* 212, 316–326.
- Sévèque, A., Gentle, L.K., Vicente López-Bao, J., Yarnell, R.W., Uzal, A., 2022. Impact of human disturbance on temporal partitioning within carnivore communities. *Mammal. Rev.* 52 (1), 67–81.
- Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L.M., Forrester, T., Green, A.M., et al., 2021. Disturbance type and species life history predict mammal responses to humans. *Glob. Change Biol.* 27 (16), 3718–3731.
- Wickham, H., 2014. Tidy Data. *J. Stat. Softw.* 59 (10), 1–23.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Wilson, M.W., Ridlon, A.D., Gaynor, K.M., Gaines, S.D., Stier, A.C., Halpern, B.S., 2020. Ecological impacts of human-induced animal behaviour change. *Ecol. Lett.* 23 (10), 1522–1536.
- Wolsko, C., Lindberg, K., Reese, R., 2019. Nature-Based Physical Recreation Leads to Psychological Well-Being: Evidence from Five Studies. *Ecopsychology* 11 (4), 222–235.
- Zanette, L.Y., Frizzelle, N.R., Clinchy, M., Peel, M.J.S., Keller, C.B., Huebner, S.E., Packer, C., 2023. Fear of the human “super predator” pervades the South African savanna. *Curr. Biol.* 33 (21), 4689–4696 e4.