Science of the Total Environment 996 (2025) 180091

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Trapped by trails: How different types of recreational trails influence seasonal space use of wildlife in a densely visited national park

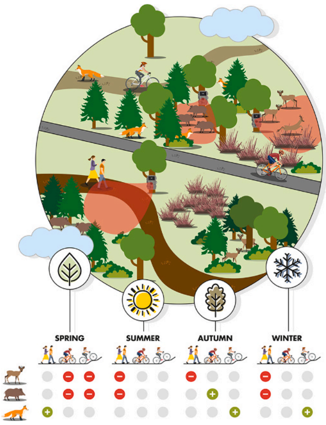
Wim Kuypers [a,b,c,*], Martijn Bollen [a,c], Jim Casaer [c], Natalie Beenaerts [a]

[a] Centre for Environmental Sciences, Hasselt University, Diepenbeek, Belgium
[b] Department of Geography, Institute of Life Earth and Environment, University of Namur, Namur, Belgium
[c] Research Institute for Nature and Forest, Brussels, Belgium

HIGHLIGHTS

- We analysed seasonal responses of wildlife to recreational trail densities.
- Species and seasonality shaped responses to hiking, cycling, and mountain biking.
- Hiking trails reduced land use of roe deer and wild boar more than cycling or mountain biking.
- Roe deer land use was more affected by recreational trails during daytime than at night.
- Red fox preferred areas with higher recreational trail density.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Human-wildlife interactions
Recreation
Camera traps
Protected areas
Spatiotemporal patterns
Seasonality
Wild boar
Roe deer
Red fox

ABSTRACT

Protected areas face the challenge of balancing conservation goals with increasing recreational use, which can strongly influence behavioural changes of wildlife and, consequently, affect ecosystem functioning. Understanding the impacts of various recreational activities on wildlife behaviour is essential for guiding targeted management strategies and supporting sustainable conservation practices. In the 60 km^2, highly visited Hoge Kempen National Park (Belgium), we assessed habitat preferences and the seasonal impact of hiking, mountain biking, and tarmac cycling trail densities on the land use of roe deer, wild boar, and red fox. From May 2018 until May 2019, camera traps were used to monitor wildlife. Since individual animals could not be uniquely identified and the detection is imperfect, we used N-mixture models to estimate spatial variation in their land use, given their detection probability. We revealed species-specific seasonal differences in the impact of recreational trails and habitats. From all recreational trail types, hiking had the most negative impact on land use of roe deer and wild boar, while the impact of cycling and mountain biking trails was only negative in Spring. Furthermore, hiking and cycling trails had a more negative impact on land use of roe deer during the day than at night. In

---

* Corresponding author at: Centre for Environmental Sciences, Hasselt University, Diepenbeek, Belgium; Department of Geography, Institute of Life Earth and Environment, University of Namur, Namur, Belgium.

E-mail address: wim.kuypers@uhasselt.be (W. Kuypers).

https://doi.org/10.1016/j.scitotenv.2025.180091
Received 26 March 2025; Received in revised form 11 June 2025; Accepted 14 July 2025

contrast, red fox selected areas with high recreational trail density in multiple seasons. These findings underscore the difference and seasonality in the impact of various recreation types on wildlife land use, highlighting the need for recreation monitoring and adaptive management strategies to mitigate or leverage recreational pressures on wildlife.

1. Introduction

The establishment of protected areas is a cornerstone of contemporary conservation strategies, aimed at preserving biodiversity and natural resources (Graham et al., 2019; Haight and Hammill, 2020). This approach is typically guided by a dual mandate: to safeguard ecosystems and species from anthropogenic pressures while simultaneously providing opportunities for public enjoyment and recreation (IUCN, 1994; Díaz et al., 2015; IPBES, 2019). Balancing these objectives necessitates careful management to ensure that recreational use does not undermine conservation goals, thereby promoting both ecological integrity and human well-being. Protected areas have become increasingly popular for outdoor recreation worldwide. This trend helps people reconnect with nature, which is especially important in our urbanised society and significantly benefits mental well-being (Barragan-Jason et al., 2022). Furthermore, nature tourism is a crucial economic factor for local communities, making visitor attraction an essential objective for protected areas alongside conservation efforts. However, despite its growing popularity, challenges regarding the negative impacts of outdoor recreation on wildlife arise (Schulze et al., 2018). These challenges are especially prominent in densely populated regions where a trade-off between conservation and recreation often exists. Human activities not only physically change landscapes through infrastructure development but also affect ecological communities.

Protected areas and their dual mandates are becoming increasingly important in our human-dominated world. While research on recreation ecology has been slowly increasing, the body of literature on this subject remains relatively small, with numerous knowledge gaps still to be addressed (Larson et al., 2016). This is particularly true for smaller protected areas located in densely populated regions with high recreational use. In these areas, it is crucial to recognize the impacts of non-consumptive recreation on wildlife for effective ecosystem management both within and beyond protected areas.

Non-consumptive recreation contributes to a “perceived risk of predation” among various wildlife species (Lasky and Bombaci, 2023). This perceived risk of predation is widely recognized to influence wildlife behaviour (Palmer et al., 2017; Prugh et al., 2019), resulting in a “landscape of fear” where species modify their behaviour or avoid areas with higher perceived risk. Within this framework, humans are often considered apex predators, possibly inducing fear-driven behavioural changes (Tolon et al., 2009; Ciuti et al., 2012). Wildlife responses to human activity can be multifaceted, ranging from fine-scale behavioural adaptations in more resilient species, such as changes in diel activities (Gaynor et al., 2018; Nickel et al., 2020; Anderson et al., 2023; Fennell et al., 2023; Burton et al., 2024; Procko et al., 2024), to avoidance of optimal habitat resulting in suboptimal habitat use, in more sensitive species (Heinemeyer et al., 2019; Procko et al., 2024). Moreover, recreational activities can adversely affect reproductive success (Beale and Monaghan, 2005; Baudains and Lloyd, 2007; Weterings et al., 2024), potentially leading to population-level consequences. These varied responses highlight the complexity of wildlife interactions with human activities, posing significant challenges for the management of protected areas striving to develop sustainable recreation systems that satisfy recreational demands while minimising ecological impacts (Miller et al., 2022). While much of the literature emphasises the negative impacts of recreation on wildlife and proposes protective conservation strategies based on these findings, it is also important to consider the potential positive role of recreational activities in managing invasive species or those with invasive characteristics. The effects of recreation could potentially be leveraged to help control invasive populations, thereby supporting broader conservation goals. The impact of human recreation on wildlife is highly species- and context-specific, varying across spatial and temporal scales (Dertien et al., 2021; Suraci et al., 2021). Studies of terrestrial recreation impacts often focus on hiking, while fewer studies investigate the impacts of other popular recreational activities like cycling and mountain biking (MTB) (Larson et al., 2016). Furthermore, most studies only focus on large areas combined with short time frames of several weeks or months without taking into account possible temporal differences (i.e. seasons, holidays, week/weekend) in the impact of recreation. Nevertheless, most wildlife species may exhibit different responses to recreational activities over time (i.e. day vs. night, seasonal changes), based on their ecology and the changing natural environment. Most studies focus on the effects of recreation on wildlife in large protected areas, often overlooking the impacts in smaller protected areas with fewer spatial refuges (Naidoo and Burton, 2020; Nickel et al., 2020; Sytsma et al., 2022; Salvatori et al., 2023; Marion et al., 2024; Procko et al., 2024). As urbanisation and population growth continue, these smaller protected areas are becoming increasingly critical for conservation (Volenec and Dobson, 2020). To manage protected areas more effectively, we need to better understand the seasonal responses of different wildlife species to a variety of non-consumptive recreational activities (Dertien et al., 2021).

We investigate the seasonal impact of different recreational trail types (hiking, cycling, and MTB) on the space use of wildlife, using a camera trap network in the Hoge Kempen National Park (NPHK) in Belgium. We hypothesise that recreation negatively affects the spatio-temporal behaviour of roe deer and wild boar, resulting in reduced space use or avoidance of areas with high trail densities compared to areas with lower trail densities. We expect this spatial avoidance to be most pronounced during the daytime when human activity peaks (Wevers et al., 2020) and also to vary seasonally based on the ecological behaviour of each species (e.g. reproductive season), the varying natural resources, and the seasonal variability in human activities. Because hiking trails and hikers are most abundant in NPHK, and hikers tend to move more slowly and often engage in conversation, which could have a more disturbing impact on wildlife (Zeller et al., 2024), we hypothesise that the avoidance of areas with high hiking trail density is greater compared to areas with high MTB and cycling trail density. For red fox, we hypothesise a preference for areas with high recreational trail density, as this species is often attracted to human presence and associated infrastructure (Erb et al., 2012; Suraci et al., 2021). Additionally, we expect the influence of recreational trails to vary seasonally, reflecting both the ecological behaviour of red fox and seasonal fluctuations in human activity. In this study, we distinguish between MTB and cycling trails because they differ in their physical characteristics and usage patterns; MTB trails in NPHK are nonlinear and naturalistic, while cycling trails are often tarmacked and straight, potentially resulting in differential impacts on wildlife.

