Trading fear for food in the Anthropocene: How ungulates cope with human disturbance in a multi-use, suburban ecosystem

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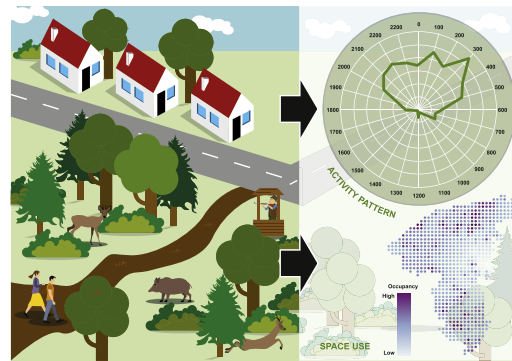[b] Research Institute Nature and Forest, Brussels 1000, Belgium
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HIGHLIGHTS

- We studied wild boar and roe deer activity and space use in an urban protected area.
- Wild boar were nocturnal, while roe deer were crepuscular.
- Forest availability was the main driver of wild boar and roe deer space use.
- Behavioural adaptations resembled those found in similarly urbanized landscapes.
- Wild boar and roe deer are able to thrive despite intensive recreation and hunting.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Resource distribution, predation risk and disturbance in space and time can affect how animals use their environment. To date few studies have assessed the spatiotemporal trade-off between resource acquisition and avoidance of risks and human disturbance in small protected areas embedded in an urban matrix. A better understanding of the forage-safety trade-off in urban protected areas (UPA) is key to the design of evidence-based approaches to deal with the ever-increasing human-wildlife impacts typical of UPA. Herein, we analyzed camera trap data to evaluate how two ungulate species trade fear for food in a 60 km² human-dominated UPA without natural predators. We found that wild boar (*Sus scrofa*) were predominantly active at night, while roe deer (*Capreolus capreolus*) showed a typical bimodal crepuscular activity pattern. Occupancy analysis indicated that deciduous forest and the presence of high seats for hunting played an important role in determining the space use of wild boar. For roe deer, we found indications that the presence of forest influenced space use, although the null model was retained among the top ranked models. Our results confirm that wild boar and roe deer are able to thrive in heavily human dominated landscapes characterized by intensive recreational use and hunting, such as protected areas embedded in an urban matrix.

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1. Introduction

In the present Anthropocene era, human disturbance mimics and can even exceed the effects of predation risk by apex predators (Ciuti et al., 2012; Zbyryt et al., 2017). Most animals tend to respond to

human disturbance by shifting their activity patterns or by altering habitat use to avoid humans on a temporal (Dupke et al., 2017; Gaynor et al., 2018; Oberosler et al., 2017; Richter et al., 2020) or spatial scale (Lone et al., 2015; Kays et al., 2016). Urbanization has led to severe habitat fragmentation, degradation and loss, and generally has brought humans and wildlife in close proximity (DeStefano and DeGraaf, 2003). Such proximity can result in severe human-wildlife interactions affecting the well-being of both parties (Treves et al., 2006). Large visitor numbers, as well as logging and hunting can add up to various degrees of human disturbance in space and time within protected areas (Marchand et al., 2014; Tolon et al., 2009). While prior research has elucidated the effects of several forms of human disturbance in large reserves and stretches of natural habitat (Ciuti et al., 2012; Kays et al., 2016), it is still poorly known how wildlife copes with human disturbance when their habitat is enclosed within an urban matrix.

Hunting, as a form of outdoor recreation as well as a management tool, does not only directly numerically impact wildlife populations, but it also induces fear that can influence game behavior (Cromsigt et al., 2013). Non-consumptive recreation, such as hiking, biking, and horseback riding, is assumed to be less harmful to wildlife. However, non-lethal disturbance has been found to affect many taxonomic groups, among which birds and ungulates (Bötsch et al., 2017; Larson et al., 2016). Due to the intensive human use of urban protected areas (UPA), the trade-off between risks and food availability is likely exacerbated in these situations. Considering the goal of UPA to provide benefits for both wildlife and humans, management requires to balance the needs of both. UPA managers need to simultaneously conserve endangered species and provide people the opportunity to experience nature while also minimizing human-wildlife conflict at the borders of the protected area (Trzyna, 2014). In addition to understanding a species' demographics, knowledge of its spatial and temporal distribution provides valuable ecological information for directing species-specific management (Guisan and Thuiller, 2005). This information is necessary to understand the possible consequences of different management scenarios such as hunting regulations or temporal and/or spatial access restrictions to particular parts of the park.

