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Quiet islands in a world of fear: Wolves seek core zones of protected areas to escape human disturbance

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A B S T R A C T

The Anthropocene continuously escalates the challenges and threats faced by large carnivores in human-dominated landscapes. Given their unique conservation and management requirements, detailed insights into their behaviour in relation to human-induced risks are crucial to designing landscapes of coexistence for people and predators, containing key features such as nature conservation areas. Adaptations like selection or avoidance of areas at certain times reveal the dynamic perception of large carnivores to risk-landscapes and the trade-offs with potential resources. This study investigates these ideas by applying a habitat-selection approach to GPS collared wolves in Belovezhskaya Pushcha National Park (Belarus) to quantify fine-scale avoidance of human disturbance. Our results indicate that wolves selected strongly for areas of higher nature protection within the national park. They also avoided human disturbance from settlements and roads, but mediated their behaviour depending on the shifting risk throughout the day and night. They selected for more open areas during darkness. Seasonal and sex-based differences shifted avoidance, such as females being more avoidant of settlements. This suggests evidence of a successful anti-predator strategy against humans. Our study offers some of the most detailed and novel insights into wolf spatio-temporal avoidance of disturbance in the context of protected areas, which is imperative for fine-tuning management measures for continued coexistence and effective conservation of this functionally important species.

1. Introduction

Large carnivores, like essentially all wild mammals, must trade-off resources (food, shelter, mates) with avoidance of human-induced disturbance and mortality risks (Basille et al., 2009; Ciucci et al., 2018; Fahrig, 2007; Mancinelli et al., 2019). This human-induced landscape of risk establishes a behavioural interplay between humans and large carnivores resembling that of predator-prey interactions and classic landscape of fear dynamics (Laundre et al., 2010; Ordiz et al., 2011, 2021; Oriol-Cotterill et al., 2015). Humans are commonly considered as “super-predators” of large carnivores (Bryan et al., 2015; Smith et al., 2017; Suraci et al., 2019) and consequently spatiotemporal avoidance of humans is a distinct expected outcome i.e. animals interpreting predator risk should allocate their behaviours accordingly (Lima and Bednekoff, 1999a, 1999b). However, in human-dominated landscapes, work quantifying large carnivore behaviour is especially pertinent given their socio-political importance and the necessity for fine-tuned management compared to other species (Kuijper et al., 2019; Trouwborst, 2010).

Wolves (*Canis lupus*) have the largest distribution of any large carnivore in the northern hemisphere (Ripple et al., 2014). In Europe, wolves are recovering their former distribution due to legal protection and shifting human densities (Boitani and Linnell, 2015; Chapron et al., 2014; Cimatti et al., 2021; Linnell et al., 2001; Trouwborst, 2010) that

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facilitate their natural re-expansion. Despite extensive wolf reestablishment in many European regions and the continuous presence of wolves in others, quantified impacts of human disturbance on wolf behaviour are still sparse given the species importance (e.g. Kuijper et al., 2019). Understanding wolf behaviour and their adaptations (i.e. spatiotemporal responses) to coexistence with humans is pivotal to improve wolf management and conservation (Kuijper et al., 2019; Mech, 2017). This necessitates monitoring and research to understand how they trade-off resources in human-dominated landscapes for continued coexistence.

Habitat selection is an adaptive behaviour that allows animals to balance the costs and benefits of resources available to them through their movement (Basille et al., 2013; Gehr et al., 2017), and offers a tried-and-tested framework for uncovering the importance of factors relating to risks and resources in the landscape (Mao et al., 2005). Studies of wolf habitat selection in Europe have stemmed from Italy quantifying the territory and rendezvous site selection in relation to tree cover and human disturbance (Ciucci et al., 2018) or anthropogenic features in the landscape across seasons and behaviours (Mancinelli et al., 2019). In Fennoscandia, recent studies have examined wolf avoidance of anthropogenic features in the landscape dependent on season and day or night (Carricondo-Sanchez et al., 2020a, 2020b), as well as show how anthropogenic features are still avoided when bears are present (Ordiz et al., 2020). Much of this work is built upon the dynamic behaviours of wolves in relation to roads dependent on behavioural processes and scale conducted by Zimmermann et al. (2014). In Greece, wolves selected rendezvous sites within their home ranges away from roads and villages (Iliopoulos et al., 2014). In Portugal, Lino et al. (2019) examined how fire disturbance does not greatly affect wolf persistence and breeding-site selection and in Spain, Llaneza et al. (2016) examined the importance of tree cover for wolves. Human infrastructure, such as roads and settlements, is a nearly universal source of disturbance in European wolf movement studies (Ciucci et al., 2018; Jędrzejewski et al., 2005; Mancinelli et al., 2019; Zimmermann et al., 2014). In Bialowieza Forest (Poland), Theuerkauf et al. (2003a, 2003b) noted that spatiotemporal segregation of wolves and humans is an adaptation of wolves that promotes coexistence, while still allowing wolves to acquire food. Indeed, photoperiod and human-induced mortality were identified among the most important variables in driving wolf activity patterns (Theuerkauf, 2009). However, analysing the fine-scale temporality of habitat selection of wolves has, to our knowledge, only been done by classifying locations into day or night (Carricondo-Sanchez et al., 2020a, 2020b; Mancinelli et al., 2019; Zimmermann et al., 2014) and as such, the true nature of fine-scale avoidance of human disturbance may be blurred. Work examing fine-scale avoidance is therefore novel and required to confirm previous work on wolves in Europe and around the world.