2. Material and methods

2.1. Study area

The study area (longitudes: 5.552°W - 5.703°W; latitudes: 50.899°N - 51.016°N) is situated in the core region of Hoge Kempen National Park (NPHK), eastern Belgium (Fig. 1). It has a total surface area of ~60km^2, consisting of large areas of planted pine forests (41 % *Pinus sylvestris* and *Pinus nigra*). These afforested regions are undergoing a systematic transition towards a more natural deciduous forest ecosystem, wherein *Quercus* spp. and *Betula* spp. dominate (9 %). The park includes valuable dry (*Calluna* sp.) and wet (*Erica* sp. and *Myrica* sp.) heathland (11 %), along with shrub vegetation (7 %) predominantly dominated by *Molinia* sp. NPHK has altitudes ranging from 50 to 100 m above sea level. The study area has a cool, temperate, and moist climate, with a mean annual temperature of 10.9 °C and 816.4 mm rainfall (Klimaatstatistieken van de Belgische gemeenten Maasmechelen (nis 73107), n.d.).

The study area is embedded in a densely populated urban matrix, with an average of 443 inhabitants per km^2 in the surrounding municipalities (Statbel, n.d.). Hence, the region is extensively utilised for recreational purposes including walking, cycling, MTB, horse riding, and hunting. The study area features an exceptionally dense network of recreational trails, with approximately 100 km of advertised hiking trails (1.657 km/km^2), 50 km of cycling paths (0.814 km/km^2), and 60 km of designated MTB routes (1.008 km/km^2). The estimated annual number of visitors within our study area exceeds 500,000 (Visitor counters from NPHK (2018)). Furthermore, there are five official entrance gates at the borders of the study area, providing visitors with parking opportunities and direct access to these various recreational trails. NPHK faces typical challenges, including increasing human recreational pressures, limited data on human usage and wildlife behaviour, and a lack of comprehensive understanding of how these factors influence management strategies. Additionally, the park is becoming increasingly isolated from other prime wildlife habitats due to surrounding road networks, fencing and urban expansion.

2.2. *Camera trapping network*

A systematic random sampling design of 40 motion-sensing camera

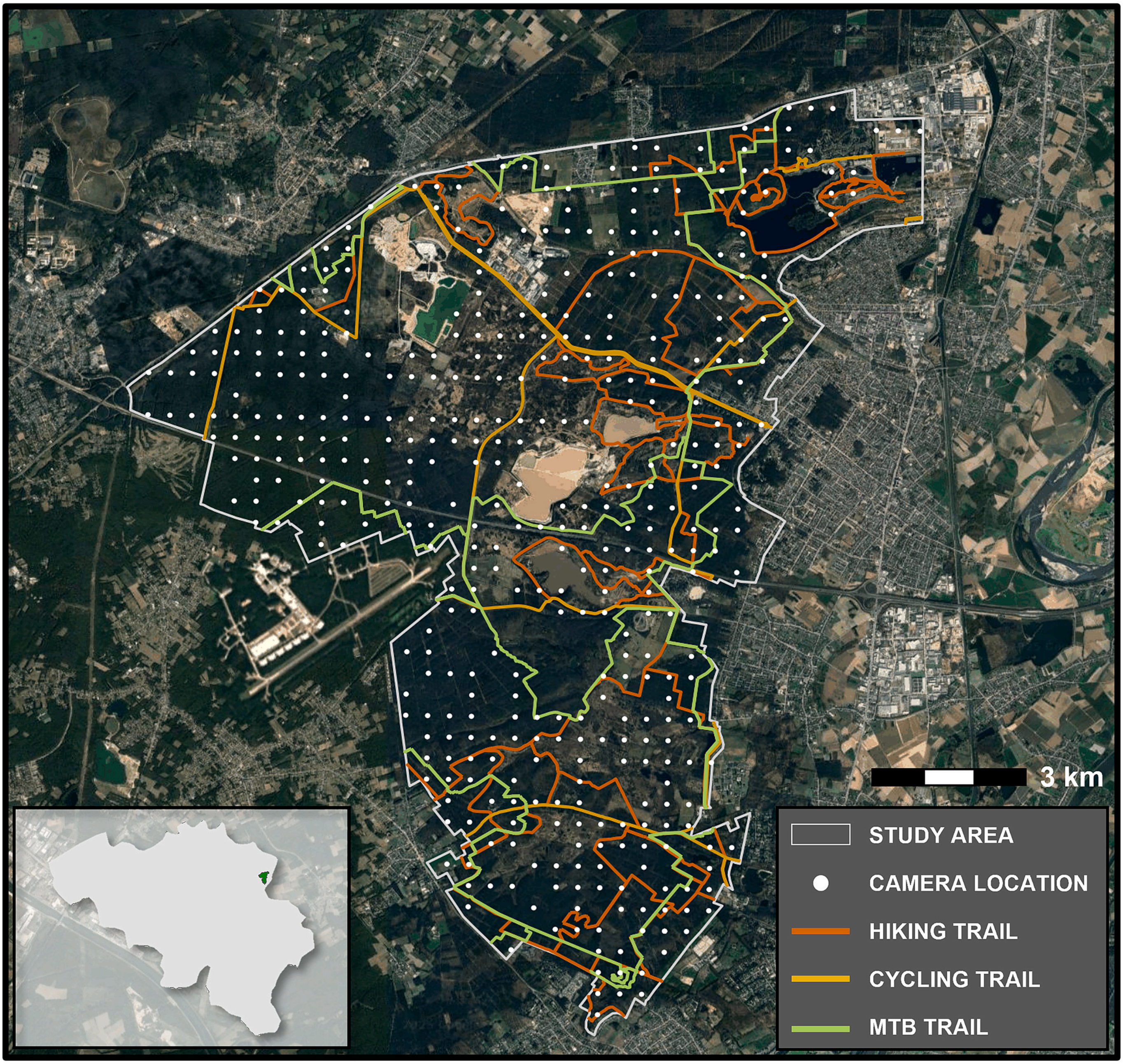


Fig. 1. Map of the study area in Hoge Kempen National Park (Belgium). Camera trap locations, officially designated hiking, cycling and mountain bike trails are illustrated on the map. The inset map (lower left) shows the study area within Belgium.

traps (CTs) (Reconyx HC600 Hyperfire) was applied in NPHK. We divided the study area into 40 compartments of approximately 1,5 km^2 and superimposed a grid of 300x300m on these compartments. Each month, we randomly selected one grid cell within each of the 40 compartments and used their midpoints as the sampling location to set up a single camera trap (Fig. B1). We deployed camera traps for three consecutive weeks and relocated them in the fourth week. This rotation scheme resulted in 12 deployments per year, with each 1.5 km^2 compartment containing three randomly selected CT locations per season, corresponding to approximately 120 sampled locations per season. The deployment duration was based on a pilot study in NPHK and sampling design guidelines developed for occupancy models for general species (MacKenzie and Royle, 2005; Shannon et al., 2014). In total, after accounting for camera malfunction or stolen devices, 471 unique sites were sampled with an average trapping effort of 29 days per site. All CTs were mounted to the nearest tree ~50 cm above ground, facing North. No bait was used to lure animals. Locations on trails or within non-accessible industrial sites were excluded. Each camera trigger initiated a series of ten successive photographs, with no interval between triggers. In addition, time-lapse pictures were taken every 12 h to control for camera malfunction. Following Bollen et al. (2024), sequences of photographs (ten photos per trigger) were deemed independent if they were separated by a minimum of 2 min (i.e. the default 'time-to-independence' for Agouti projects). Each independent sequence was regarded as representing a distinct observation of roe deer, wild boar or red fox and the raw counts were defined as the sum of unique individuals within these sequences (Wevers et al., 2020; Bollen et al., 2024). Annotation of photograph sequences was done using the Agouti software platform (Casaer et al., 2019; Bubnicki et al., 2023). For this paper, we focused on images obtained from May 2018 to May 2019. This selection encompassed a total of 13,585 operational camera days. Within these periods, we identified and documented observations of 12 wildlife species (excluding birds, domestic species and humans, Table A1). Among these, roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and red fox (*Vulpes vulpes*) provided sufficient data to model the seasonal effect of covariates on space use. Moreover, we observed 5092 roe deer, 1189 wild boar and 921 red fox.

2.3. Recreational pressure and habitat metrics

To develop a metric for recreational pressure, we used trail density from officially designated, marked trails as a proxy for various recreational activities, including hiking, cycling, and MTB. Using NPHK's official website data, we mapped all officially designated hiking trails, MTB trails, and biking routes. More specifically, the density of each type of recreational trail within each 300x300m grid cell was calculated by summing the total length of trails in metres within the cell boundaries. The distribution of trail length covariates within grid cells can be consulted in Fig. B2. Trail length variables were standardised (i.e. z-transformed) using the 'scale' function in R to ensure comparability across covariates. These trails are actively promoted by NPHK management and are well-known to visitors through multiple sources such as signposts, the NPHK website, and popular sports applications like Komoot and Fietsnet (Fietsnet, n.d.; Hoge Kempen National Park, n.d.; Komoot, n.d.).