Two species known to thrive in European human-dominated landscapes and requiring management are wild boar [*Sus scrofa* (Linnaeus, 1758)] and roe deer [*Capreolus capreolus* (Linnaeus, 1758)](Linnell et al., 2020). Wild boar and roe deer populations have increased extensively in the recent decades, and their plasticity allowed them to adjust to human presence (Cahill et al., 2003; Castillo-Contreras et al., 2018; Ditchkoff et al., 2006; Linnell et al., 2020; Morelle et al., 2016; Stillfried et al., 2017). Wild boar are diurnal in undisturbed environments but human pressure in general causes wild boar to become more crepuscular or even nocturnal (Fischer et al., 2016; Keuling et al., 2008; Podgorski et al., 2013). Continuous high human pressure tends to lead to a spatial shift in wild boar habitat use to avoid disturbed areas (Fischer et al., 2016; Tolon et al., 2009). However, landscape variables such as habitat, food availability and cover seem to modulate the magnitude of this response (Fattebert et al., 2017). Roe deer activity shifts from a crepuscular pattern with regular daytime activity to a more nocturnal activity pattern under human disturbance (Bonnot et al., 2013; Oberosler et al., 2017). Roe deer are also found to adapt their habitat selection to human disturbance by shifting from open habitats to more forested habitats, depending however highly on the type of landscape available (Bonnot et al., 2013; Benhaiem et al., 2008). While several studies have been conducted on the effect of human disturbance on the spatial or temporal behavior of wild boar and roe deer, to our knowledge, none of them consider the trade-off between resources and human disturbances within small UPA.

Herein, we used camera trap data to evaluate the activity and space use patterns of wild boar and roe deer in response to habitat and human disturbance in a small protected area (60 km^2). We hypothesized that due to the extensive degree of utilization of the urban protected area by humans, both species would show adaptations in their activity pattern (H1) and habitat selection (H2). First, we predicted that wild boar would show a high degree of activity at dusk and at night, while
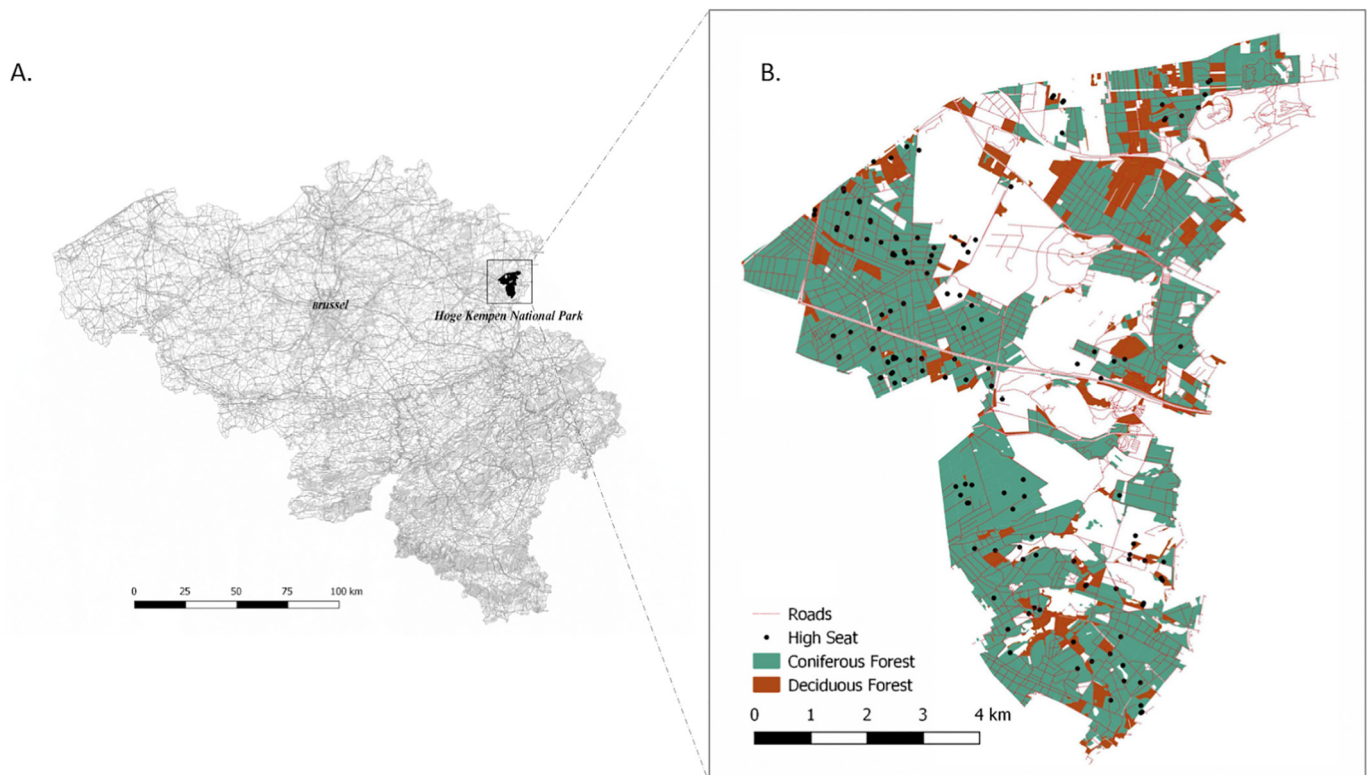