Moreover, we collected data from twelve strategically placed visitor counters along the officially designated hiking trails, recording daily visitor numbers throughout the study period, which were used to calculate the seasonal average daily visitor counts to understand the seasonal variation in hiker numbers (Fig. B3). This information provided additional context for interpreting the seasonal impact of hiking trail density on our results. Data on visitor numbers for cycling and MTB were unavailable.

In addition to recreational trail data, we integrated habitat-related landscape metrics using Belgium's Corine Land Cover map (EEA, 2020). We determined the proportion of coniferous forest, deciduous forest, mixed forest, heathland, transitional woodland-shrub, wetland, and urban areas for each grid cell. These habitat metrics allowed us to control for landscape composition when assessing the impact of recreational trails on wildlife behaviour, ensuring that our findings accounted for both recreational and habitat-related factors. Habitat covariates, calculated as proportions between 0 and 1, were standardised (i.e. z-transformed) using the 'scale' function in R to ensure comparability across covariates.

2.4. Spatial analysis

The collected CT data were analysed using binomial N-mixture models via the R package *unmarked* (Fiske and Chandler, 2011) to assess the relationship between habitat and human disturbance covariates, and relative abundance of wild boar, roe deer and red fox. N-mixture models are frequently used to study the abundance of animals in relation to human disturbance and environmental covariates while accounting for imperfect detection (Bubnicki et al., 2019; Chaudhuri et al., 2022; Bollen et al., 2024; Rozylowicz et al., 2024). While N-mixture models are typically applied in large-scale designs with grid cells equal to or larger than the animals' home ranges, we used them in a small-scale design with grid cells much smaller than the animals' home ranges, necessitating a relaxation of the assumption that sampling units remain closed to changes in abundance during the survey period. We therefore interpreted estimated abundance as the predicted land-use intensity, while detection probability was defined as the probability that an individual of one of the studied species being present in a grid cell is detected (MacKenzie and Nichols, 2004; Efford and Dawson, 2012).

We generated species detection histories by grouping the number of observed individuals at daily intervals, utilising the *camtrapR* package (Niedballa et al., 2016). Furthermore, we segregated observations into day and night categories using sunset and sunrise times relative to the centre of the study area through the R package *overlap* (Ridout and Linkie, 2009), resulting in a 24-hour detection history and two separate day and night detection histories. This approach aimed to explore temporal disparities in the influence of recreational trail density and habitat on land-use intensity of wildlife, given the diel activity patterns of recreationists in NPHK (Wevers et al., 2020).

Before fitting N-mixture models, we screened all covariates for collinearity using the Spearman's rank correlation with a threshold of $\rho = |0.7|$ (Dormann et al., 2013). An important aspect of fitting N-mixture models is the choice of the parameter 'K'. The parameter 'K' represents the upper bound on the possible population size (abundance) at each site. It is crucial to select an appropriate value for 'K' since it influences the stability and accuracy of the parameter estimates produced by the model. To determine a suitable value for 'K', we evaluated the stability of parameter estimates across a range of 'K' values. Specifically, we fit a series of null models (i.e. models without covariates) to the data, varying 'K' between 25, 50, 100, 200, and 500, ensuring that these values encompassed the maximum number of observations per day in a grid cell for a given wildlife species (Fiske and Chandler, 2011; Kéry, 2018). We developed a set of 23 a priori abundance models containing a null model and 22 multivariate models (Table A2). Using a two-step approach as described by MacKenzie et al., 2017; we started by identifying the optimal detection model. This detection model was then used to determine the best-fitting abundance model. After model fitting, model selection was conducted using Akaike's Information Criterion (AIC) to assess the relative quality of the models (Akaike, 1974). Top-ranked models with $\Delta AIC < 2$ and greater weight than the null model were deemed competitive. We evaluated the significance of covariate effects of the top-performing model using 95 % confidence intervals (CIs) based on the covariate estimates and standard errors from the model summary (Supplementary Tables A6, A7, A8, A9, A10), considering intervals that did not overlap zero as statistically significant.

Detection was modelled using three potential covariates: month of the year, julian day of the year, and transformed julian day of the year

(Table A3). These date-related variables in the detection model allowed for correction of variation in detectability due to seasonal changes in cover, temperature, foliage, and animal behaviour. To address the circularity of time, Julian dates were sine- and cosine-transformed (Richter et al., 2020). Land-use intensity was modelled using selected candidate environmental covariates to account for factors such as cover, food availability, seasonality, and human recreational disturbance. To assess the impact of various recreational trail densities, we incorporated covariates such as hiking trail length, MTB trail length, and cycling trail length within a grid cell. As mentioned earlier, these trail lengths only encompass officially designated trails promoted and visualized by the National Park (Fig. 1). To ensure that the effects of recreation were not over- or underestimated due to omission of key environmental factors, we incorporated landscape covariates representing habitat composition, including the proportions of coniferous forest, deciduous forest, mixed forest, transitional woodland-shrub, heathland, wetland, and urban areas. To evaluate potential seasonal variations in the effects of recreational trails and habitat on wildlife land-use intensity, we included interaction terms between recreational trail densities and seasons, as well as habitat and season (spring, summer, autumn, winter, based on the meteorological seasons in Western Europe) (Table A2).

To account for potential spatial autocorrelation, we incorporated spatial random effects using the *ubms* package in R (Kellner et al., 2022). We first evaluated models including a spatial random effect defined by neighbouring cells at three scales (i.e. 300 m, 600 m, and 900 m), and compared model performance based on differences in expected log predictive density (elpd). The best-performing spatial scale was then added as a random effect to the previously selected top N-mixture model. We assessed whether this addition improved model fit by comparing elpd differences between models with and without the spatial random effect. The final model was then used to evaluate the estimated effects of covariates on wildlife space use intensity.

3. Results

In the following analyses, we will use the terms “negative effect” and “positive effect” to describe how various covariates influence the land-use intensity of roe deer, wild boar and red fox in NPHK. A “negative effect” refers to a situation where an increase in the covariate metric results in a decrease in the intensity with which a wildlife species uses a specific site or space, suggesting avoidance. Conversely, a “positive effect” indicates that an increase in the covariate metric leads to an increase in the land-use intensity of the wildlife species, suggesting preference. Statistical significance will be framed as explained in Section 2.4.

For roe deer, given its crepuscular lifestyle (Fig. B4), we were able to fit a daytime and night-time model with a high number of observations (2059 daytime, 3033 night-time). Unfortunately, due to the almost complete nocturnal nature of wild boar and red fox in NPHK (Fig. B4), we lacked sufficient daytime observations to effectively compare daytime to night-time spatial behaviour for those species using our modelling approach (Wild boar 153 daytime, 1036 night-time; Red fox 100 daytime, 821 night-time). Consequently, only 24-h models were applied to wild boar and red fox.

3.1. *Roe deer*

3.1.1. *24-hour model*

For roe deer (*Capreolus capreolus*), the “Month” detection model outranked the others (Table A4). The resulting monthly variation in detection probability is presented in Fig. B5. The top-ranked N-mixture model was the “habitat7_recreation_season_int” model including the following habitats: urban, coniferous forest, mixed forest, deciduous forest, transitional woodland shrub, wetland and heathland. Moreover the model included the following recreational covariates: hiking, MTB and cycling trail density. For both habitat and recreation covariates, the top-performing model also incorporated an interaction term with the seasons (i.e. spring, summer, autumn and winter) (Table A5). This model was more parsimonious than all the other models ($\Delta\mathrm{AIC}>2$). To account for spatial autocorrelation, a spatial random effect based on neighbouring cells within a 900 m radius was included, as this scale yielded the best model fit based on elpd comparisons.

Roe deer exhibited a significant reduction in land-use intensity with increasing hiking trail density during summer, autumn and winter, with the most pronounced negative effect observed in autumn (Fig. 2). In spring, there was no significant effect of hiking trail density on land-use intensity for roe deer.

Cycling trail density showed a significant negative effect on land-use intensity of roe deer in spring. In all other seasons, there was no significant impact. Mountain bike trail density did not significantly affect land-use intensity for roe deer with exception for the spring months. During those months there was a significant negative impact.

The impact of habitat on roe deer land-use intensity showed clear seasonal variation (Fig. B6). Urban areas had a significant negative effect in autumn but a positive effect in winter. Coniferous forest was associated with reduced land-use intensity in spring, yet showed a positive effect in winter. Mixed forests had a negative effect in spring, while deciduous forest was linked to increased land-use intensity only during winter. Woodland-shrub areas negatively influenced space use in both spring and autumn but had a positive effect in winter. Heathland consistently showed a significant negative effect in spring and autumn. No significant effects were observed for wetlands.

3.1.2. *Daytime vs night-time model*

When the same model was run for day and night time observations separately, a shift in coefficients was observed, showing a notable difference in significant coefficient values between daytime and night time (Fig. 3). In the daytime model, hiking trail density coefficients revealed significant negative effects in summer, autumn, and winter, while there was no significant effect in spring. The most pronounced negative effect of hiking trail density was observed in autumn. Conversely, during night time, the negative effect of hiking trail density was significant solely in autumn, while in spring a positive effect was observed.