Fig. 1. Location of NPHK, eastern Belgium, 2018 (A). Inset (B) shows the distribution of roads, high seats, coniferous forest and deciduous forest in the study area, NPHK, Belgium, 2018.

roe deer would show a high degree of activity during the night (P1). Second, we predicted that different food preferences would lead roe deer and wild boar to use different habitats, but that space use would be primarily driven by human disturbance caused by risks associated with hunting and recreation (P2).

2. Methods

2.1. Study area

Hoge Kempen National Park (NPHK, ca 60km², Fig.1), northeastern Belgium, was officially gazetted as a national park in 2006. To optimize conservation, NPHK management adopted an approach with zones dedicated to nature conservation, to recreation or both. NPHK has six heavily-visited entrance gates, only one of which actually gives direct access to the park. The estimated number of visitors to the park exceeds 300′000 visitors each year (Van Den Bosch, 2012). While few roads are accessible to cars, recreational pressure in the park is considerably high due to its vast network of cycling paths (~ 240 km) and hiking trails (~ 200 km) (Fig. 1). The park consists of large areas of planted pine forest (41% covered with *Pinus sylvestris* and *Pinus nigra*). These areas are gradually being transformed into a more natural deciduous forest dominated by *Quercus* spp. and *Betula spp.* (9%). It also contains stretches of valuable dry (*Calluna sp.*) and wet (*Erica* sp. and *Myrica sp.*) heathland (11%), as well as patches of shrub vegetation (7%), dominated by *Molinia sp.*

Flemish hunting laws state that roe deer hunting is restricted to a predefined hunting bag. Only day time hunting is allowed and the hunting season is confined to a doe and fawn season between January and March and a buck only season from May until September. Wild boar can be hunted year round, and in contrast to roe deer, can be hunted during the day and the night (Agency for Nature and Forest, 2020). As different parts of the park are owned by different parties [Agency for Nature and Forest (ANB), municipality or private], hunting pressure varies significantly throughout the park and ranges from no hunting to hunting all year round (Fig. A1). For private leased areas (Fig. A1), wild boar hunting bags in the period 2014–2019 ranged from a minimum of 107 to a maximum of 221 individuals while roe deer hunting bags ranged from 205 to 328 individuals (Research Institute for Nature and Forest, 2020b). In parts of the park managed by ANB (Fig. A1), a total of 85 roe deer and 128 wild boar were shot between 2017 and 2019 (Research Institute for Nature and Forest, 2020a).