Examining the impact of cycling trail density, the daytime model revealed significant negative effects on roe deer land-use intensity in spring, and winter. No significant effect was observed in summer and autumn. The night-time model, however, did not show significant effects of cycling trail density in any season. For MTB trail density, the daytime model indicated no significant effects on roe deer land-use in any season. Contrastingly, in the night-time model, MTB trail density had significant negative effects on land-use intensity in spring and summer, while no effect was detected in autumn and winter.

Comparing daytime and night-time models (Fig. B7) revealed clear differences in habitat effects on roe deer land-use intensity. Urban areas had a negative effect in spring during the day and in autumn at night, but a positive effect in winter at night. Coniferous and mixed forests showed positive effects during the day in winter, but significant negative effects at night in spring and autumn. Deciduous forest consistently had a positive effect in winter across both models. Woodland-shrub areas had a positive effect during the day in winter, but negative effects at night in spring and autumn. Heathland had a negative effect in spring during the day and in both spring and autumn at night. No significant effects were found for wetlands.

3.2. *Wild boar*

3.2.1. *24-hour model*

For wild boar (*Sus scrofa*), the “Month” detection model outranked the other models (Table A4). The resulting monthly variation in detection probability is presented in Fig. B5. The top-ranked N-mixture model was again the “habitat7_recreation_season_int” model. For both the habitat and recreation covariates, the top-performing model included an

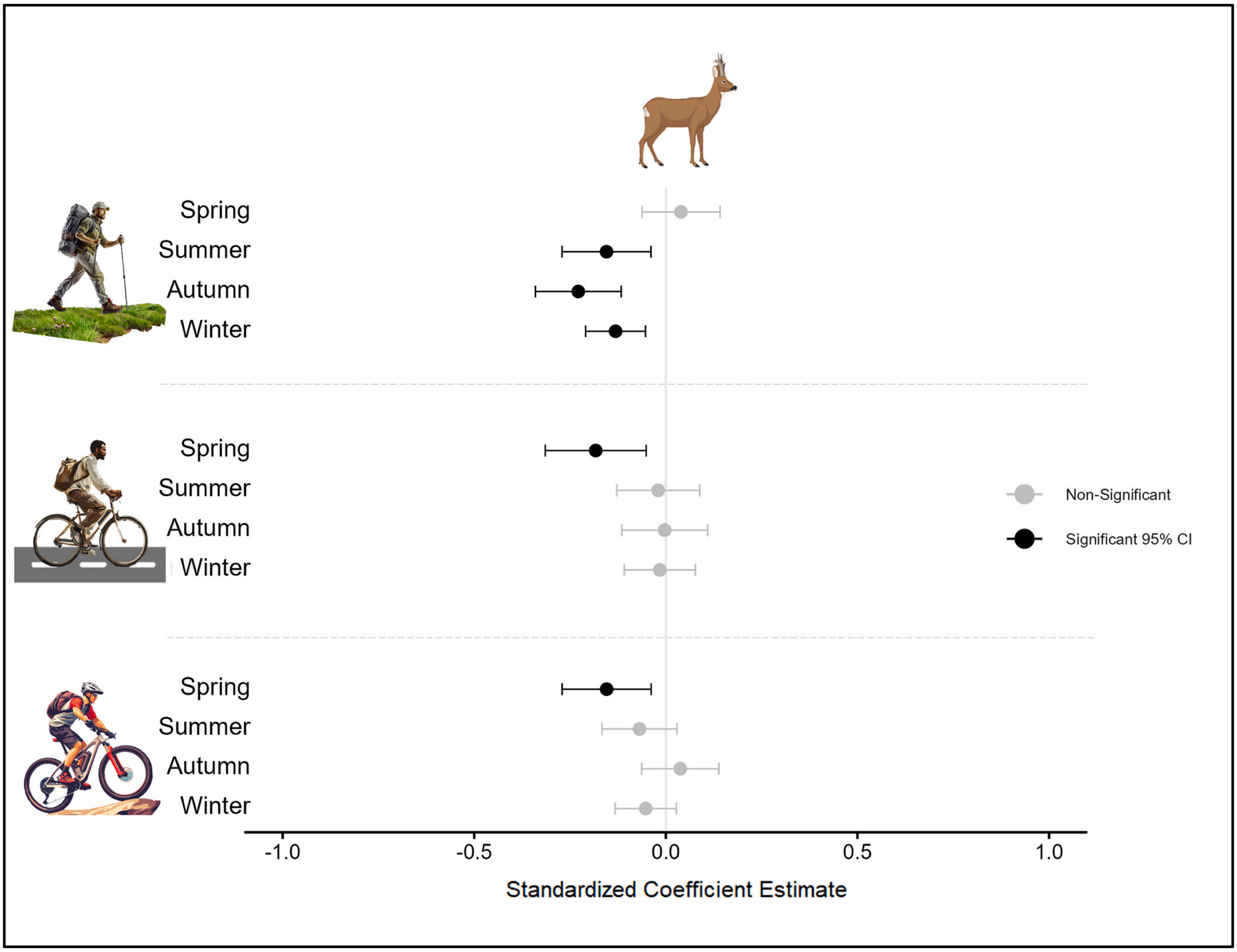


Fig. 2. Seasonal effects of different types of recreation on land-use intensity of roe deer. Shown are N-mixture model coefficient estimates for the effects of hiking, MTB and cycling trail densities based on 24-hour time intervals. Error bars are 95 % confidence intervals (CI). Black-colored estimates indicate statistical significance at a 95 % CI, and light grey-colored estimates indicate no significance at a 95 %.

interaction term with the seasons (i.e. spring, summer, autumn and winter) (Table A5). This model was more parsimonious than all the other models (ΔAIC>2). To account for spatial autocorrelation, a spatial random effect based on neighbouring cells within a 900 m radius was included, as this scale yielded the best model fit based on elpd comparisons.

Wild boar exhibited a significant reduction in land-use intensity with increasing hiking trail density during summer and winter (Fig. 4). In spring and autumn, there was no significant effect of hiking trail density on land-use intensity for wild boar. The impact of cycling trail density on wild boar land-use intensity varied by season. In spring, cycling trail density had a significant negative effect, while in autumn there was a positive effect. There were no significant effects of cycling trail density in summer or winter. MTB trail density had a strong significant negative impact on land-use intensity for wild boar in spring. No significant effects of MTB trail density were observed in summer, autumn or winter. Wild boar land-use intensity showed a significant positive relationship with coniferous, mixed, and deciduous forests, transitional woodland-shrub, and wetlands across seasons (Fig. B8). In contrast, heathland had a strong negative effect in spring.

3.3. Red fox

3.3.1. 24-hour model

For red fox (*Vulpes vulpes*), the “Month” detection model outranked the other models (Table A4) and again the “habitat7_recreation_season_int” model was the top-ranked N-mixture model. The resulting monthly variation in detection probability is presented in Fig. B5. For both the habitat and recreation covariates, the top-ranked model included an interaction term with the seasons (Table A5). This model was not more parsimonious than the “habitat7_ season” model (ΔAIC<2), where no recreation variables were included. Nevertheless, we will use the top-ranked model “habitat7_recreation_season_int” to explain relationships between land-use intensity and recreational covariates. To account for spatial autocorrelation, a spatial random effect based on neighbouring cells within a 600 m radius was included, as this scale yielded the best model fit based on elpd comparisons.

Red fox exhibited a significant increase in land-use intensity in response to recreational trail density, but only three specific combinations showed a significant positive effect (Fig. 5). Hiking trail density had a significant positive effect in summer, cycling trail density had no significant effects in any season, and MTB trail density had a significant positive effect in autumn and winter. In all other cases, no significant effects on red fox land-use intensity were observed. Regarding habitat

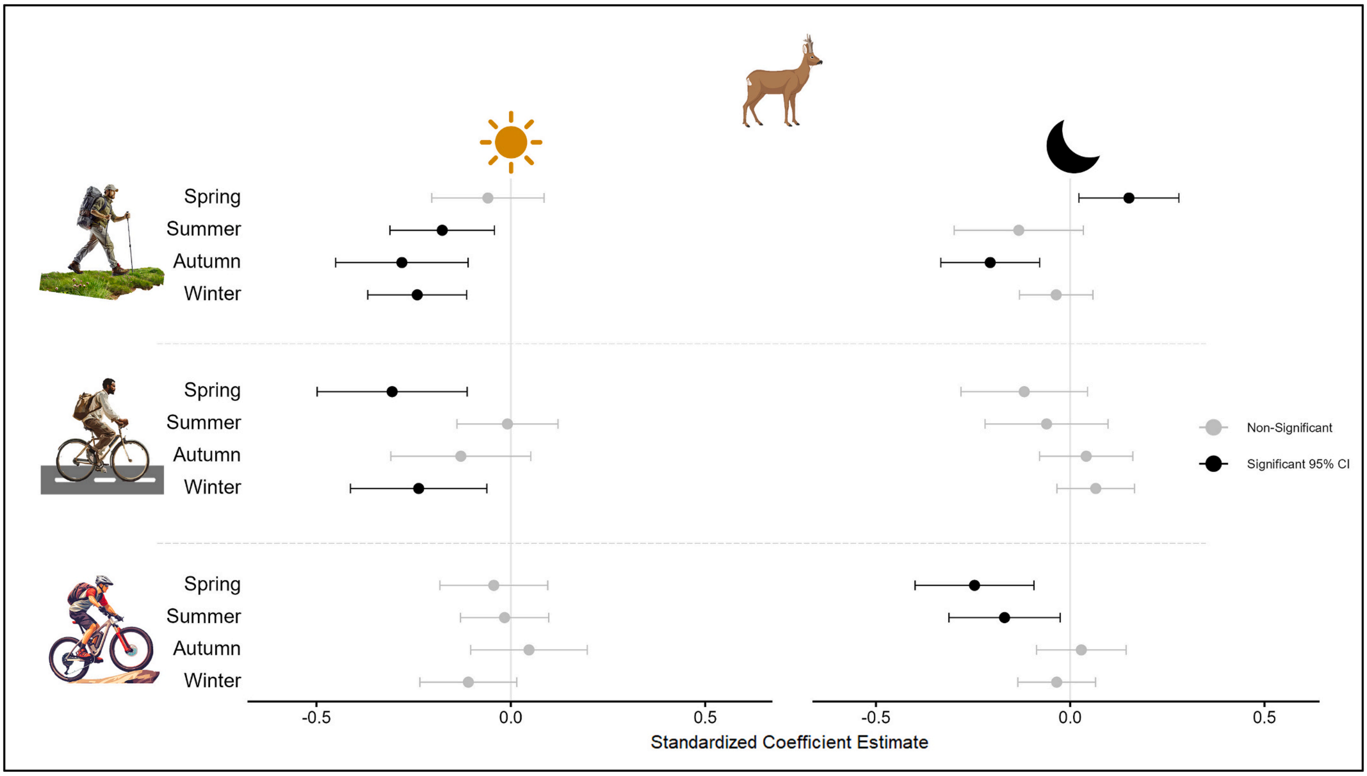


Fig. 3. Seasonal effects of different types of recreation on diel (left) or nocturnal (right) land-use intensity of roe deer. Shown are N-mixture model coefficient estimates for the effects of hiking, MTB and cycling trail densities based on diel and nocturnal time intervals. Error bars are 95 % confidence intervals (CI). Black-colored estimates indicate statistical significance at a 95 % CI, and light grey-colored estimates indicate no significance at a 95 %.

variables (Fig. B9), red fox land-use intensity exhibited a significant positive effect from the proportions of urban area in summer. Area mixed forest, transitional woodland-shrub, and heathland showed a negative effect in winter. Conversely, for the summer and spring, area wetland showed significant positive effects.

4. Discussion

Using an intensive year-long camera trap study and the application of N-mixture models, we assessed the seasonal impact of recreational trail densities (hiking, cycling and MTB) and the influence of habitat on space use of roe deer, wild boar, and red fox. While most studies primarily focus on large, sparsely populated regions with relatively low trail densities (Naidoo and Burton, 2020; Nickel et al., 2020; Sytsma et al., 2022; Salvatori et al., 2023; Marion et al., 2024; Procko et al., 2024) and/or short observation periods (typically spanning only a few months), we provide a year-round perspective in a small, highly visited national park embedded in a densely populated urban matrix, a scenario increasingly common in the western world. By considering seasonality and different trail types, including hardened, tarmac cycling trails, we contribute to a broader understanding of how diverse recreational trails may influence wildlife in such landscapes. This study for the first time investigated the impact of tarmac cycling trails, including a comparison between different types of recreational trails, as these features are particularly relevant to the region's landscape and to regions experiencing growing recreational pressure and evolving trail infrastructure. Incorporating habitat covariates allowed us to better isolate the effects of recreation and improve model performance. While habitat variables showed clear seasonal effects on wildlife space use, we do not further elaborate on these patterns here, as they fall outside the main scope of this study.

We revealed species-specific spatiotemporal responses, or lack thereof, to recreational trail density, with variations depending on the type of recreational trail and the season. For roe deer specifically, responses also varied with the time of day. For wild boar and red fox, this could not be investigated due to low numbers of observations during the day. It is important to note that these lower observation numbers during daylight hours may already reflect a temporal avoidance of human activity rather than an absence of a spatiotemporal response (Podgórski et al., 2013; Díaz-Ruiz et al., 2016). Our results suggest that both the season and the type of recreational trail or activity are critical factors in determining the effects of recreation on wildlife. Due to the setup of this research, we were however not able to differentiate between the impact of the physical presence of a trail and the recreational activity itself. Overall, hiking trail density had the most constant negative impact on space use of ungulates throughout all seasons, meaning ungulates tend to avoid zones with higher densities of hiking trails more than other recreational trails. Red fox showed a tendency to prefer areas with dense recreational trail networks (Fig. 5).

4.1. *Species-specific seasonal responses to recreational trails*

4.1.1. *Ungulates: roe deer and wild boar*

Overall, roe deer and wild boar exhibited avoidance of areas with higher hiking trail densities more than areas with high cycling or MTB trails, indicating the potentially more disturbing impact of hiking on space use of ungulates compared to cycling and MTB. This pattern aligns with our hypothesis, as hiking trails in NPHK are most common and meander through multiple key habitats. In contrast, cycling and MTB trails are less common and more linear (Fig. 1), reducing overall density and potentially keeping recreational disturbance lower. Furthermore, hikers generally move more slowly than cyclists or MTB, and when combined with noise from communication, this could create a more unpredictable and disruptive effect on wildlife (Zeller et al., 2024). Other studies have also documented adverse effects of hiking activities

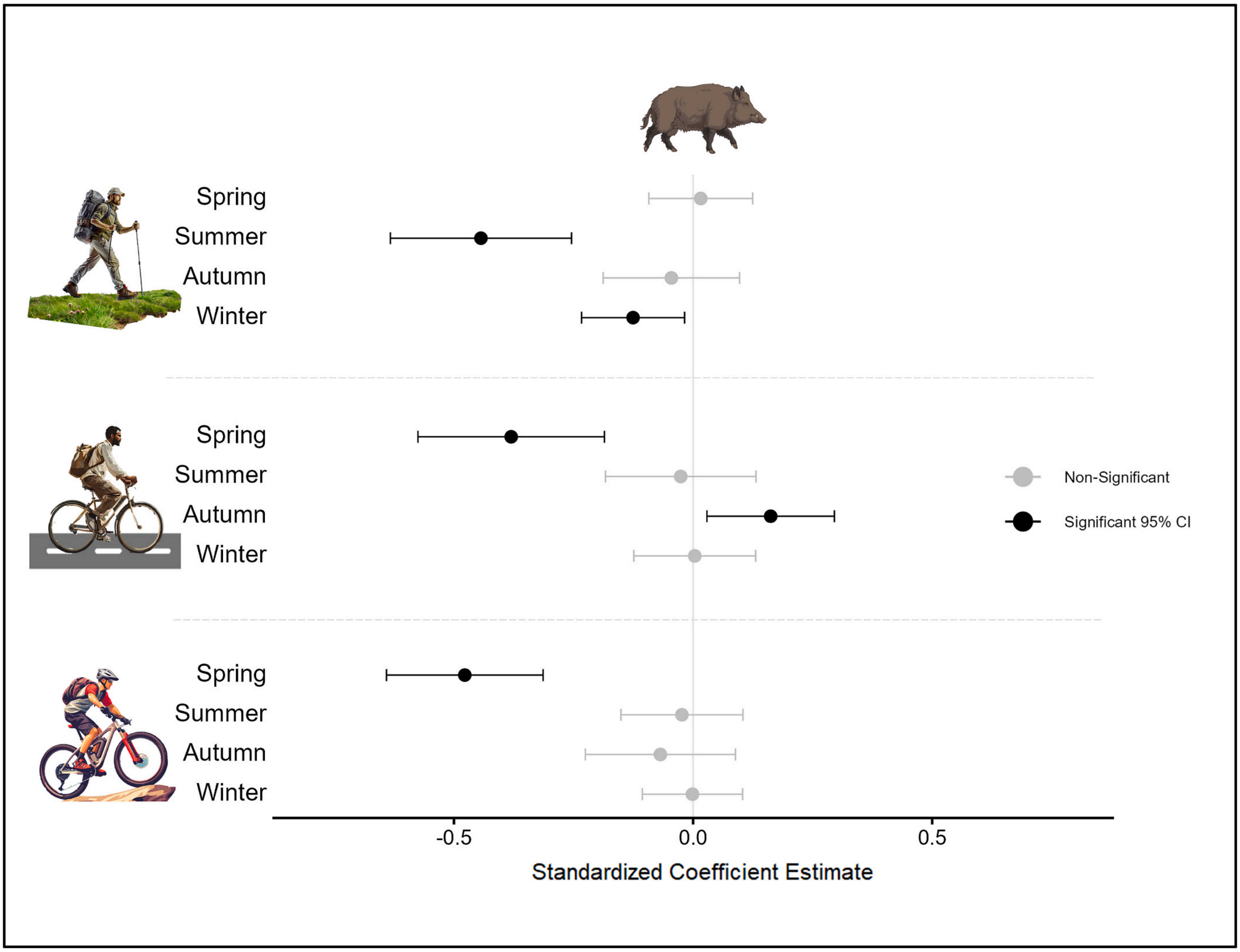


Fig. 4. Seasonal effects of different types of recreation on land-use intensity of wild boar. Shown are N-mixture model coefficient estimates for the effects of hiking, MTB and cycling trail densities based on 24-hour time intervals. Error bars are 95 % confidence intervals (CI). Black-colored estimates indicate statistical significance at a 95 % CI, and light grey-colored estimates indicate no significance at a 95 %.

and trails on space use of various wildlife species (Larson et al., 2016; Coppes et al., 2017; Lewis et al., 2021; Sytsma et al., 2022; Fennell et al., 2023; Marion et al., 2024). However, these studies never compared between different recreation types. Nevertheless, in spring, wild boar seemed to avoid MTB and cycling trail-rich areas more than hiking trail-rich areas.