2.2. Camera-trap placement

We used a systematic-random sampling design to place camera traps. We divided the study area into 40 compartments of approximately 1.5 km², and superimposed a grid of 300 m × 300 m on these compartments. Each month, we randomly selected one grid cell within each of the 40 compartments, and used their midpoints as the sampling locations to set up a single camera trap (Reconyx HC600 Hyperfire) at the nearest tree. We did not use bait nor did we select for trails. We placed camera traps on a height of 50 cm facing North without altering the surroundings unless some vegetation was directly in front of the camera. Cameras were set up to the fastest trigger speed for a burst of ten pictures without delay between triggers and with time-lapse pictures every 12 h to control for malfunction. We deployed camera traps for three consecutive weeks and relocated them in the fourth week, which resulted in 13 deployments per year. 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). For this manuscript, we sampled 480 locations from May 8, 2017 to April 13, 2018 (Fig. B1). This results in a total of 11,603 24-h observation periods. We discarded data from 15 (3.1%) locations due to camera malfunction.

2.3. Activity patterns

We evaluated the activity patterns of wild boar, roe deer and humans using the *CamtrapR* (Niedballa et al., 2016) and *activity* packages (Rowcliffe et al., 2014). We used average anchoring as outlined by Vazquez et al. (2019) to correct for the variation in day length during the year. We plotted uncorrected activity as the count of observations clustered per hour. Next we plotted corrected activity as the overlapping of the kernel density functions of the species and calculated the coefficient of overlap ($\hat{d}$) between activity patterns of wild boar, roe deer and humans (Rowcliffe et al., 2014).

2.4. Space use

We modelled the impact of resources and human disturbance on the space use of wild boar and roe deer in an occupancy framework (MacKenzie et al., 2017). Occupancy models are frequently used to study the distribution of animals in relation to human pressure and landscape covariates (e.g. Kays et al., 2016; Oberosler et al., 2017). While occupancy is often used in large landscape sampling designs (e.g. Steenweg, 2016), we used occupancy models on observations collected in grid cells smaller than the animals' home ranges. Based on the assumption that both species move randomly in and out of the sampling grid cells, we therefore interpret occupancy as a measure of habitat use rather than occupancy *per se* (MacKenzie et al., 2017).

We constructed detection histories for each sample location using *CamtrapR* (Niedballa et al., 2016). Before fitting occupancy models, we screened for collinearity among resource variables and used a threshold Spearman rho $|r_s| = 0.7$ (Dormann et al., 2013). We used the R-package *Unmarked* (Fiske and Chandler, 2017) to rank our *a priori* defined models (Table 1). Applying a two-step approach (MacKenzie et al., 2017) we first selected the best detection model and subsequently used this to fit the best occupancy model. Model selection throughout was based on Akaike's Information Criterion (AIC), while the importance of covariates was determined by comparing AIC weights. When

Table 1

A priori occupancy models and predictions of the effect of human activities and landscape on wild boar and roe deer space use in NPHK, Belgium, 2018. DOY = Day Of Year, percDec = percentage Deciduous forest, percCon = percentage Coniferous forest, distHS = distance to the nearest High Seat, distR = distance to the nearest Trail.

Model name	Model structure	Prediction
Null	~p(sine(DOY) + cosine(DOY) ~ Ψ(.)	No selection
Deciduous	p(sine(DOY) + cosine(DOY) ~ Ψ (percDec)	Selection for food (both species)
Coniferous	~p(sine(DOY) + cosine(DOY) ~ Ψ (percConf)	Selection for food (roe deer)
Forest	~p(sine(DOY) + cosine(DOY) ~ Ψ (percDec + percConif)	Selection for food (roe deer)
Hunting	~p(sine(DOY) + cosine(DOY) ~ Ψ (distHS)	Avoidance of high seats
Recreation	~p(sine(DOY) + cosine(DOY) ~ Ψ (distR)	Avoidance of trails
Human	~p(sine(DOY) + cosine(DOY) ~ Ψ (distHS + distR)	Avoidance of high seats and trails
Hunting & Food Wild Boar	~p(sine(DOY) + cosine(DOY) ~ Ψ (distHS + percDecid)	Avoidance of highs seats, selection for food
Hunting & Food Roe deer	~p(sine(DOY) + cosine(DOY) ~ Ψ (distHS + percDecid + percConif)	Avoidance of highs seats, selection for food
Human & Food Wild boar	~p(sine(DOY) + cosine(DOY) ~ Ψ (distHS + distR + percDecid)	Avoidance of high seats and trails, selection for food
Human & Food Roe deer	~p(sine(DOY) + cosine(DOY) ~ Ψ (distHS + distR + percDecid + percConif)	Avoidance of high seats and trails, selection for food

top ranked models did not differ significantly (Δ AIC < 2) we used model averaging (R-package *AICcmodavg*; Mazerolle, 2019) to analyze the functional response between the most important covariates and occupancy based on the averaged top models. All statistical procedures were performed in the R environment (R Core Team, 2019).

We modelled detection using three different possible detection covariates: month of the year, day of the year or transformed day of the year. The date-related variables used in the detection model allowed to correct for possible variation in detectability as a consequence of variation throughout the year in cover, temperature, foliage or animal behavior (Richter et al., 2020). To account for circularity of time, we sine- and cosine transformed Julian dates (Richter et al., 2020; Zar, 2010). We modelled occupancy with selected candidate environmental covariates to account for food availability and human disturbance (Table 1). We identified deciduous forest as food-rich habitat for wild boar and deciduous and coniferous forest as food-rich habitat for roe deer based on the presence of preferred plant species in both habitats (Cornelis et al., 1999; Henry, 1978; Massei et al., 1996). We used the biological valuation map of Belgium (Vriens et al., 2011) to characterize the landscape. For each grid cell, we extracted the percentage of deciduous and coniferous forest in a Geographic Information System (GIS; ArcMap Desktop version 10.1 ESRI, 2011).

We used distance to hiking trails and cycling paths as a covariate for recreational pressure (Bonnot et al., 2013; Kays et al., 2016). For this purpose, we calculated the distance of the center of each grid cell to the nearest trail or path. We mapped the exact locations of high seats, which are elevated stands from which wild boar and roe deer are hunted. As high seats can be considered a source of fear even when hunting is not taking place (Cromsigt et al., 2013), we used the distance of the center of each grid cell to the nearest high seat as a surrogate for hunting pressure. As the high seats on land owned by ANB are solely used for hunting in January and February, and thus impose little risk in the rest of the year, they were only included in the dataset for these two months.

3. Results & discussion

3.1. Activity patterns

3.1.1. Wild boar

Wild boar in NPHK exhibit an activity range between 18:00 and 06:00 h, but show a marked activity peak at 03:00 h (Fig. 2; Fig. C1). Wild boar activity overlapped only 17% with humans (ȡ=0.17), who are observed to be most active between 09:00 and 17:00 with a peak at 15:00. These results suggest that wild boar in the area apparently utilize the cover of dark to avoid interactions with humans, which is in line with our prediction (P1). Other studies confirmed that in areas with human disturbance the species is indeed frequently more active at night in order to circumvent the risks associated with human presence (Keuling et al., 2008; Fischer et al., 2016; Gaynor et al., 2018; Podgorski et al., 2013).

3.1.2. Roe deer

Activity of roe deer followed a crepuscular pattern ranging from 17:00 until 08:00 h with a peak at dusk and dawn. The highest activity was registered at dawn (Fig. 2; Fig. C1), and showed 40% overlap of (ȡ= 0.40) with humans, while not displaying spatial segregation (Fig. D1; see *3.2.2 Roe deer* below). Roe deer in our study area appeared to display activity patterns similar to other areas in Europe, as reported by e.g. Pagon et al. (2013) and Oberosler et al. (2017). Activity overlap indicates roe deer were frequently active at the same time as humans, although crepuscular peaks of roe deer fell outside the human activity range (Fig. 2). Thus, contrary to our prediction (P1), roe deer did not seem to be nocturnal in response to human disturbance. While increased nocturnality has been previously found in roe deer in response

to human disturbance, roe deer is also known to use more forested, and therefore secluded, habitats during the day to avoid human contact (Bonnot et al., 2013).

Human disturbance can have a strong effect on the activity patterns of mammals in general (Gaynor et al., 2018), and several studies have confirmed this effect for European ungulates other than roe deer and wild boar. For example, red deer [*Cervus elaphus* (Linnaeus 1758)] in an urban green area in the Netherlands showed a similar two peaked crepuscular activity pattern but were mostly active at night due to human disturbance (Ensing et al., 2014). Increased nocturnality was also found in mouflon [*Ovis orientalis* (Linnaeus 1758)] in response to hunting and tourism in southern France (Marchand et al., 2014). Similarly, a low amount of activity overlap was found between red deer and humans in the Alps, while increasing human disturbance was linked to increased nocturnality in chamois [*Rupicapra rupicapra* (Linnaeus 1758)] (Oberosler et al., 2017).