Contrastingly, areas with a higher cycling trail density showed an intensified space use of wild boar in autumn. This could be explained by seasonal changes in food availability in some cycling or MTB trail-rich zones, making them more attractive to wild boar in autumn when food availability is at its peak. Although we used habitat percentages based on the Corine land cover to capture the variability for food availability and cover year-round, these habitat metrics are rather general and do not specify detailed seasonal differences in food availability. Hence, we suggest the incorporation of seasonal fine-scale landscape and food availability measurements to help better understand seasonal preferences for certain areas. Alternatively, interspecific competition for resources may force wild boar to visit locations with higher cycling trail densities in specific seasons (Ballari and Barrios-García, 2014; Borkowski et al., 2021). Moreover, we emphasize that the spatiotemporal variability in trail use intensity likely plays a key role in shaping seasonal wildlife responses, as the impact of trails is not solely determined by their density but also by how, when, and by whom they are used. Nevertheless, the observed space use patterns could also be influenced by an unobserved spatial driver that co-varies with trail densities (e.g. traffic roads or food availability).

4.1.2. *Red fox*

Interestingly, model selection for red fox identified a top model that included recreational trail densities (Table A5). However, based on AIC criteria, this model was not substantially more parsimonious (ΔAIC = 1.84) than a model containing the same habitat variables but without recreational trail densities. This suggests that incorporating recreational trail densities did not notably improve the explanatory power of the model for red fox space use. Nevertheless, we selected the top model including recreational variables to explore potential associations between recreation and red fox space use. Red fox exhibited seasonally dependent positive associations with recreational trail densities. In summer, red fox showed a preference for hiking trail rich areas. During autumn and winter, red fox showed a clear preference for areas with high MTB trail densities, whereas in spring, no preference or avoidance was observed. This pattern may be linked to reproductive behaviour, as during the denning season, red foxes balance the need to protect their offspring with accessing nearby resources, resulting in neither a strong preference nor avoidance during the denning season (Storm et al., 1976). Red fox's preference for urban areas in summer aligns with its

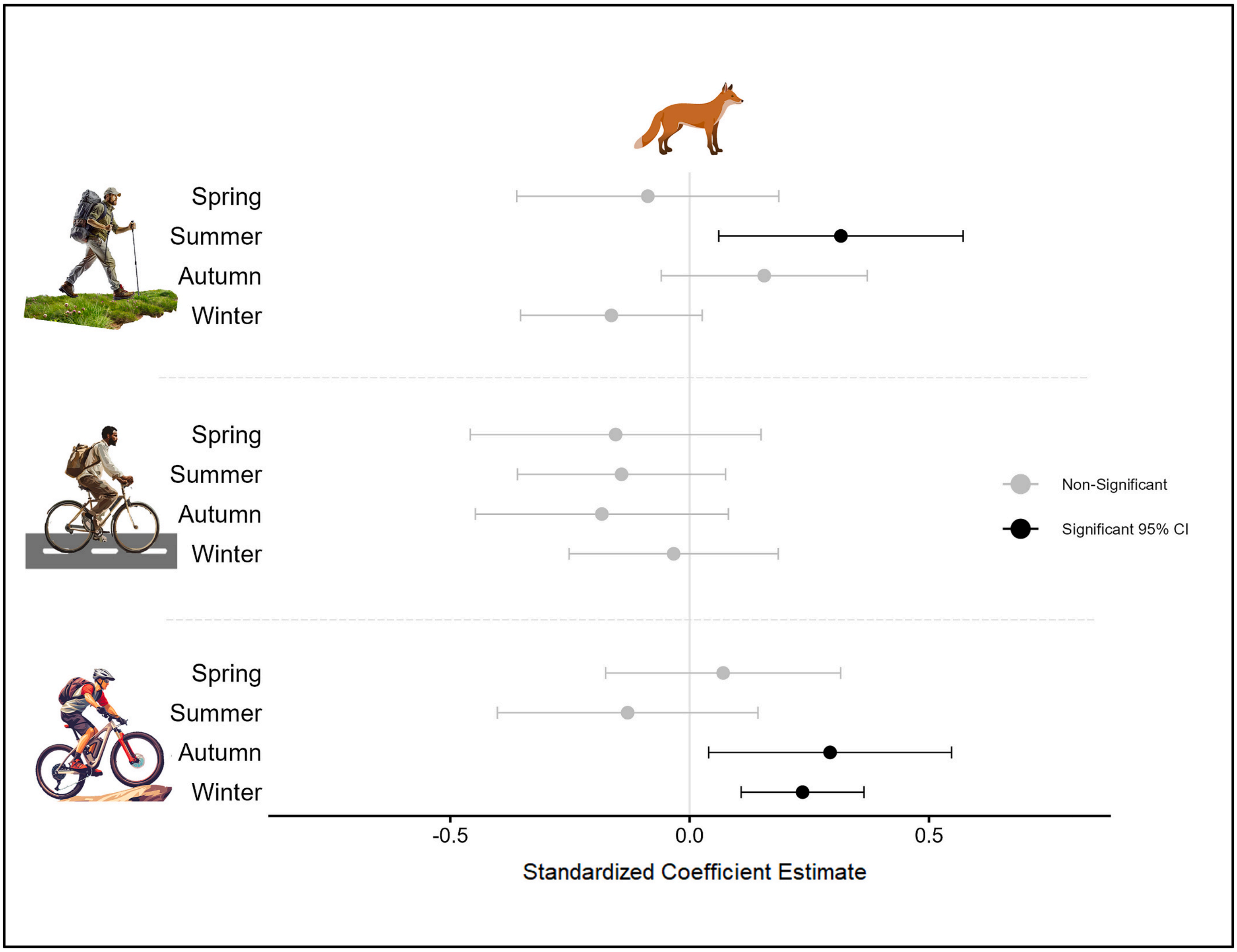


Fig. 5. Seasonal effects of different types of recreation on land-use intensity of red fox. Shown are N-mixture model coefficient estimates for the effects of hiking, MTB and cycling trail densities based on 24-hour time intervals. Error bars are 95 % confidence intervals (CI). Black-colored estimates indicate statistical significance at a 95 % CI, and light grey-colored estimates indicate no significance at a 95 %.

characterization as an urban adapter, a species that readily exploits human-altered environments due to their adaptability in diet and denning sites (DeCandia et al., 2019; Gil-Fernandez et al., 2020; Handler et al., 2020). This adaptability enables them to coexist in close proximity to human populations, further supporting their tendency to prefer areas with human-made features (Erb et al., 2012; Suraci et al., 2021). However, it is difficult to compare our seasonal results to other studies also showing the attraction of red fox towards human-made features and use of trails to navigate (Naidoo and Burton, 2020; Lewis et al., 2021; Anderson et al., 2023), as they lack to include the seasonal impact of a variety of recreational activities or trails.

4.1.3. *Visitor data*

The 24-hour responses of roe deer and red fox to hiking trail density throughout the seasons exhibit a pattern that parallels the seasonal average daily visitor counts on hiking trails. The visitor data indicate an increase in average daily visitor numbers from spring to summer, followed by a decline in winter (Fig. B3). Similarly, roe deer show a more negative response to hiking trail density from spring to summer, with this effect diminishing in winter, while red foxes exhibit increased effect sizes of hiking trail density from spring to summer, which then decrease during winter. Although our analyses did not directly incorporate visitor numbers, the observed similarity in trends suggests a potential relationship between hiking trail visitation and wildlife responses (Procko et al., 2024). We assumed that the officially marked and promoted trails serve as a proxy for the bulk of the recreational activity they are intended for, though it is important to keep in mind that specific trails may be used by multiple types of recreationists, which could influence these patterns. Therefore, future research should consider including visitor counts for specific types of recreation on a gradient of trails to better understand the effects of varying recreational pressures across different seasons and distinguish the effect of recreational intensity from seasonal species-specific habitat use. We used trail densities in each grid cell as proxies for recreational pressure. These densities are constant, while in fact, recreational pressure throughout a national park is often highly dynamic. Although we analysed seasonal impacts of recreational trail densities, the lack of spatiotemporal data on human presence creates uncertainty in the interpretation of results about seasonal impacts of static proxies for recreation. As such, it would be beneficial for nature management and conservation to investigate more specific spatiotemporal data on human presence/abundance and activity, including differentiation between recreational activities (i.e. hiking, cycling, MTB) to better understand the spatiotemporal dynamic interactions taking place between human activities and wildlife. This would allow us to eventually design useful thresholds at which certain species show behavioural adaptations towards recreational pressures.

Therefore, we propose the incorporation of social media and mobile phone data combined with camera traps to estimate visitor pressure on trails over large areas (Dertien et al., 2021; Procko et al., 2024).

Given that some wildlife species exhibit flexibility in their activity patterns and can seek temporal refuge from human disturbance at night, like wild boar, it might be assumed that wildlife and humans can coexist in recreational areas through temporal avoidance (Gaynor et al., 2018; Nickel et al., 2020; Lewis et al., 2021; Anderson et al., 2023; Fennell et al., 2023; Burton et al., 2024; Procko et al., 2024). However, despite their nocturnal behaviour, wild boar consistently avoided areas with high recreational trail densities across multiple seasons, particularly those with hiking trails. This suggests that human disturbance can significantly displace nocturnal species from areas with high levels of recreational activity. While temporal refuge from human recreation can be effective for some species, providing spatial refuge is equally crucial for wildlife survival (Larson et al., 2019; Lewis et al., 2021). This is especially important for species with diurnal or crepuscular activity patterns. For instance, in multiple seasons roe deer demonstrated spatial avoidance of hiking and cycling trail-dense areas during the day, while their response at night was less pronounced or even neutral. This indicates a potential spatiotemporal adaptation to recreational pressure, where wildlife may use spatial refuges during the day and access areas associated with recreational trails at night.

4.2. Considerations for management

To effectively mitigate the negative impacts of recreational activities on wildlife, management strategies often focus on creating spatial and temporal refuges (Lewis et al., 2021). Spatial refuges, such as restricted zones, and temporal refuges, like time-based access restrictions, provide wildlife with undisturbed areas for essential behaviours. In NPHK, three protected zones and night-time access restrictions already serve as such refuges. However, monitoring visitor behaviour is essential to ensure these areas or time zones remain undisturbed. Comprehensive monitoring of both visitor and wildlife behaviour would enhance future research on recreation-wildlife interactions, facilitating more effective management strategies.

Nevertheless, while much of the literature focuses on the negative effects of recreation, it is also important to consider its potential to manage overabundant species, such as roe deer, wild boar, and red fox, which can disrupt ecosystems from a top-down perspective and create human-wildlife conflicts (Moll et al., 2020; Castañeda et al., 2022; Afonso et al., 2024). For example, high roe deer populations hinder forest regeneration, but higher trail density in specific zones may reduce browsing pressure on young deciduous trees, aiding forest diversity (Stokely et al., 2020). Conversely, undisturbed zones could lead to overbrowsing and hinder natural regeneration (Mols et al., 2022).

Managing the spatiotemporal use of wildlife by designing recreational zones around protected areas can also concentrate ungulate populations, providing hunters with more focused areas for population control. Finally, species-specific thresholds for recreational activities and trail densities could help manage recreational pressure and achieve conservation goals (Dertien et al., 2021). However, it is crucial to consider the potential negative impacts on endangered species and critical habitats when implementing such management practices (Larson et al., 2016).

5. Conclusion

This year-long camera trap study, using N-mixture models, revealed clear species-specific and seasonal variation in how recreational trail density influences wildlife space use in the highly visited Hoge Kempen National Park (Belgium). Hiking trails had the most consistent negative impact on roe deer and wild boar, while cycling and MTB trails only showed negative effects in spring. For roe deer specifically, the influence of recreational trails differed notably between daytime and night-time. In contrast, red fox appeared to prefer areas with higher trail densities. These findings highlight the importance of considering both seasonality and the type of recreational activity or trail when designing conservation strategies and managing recreational access to support coexistence between wildlife and recreation.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.180091.

CRediT authorship contribution statement

Wim Kuypers: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Martijn Bollen:** Writing – review & editing, Validation, Supervision, Methodology. **Jim Casaer:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition. **Natalie Beenaerts:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgements

This work makes use of data and/or infrastructure provided by INBO and UHasselt and funded by Research Foundation Flanders (FWO) as part of the Belgian contribution to LifeWatch. Wim Kuypers is a joint PhD fellow funded by a BOF mandate at Hasselt University and the University of Namur. We are grateful to ANB, Regionaal Landschap Kempen & Maasland, the municipalities of As, Dilsen-Stokkem, Lanaken, Maasmechelen and Zutendaal, the tourist offices of NPHK, hunters and residents for allowing us to place camera traps on their property. We would also like to thank Dave Bosmans for helping us with the finalisation of the graphical abstract. Further, we thank all colleagues, students and volunteers who aided in the field or processed and annotated pictures.

Data availability

Data will be made available on request.

References

Afonso, B.C., et al., 2024. The effects of wild ungulates on small mammals: a systematic review and meta-analysis. Mammal Rev. 54 (2), 121–132. https://doi.org/10.1111/mam.12331.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19 (6), 716–723. https://doi.org/10.1109/TAC.1974.1100705.

Anderson, A.K., Waller, J.S., Thornton, D.H., 2023. Partial COVID-19 closure of a national park reveals negative influence of low-impact recreation on wildlife spatiotemporal ecology. Sci. Rep. 13 (1), 687. https://doi.org/10.1038/s41598-023-27670-9.

Ballari, S.A., Barrios-García, M.N., 2014. A review of wild boar S us scrofa diet and factors affecting food selection in native and introduced ranges. Mammal Rev. 44 (2), 124–134. https://doi.org/10.1111/mam.12015.

Barragan-Jason, G., et al., 2022. Human–nature connectedness as a pathway to sustainability: a global meta-analysis. Conserv. Lett. 15 (1), e12852. https://doi.org/10.1111/conl.12852.

Baudains, T.P., Lloyd, P., 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Anim. Conserv. 10 (3), 400–407. https://doi.org/10.1111/j.1469-1795.2007.00126.x.

Beale, C.M., Monaghan, P., 2005. Modeling the effects of limiting the number of visitors on failure rates of seabird nests. Conserv. Biol. 19 (6), 2015–2019. https://doi.org/10.1111/j.1523-1739.2005.00256.x.

Bollen, M., et al., 2024. Impacts of zoning and landscape structure on the relative abundance of wild boar assessed through a Bayesian N-mixture model. Sci. Total Environ. 911, 168546. https://doi.org/10.1016/j.scitotenv.2023.168546.

Borkowski, J., et al., 2021. There is only one winner: the negative impact of red deer density on roe deer numbers and distribution in the Słowiński National Park and its vicinity. Ecol. Evol. 11 (11), 6889–6899. https://doi.org/10.1002/ece3.7538.

Bubnicki, J.W., et al., 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. Elife 8, e44937. https://doi.org/10.7554/eLife.44937.

Bubnicki, J.W., et al., 2023. Camtrap DP: an open standard for the FAIR exchange and archiving of camera trap data. Remote Sens. Ecol. Conserv. https://doi.org/10.1002/rse2.374.

Burton, A.C., et al., 2024. Mammal responses to global changes in human activity vary by trophic group and landscape. Nature Ecology & Evolution. https://doi.org/10.1038/s41559-024-02363-2.

Casaer, J., et al., 2019. Agouti: a platform for processing and archiving of camera trap images. Biodiversity Information Science and Standards. https://doi.org/10.3897/biss.3.46690.

Castañeda, I., et al., 2022. Variation in red fox *Vulpes vulpes* diet in five continents. Mammal Rev. 52 (3), 328–342. https://doi.org/10.1111/mam.12292.

Chaudhuri, S., et al., 2022. N-mixture model-based estimate of relative abundance of sloth bear (*Melursus ursinus*) in response to biotic and abiotic factors in a human-dominated landscape of central India. PEERJ 10. https://doi.org/10.7717/peerj.13649.

Ciuti, S., et al., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS One 7 (11), e50611. https://doi.org/10.1371/journal.pone.0050611.

Coppes, J., et al., 2017. Human recreation affects spatio-temporal habitat use patterns in red deer (Cervus elaphus). PLoS One 12 (5), e0175134. https://doi.org/10.1371/journal.pone.0175134.

DeCandia, A.L., et al., 2019. Urban colonization through multiple genetic lenses: the city-fox phenomenon revisited. Ecol. Evol. 9 (4), 2046–2060. https://doi.org/10.1002/ece3.4898.

Dertien, J.S., Larson, C.L., Reed, S.E., 2021. Recreation effects on wildlife: a review of potential quantitative thresholds. Nature Conservation 44, 51–68. https://doi.org/10.3897/natureconservation.44.63270.

Díaz, S., et al., 2015. The IPBES Conceptual Framework—connecting nature and people. Curr. Opin. Environ. Sustain. 14, 1–16. https://doi.org/10.1016/j.cosust.2014.11.002.

Díaz-Ruiz, F., et al., 2016. Drivers of red fox (Vulpes vulpes) daily activity: prey availability, human disturbance or habitat structure? J. Zool. 298 (2), 128–138. Available at: https://doi.org/10.1111/jzo.12294.

Dormann, C.F., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

EEA, 2020. Corine land cover. Available at: https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download%20(CLC).