3.2. Space use

3.2.1. Wild boar

For wild boar, a "Circular" detection model including sine- and cosine-transformed day of the year ranked better than the null model and the "Month" or "Julian" models (Table A1). The four top ranked occupancy models, having differences in AIC values smaller than 2, were "Hunting and Food", "Deciduous", "Recreation" and "Human and Food". According to AIC weights of the top ranked models, the percentage of deciduous forest and distance to high seats are the most important factors, while distance to trails had a negligible effect on wild boar space use (Table 2, Fig. 3a).

Our occupancy models indicate that wild boar space use was directed towards deciduous forest (Fig. 3a). We consider deciduous forest to be a proxy for food availability for wild boar, as it harbors nut bearing trees that provide high energy food such as acorns, chestnut and beechnut (Massei et al., 1996). Nuts, however, are primarily available in autumn. Although our findings show the general importance of deciduous forest in directing space use of wild boar, future research would benefit greatly from including a temporal component to allow analyzing the importance of changes in habitats providing food resources.

Contrary to our second prediction (P2), we found a negative relationship between wild boar occupancy and the distance to high seats (Fig. 3a). This would imply that places closer to high seats are used more than places further away from high seats. During the study period, we often observed bait and scent marks used by hunters to lure the
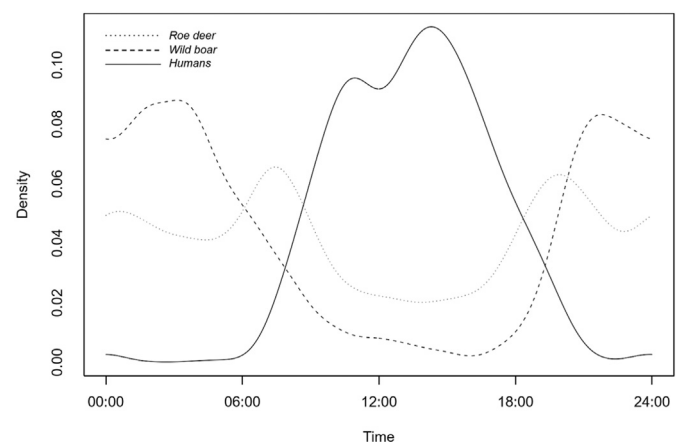

Fig. 2. Activity density distribution of Roe deer, Wild boar and Humans in NPHK, Belgium, 2018.
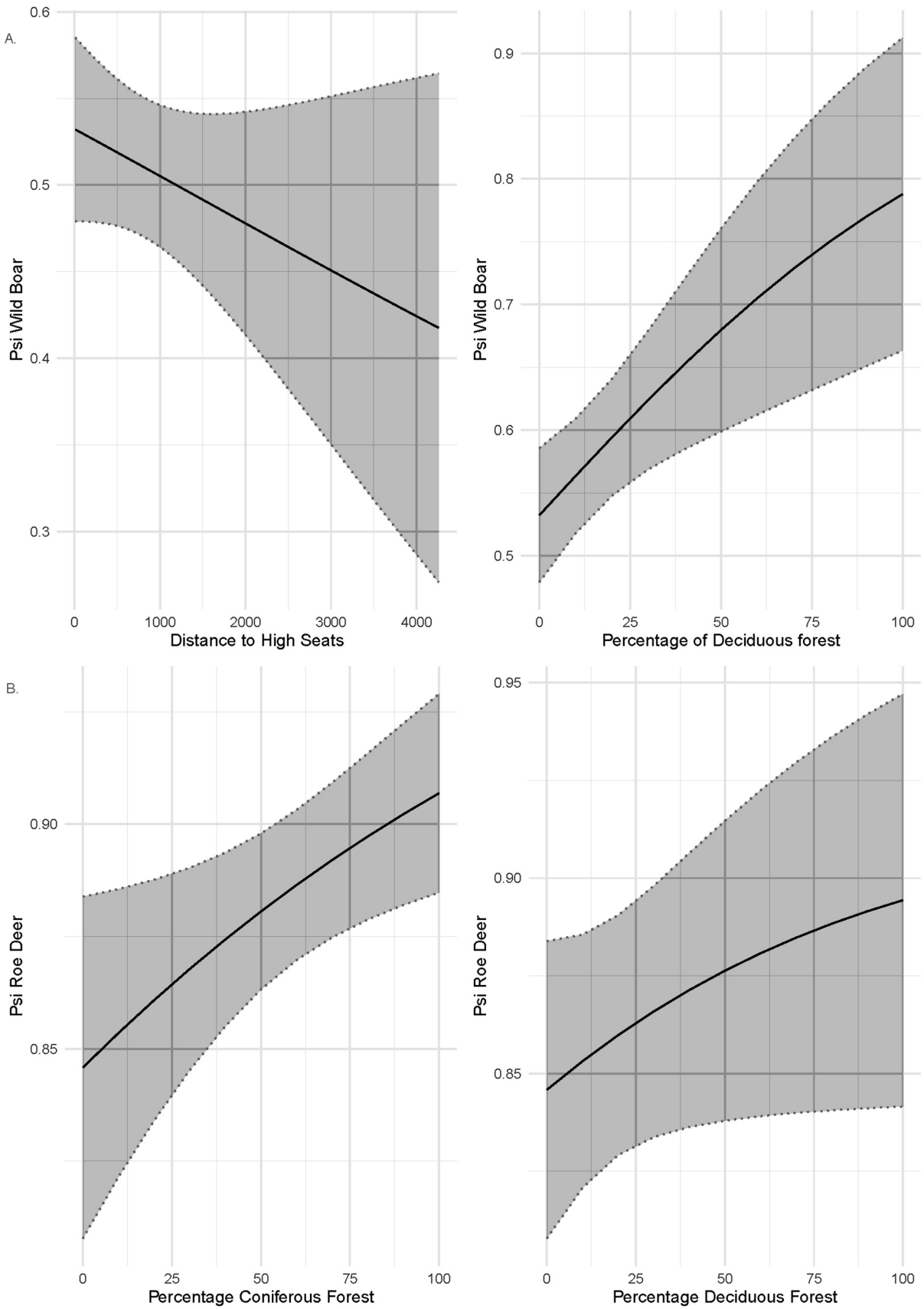
Fig. 3. Predictions of the most important covariates influencing wild boar (a) and roe deer (b) occupancy based on the averaged top models in NPHK, Belgium, 2018.

Table 2
Model selection of the candidate occupancy models regarding the effect of human activities and habitat on wild boar and roe deer space use in NPHK, Belgium, 2018.

Species	Model Name	Parameters	AIC	Delta AIC	AIC weights
Wild boar	Hunting & Food	6	4389.44	0	0.285
	Deciduous	5	4390.32	0.88	0.183
	Hunting	5	4390.70	1.25	0.152
	Human & Food	7	4390.87	1.43	0.140
	Forest	6	4391.92	2.48	0.082
	Human	6	4392.88	3.43	0.051
	Null	4	4393.33	3.88	0.041
	Coniferous	5	4393.71	4.26	0.034
	Recreation	5	4393.82	4.38	0.032
Roe deer	Forest	6	11,476.07	0	0.35
	Coniferous	5	11,476.10	0.033	0.34
	Null	4	11,477.21	1.141	0.2
	Deciduous	5	11,478.37	2.309	0.11
	Hunting	5	11,816.13	340.061	<0.001
	Recreation	5	11,816.18	340.118	<0.001
	Human	6	11,818.13	342.061	<0.001
	Hunting & Food	7	11,820.13	344.061	<0.001
	Human & Food	8	11,822.13	346.061	<0.001

animals to open areas near high seats. Baits and scent lure are known to modify space use of animals (Braczkowski et al., 2016; Mills et al., 2019), and could explain why wild boar were apparently selecting for areas in proximity to high seats. Wild boar in our study area were therefore not avoiding hunting areas spatially, either because they are mostly active at night, because hunting pressure was too low to induce a fear response (Cromsigt et al., 2013; Tolon et al., 2009), or because high seats were so prevalent in our study area that they could not be avoided spatially (Table B1).