Efford, M.G., Dawson, D.K., 2012. Occupancy in continuous habitat. ECOSPHERE 3 (4). https://doi.org/10.1890/ES11-00308.1.

Erb, P.L., McShea, W.J., Guralnick, R.P., 2012. Anthropogenic Influences on Macro-level Mammal Occupancy in the Appalachian Trail Corridor. https://doi.org/10.1371/journal.pone.0042574.

Fennell, M.J.E., et al., 2023. Assessing the impacts of recreation on the spatial and temporal activity of mammals in an isolated alpine protected area. Ecol. Evol. 13 (11), e10733. https://doi.org/10.1002/ece3.10733.

Fietsnet. Fietsnet. https://www.fietsnet.be/routeplanner/default.aspx (n.d.).

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23. https://doi.org/10.18637/jss.v043.i10.

Gaynor, K.M., et al., 2018. The influence of human disturbance on wildlife nocturnality. Science 360 (6394), 1232–1235. https://doi.org/10.1126/science.aar7121.

Gil-Fernandez, M., et al., 2020. Adaptations of the red fox (*Vulpes vulpes*) to urban environments in Sydney, Australia. J. Urban Ecol. 6 (1), juaa009. https://doi.org/10.1093/jue/juaa009.

Graham, V., et al., 2019. Prioritizing the protection of climate refugia: designing a climate-ready protected area network. J. Environ. Plan. Manag. 62 (14), 2588–2606. https://doi.org/10.1080/09640568.2019.1573722.

Haight, J., Hammill, E., 2020. Protected areas as potential refugia for biodiversity under climatic change. Biol. Conserv. 241, 108258. https://doi.org/10.1016/j.biocon.2019.108258.

Handler, A.M., Lonsdorf, E.V., Ardia, D.R., 2020. Evidence for red fox (*Vulpes vulpes*) exploitation of anthropogenic food sources along an urbanization gradient using stable isotope analysis. Can. J. Zool. 98 (2), 79–87. https://doi.org/10.1139/cjz-2019-0004.

Heinemeyer, K., et al., 2019. Wolverines in winter: indirect habitat loss and functional responses to backcountry recreation. Ecosphere 10 (2), e02611. https://doi.org/10.1002/ecs2.2611.

Hoge Kempen National Park. Hoge Kempen National Park. Available at: https://www.nationaalparkhogekempen.be/en. (Accessed 5 July 2024) (n.d.).

Klimaatstatistieken van de Belgische gemeenten Maasmechelen (nis 73107). Available at: https://www.meteo.be/resources/climatology/climateCity/pdf/climate_INS73107_9120_nl.pdf. (Accessed 15 July 2024) (n.d.).

IPBES, 2019. The global assessment report on biodiversity and ecosystem services. www.ipbes.net.

IUCN, 1994. Guidelines for Protected Area Management Categories.

Kellner, K.F., et al., 2022. ubms: an R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. Methods Ecol. Evol. 13 (3), 577–584. https://doi.org/10.1111/2041-210X.13777.

Kéry, M., 2018. Identifiability in *N*-mixture models: a large-scale screening test with bird data. Ecology 99 (2), 281–288. https://doi.org/10.1002/ecy.2093.

Komoot. Komoot. https://www.komoot.com/ (n.d.).

Larson, C.L., et al., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS One 11 (12), e0167259. https://doi.org/10.1371/journal.pone.0167259.

Larson, C.L., et al., 2019. A meta-analysis of recreation effects on vertebrate species richness and abundance. Conserv. Sci. Pract. 1 (10), e93. https://doi.org/10.1111/csp2.93.

Lasky, M., Bombaci, S., 2023. Human-induced fear in wildlife: a review. J. Nat. Conserv., 126448 https://doi.org/10.1016/j.jnc.2023.126448.

Lewis, J.S., et al., 2021. Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. Ecosphere 12 (5), e03487. https://doi.org/10.1002/ecs2.3487.

MacKenzie, D.I., Nichols, J.D., 2004. Occupancy as a surrogate for abundance estimation. Anim. Biodivers. Conserv. 27 (1), 461–467. https://doi.org/10.32800/abc.2004.27.0461.

MacKenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42 (6), 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x.

MacKenzie, D.I., et al., 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier.

Marion, S., et al., 2024. Mammal responses to human recreation depend on landscape context. PLoS One 19 (7), e0300870. https://doi.org/10.1371/journal.pone.0300870.

Miller, A.B., et al., 2022. From recreation ecology to a recreation ecosystem: a framework accounting for social-ecological systems. J. Outdoor Recreat. Tour. 38, 100455. https://doi.org/10.1016/j.jort.2021.100455.

Moll, R.J., et al., 2020. Dynamic rodent behavioral response to predation risk: implications for disease ecology. Oecologia 192, 67–78. https://doi.org/10.1007/s00442-019-04565-z.

Mols, B., et al., 2022. Recreation and hunting differentially affect deer behaviour and sapling performance. Oikos 2022 (1). https://doi.org/10.1111/oik.08448.

Naidoo, R., Burton, A.C., 2020. Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conserv. Sci. Pract. 2 (10), e271. https://doi.org/10.1111/csp2.271.

Nickel, B.A., et al., 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biol. Conserv. 241, 108383. https://doi.org/10.1016/j.biocon.2019.108383.

Niedballa, J., et al., 2016. camtrapR: an R package for efficient camera trap data management. Methods Ecol. Evol. 7 (12), 1457–1462. https://doi.org/10.1111/2041-210X.12600.

Palmer, M.S., et al., 2017. A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecol. Lett. 20 (11), 1364–1373. https://doi.org/10.1111/ele.12832.

Podgórski, T., et al., 2013. Spatiotemporal behavioral plasticity of wild boar (Sus scrofa) under contrasting conditions of human pressure: primeval forest and metropolitan area. J. Mammal. 94 (1), 109–119. https://doi.org/10.1644/12-MAMM-A-038.1.

Procko, M., et al., 2024. Quantifying impacts of recreation on elk (*Cervus canadensis*) using novel modeling approaches. Ecosphere 15 (6), e4873. https://doi.org/10.1002/ecs2.4873.

Prugh, L.R., et al., 2019. Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biol. Conserv. 232, 194–207. https://doi.org/10.1016/j.biocon.2019.02.011.

Richter, L., et al., 2020. So close and yet so different: the importance of considering temporal dynamics to understand habitat selection. Basic and Applied Ecology 43, 99–109. https://doi.org/10.1016/j.baae.2020.02.002.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14 (3), 322–337. https://doi.org/10.1198/jabes.2009.08038.

Rozylowicz, L., et al., 2024. Occupancy and N-mixture modeling applications in ecology: a bibliometric analysis. Global Ecology and Conservation, e02838. https://doi.org/10.1016/j.gecco.2024.e02838.

Salvatori, M., et al., 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. https://doi.org/10.1007/s13280-022-01825-w.

Schulze, K., et al., 2018. An assessment of threats to terrestrial protected areas. Conserv. Lett. 11 (3), e12435. https://doi.org/10.1111/conl.12435.

Shannon, G., Lewis, J.S., Gerber, B.D., 2014. Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data. PeerJ 2, e532. https://doi.org/10.7717/peerj.532.

Statbel. Statbel. https://statbel.fgov.be/nl/themas/bevolking/structuur-van-de-bevolking/bevolkingsdichtheid#figure (n.d.).

Stokely, T.D., Kormann, U.G., Betts, M.G., 2020. Synergistic effects of wild ungulates and management intensification suppress native plants and promote exotics. For. Ecol. Manag. 460, 117772. https://doi.org/10.1016/j.foreco.2019.117772.

Storm, G.L., et al., 1976. Morphology, reproduction, dispersal, and mortality of midwestern red fox populations. Wildl. Monogr. 49, 3–82. http://www.jstor.org/stable/3830425.

Suraci, J.P., et al., 2021. Disturbance type and species life history predict mammal responses to humans. Glob. Chang. Biol. 27 (16), 3718–3731. https://doi.org/10.1111/gcb.15650.

Sytsma, M.L.T., et al., 2022. Low levels of outdoor recreation alter wildlife behaviour. People and Nature 4 (6), 1547–1559. https://doi.org/10.1002/pan3.10402.

Tolon, V., et al., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Can. J. Zool. 87 (12), 1129–1137. https://doi.org/10.1139/Z09-101.

Volenec, Z.M., Dobson, A.P., 2020. Conservation value of small reserves. Conserv. Biol. 34 (1), 66–79. https://doi.org/10.1111/cobi.13308.

Weterings, M.J.A., et al., 2024. Insights from a 31-year study demonstrate an inverse correlation between recreational activities and red deer fecundity, with bodyweight as a mediator. Ecol. Evol. 14 (4), e11257. https://doi.org/10.1002/ece3.11257.

Wevers, J., et al., 2020. Trading fear for food in the Anthropocene: how ungulates cope with human disturbance in a multi-use, suburban ecosystem. Sci. Total Environ. 741, 140369. https://doi.org/10.1016/j.scitotenv.2020.140369.

Zeller, K.A., et al., 2024. Experimental recreationist noise alters behavior and space use of wildlife. Curr. Biol. https://doi.org/10.1016/j.cub.2024.05.030.