We suggest that space use of wild boar in respect to human disturbance could be further elucidated by incorporating additional fine-scale landscape variables, such as the distribution of hiding cover provided by shrubs that could have a pronounced influence on the fear effects brought about by human disturbance (Rutten et al., 2019). Additionally, temporal models could contribute to explaining in detail the impact of a fluctuating hunting pressure on the perception of the risks due to human disturbance (Tolon et al., 2009).

3.2.2. Roe deer

For roe deer, the "Month" detection model outranked the others (Table A1). However, modelling roe deer occupancy with detection varying by month of the year resulted in convergence failures for several of the *a priori* models. We therefore used the second best "Circular" model to model detection in all further occupancy analyses, as for wild boar. The top ranking occupancy model was the "Forest" model including percentage of coniferous forest and percentage of deciduous forest (Table 2). This model was not significantly more parsimonious than the "Coniferous" model or the null model (ΔAIC<2). AIC weights indicate however that, although not different from the null model, the presence of coniferous forest and deciduous forest did have somewhat of an influence on roe deer space use (Table 2, Fig. 3b).

Fig. 3 represents the relationship between occupancy and the percentages of coniferous and deciduous forest for roe deer. We consider coniferous as well as deciduous forests to be a proxy for food for roe deer in different seasons as they provide resources in the form of blueberries and blackberries in autumn while ferns, grasses and young trees such as American bird cherry (*Prunus serotina*), rowan (*Sorbus aucuparia*) and American oak (*Quercus rubra*) provide fresh leaves and are available throughout spring and summer (Henry, 1978).

Furthermore, for roe deer, our results contradict our prediction (P2) as we found no significant effect of hunting pressure or recreation on their space use, given than none of the models including covariates of human activities were selected (Table 2). Note, however, that trails in our study area are so numerous that the distance from the center of a

grid cell was on average only 51 m from a trail, with a maximum distance of 335 m (Table B1). Bonnot et al. (2013) found that distance to road did have an effect on roe deer space use. However, these authors reported distances ranging between 0.2 m and 818 m, with an average distance of 247 m. Spatial avoidance of trails, and therefore recreation, may therefore simply not be feasible for roe deer at our study site.

Several negative effects of recreation have been demonstrated in ungulates (Larson et al., 2016). Roe deer, as well as red deer can exploit forested habitats in order to avoid human disturbance during the day while using open habitat at night (Bonnot et al., 2013; Richter et al., 2020). Red deer in the Alps were found to avoid places with high human activity and human settlements in general (Oberosler et al., 2017). Moreover, hunting, whether for subsistence, sport or management, was shown to generally influence different aspects of large herbivore physiology and behavior, including space use (Cromsigt et al., 2013). For example, red deer were found to shift their space use to habitat with more dense cover in response to hunting (Fattebert et al., 2019; Lone et al., 2015). An indirect effect of human activities on the spatial behavior of roe deer in our study can thus not be excluded, as the positive effect of forest on space use could be the result of a selection for cover to hide from humans. Future studies could separately model space use during the day and night in a hunted and non-hunted context to elucidate whether selection of forest habitat would remain under low human disturbance.

4. Conclusion

In a world becoming progressively more human-dominated, understanding the impact of human pressure on wildlife behavior will become increasingly important to mitigate human-wildlife conflicts. When looking at activity patterns of roe deer and wild boar in our study area, we found that wild boar were mostly active during the night and have a minimal temporal overlap with humans. Roe deer showed a typical bimodal crepuscular activity pattern and a high temporal overlap with humans. Both wild boar and roe deer showed trends for selecting forest habitats. Their space use does not seem to be impacted negatively by human activities, although responses may be hidden by the selection for cover in forest habitats providing seclusion from humans. Our study highlights the opportunism of wild boar and roe deer, suggesting that the local availability of forest habitat affects their ability to thrive in a human dominated landscape characterized by intensive recreational use combined with fluctuating hunting pressure.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.140369.

CRediT authorship contribution statement

Jolien Wevers: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Julien Fattebert:** Conceptualization, Methodology, Writing - review & editing. **Jim Casaer:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition. **Tom Artois:** Supervision. **Natalie Beenaerts:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

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.

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