European landscapes also include protected areas (PAs) within which wolves will undoubtedly establish where their presence is not already sporadic or permanent (Pavel Hulva, unpublished results; but see Reinhardt et al., 2019). Approximately 18.5 % of EU land area was protected under the Natura 2000 network in 2020 (Diserens et al., 2017; European Environment Agency, 2022), but it should be noted not all European national parks are protected under this network. The limited size of PAs and the nature of wolf territories implies nearly all wolves in Europe inhabit a land-sharing matrix of PAs and unsympathetic land uses (Santini et al., 2016). Within this matrix they contend with many facets of human disturbance (Cimatti et al., 2021; Cretois et al., 2021; López-Bao et al., 2017). PAs can increase the prey base and prevent the direct persecution of wolves (Apollonio et al., 2004), but few PAs are alone large enough for viable populations of large carnivores (Wolf and Ripple, 2018). The importance of PAs as refugia for wolves in Europe (and the world) is under-represented in the scientific literature (Diserens et al., 2017; Mech, 2017), despite their obvious importance for conservation. A better understanding of how wolves use PAs and their vicinity is therefore important for their conservation management. Based on such knowledge PAs could serve an even more important role for wolves in the future, or be adapted appropriately given their importance as refugia is adequately quantified.

Wolf presence has been continuous in time in numerous landscapes, including PAs, in eastern Europe and Baltic states (e.g. Belarus, Poland, Ukraine, Latvia, Lithuania, Estonia), highlighting an interesting contrast to their reestablishment in other European regions. It is of interest that many of these countries maintain wolf hunting or population control (outside protected areas). This pressure may push wolves towards distinct behavioural strategies to avoid persecution and interactions with humans. Our study is centered around the primeval Bialowieza Forest complex, a transboundary PA network between Belarus and Poland considered the largest remnant of lowland old-growth forest in Europe. It is one such place that has been a stronghold for wolves, with its current inhabitants forming part of the Baltic population (Szewczyk et al., 2019). This makes it an important case study for understanding wolf ecology and behaviour as the history and ecology make it possible to test multiple hypotheses (e.g. Kuijper et al., 2016). It is also crucial for understanding the transboundary conservation of wolves due to the differing legislation which governs their protection, or lack thereof (i.e. strictly protected in Poland (Trouwborst, 2010), minimal protection in Belarus (Fenchuk et al., 2017)), and the impact of "hard borders" (or fences) on wolves (Bull et al., 2019; Kuijper et al., 2019). Transboundary wolf conservation is a common theme for many European countries (e.g. Wolf LIFE Alps, Scandinavia, Bavarian-Bohemian Forest Ecosystem) due to the dispersal capability of wolves and their large territories, highlighting the importance of transferable research for the conservation and management of the species across all European contexts (Boitani and Linnell, 2015; Kuijper et al., 2019).

Here we examine for the first time the effect of a strictly protected area on the fine-scale spatio-temporal habitat selection of GPS-tagged wolves avoiding human disturbance in western Belarus. We simultaneously predicted that wolves (1) select for core zones over other park zonation and areas outside of the national park (low human disturbance in areas with an higher protections staus) while they (2) avoid human infrastructure during the day (higher human disturbance closer to roads during the day), and (3) mediate this behaviour given the available tree cover (closer to disturbance with high tree cover that provides better opportunities to hide), and (4) show strong avoidance of human infrastructure seasonally (depending on when humans are more active). We also predicted (5) sex-based differences between wolf perception of human risk (males showing taking greater risk than females for dispersal or hunting opportunities (Milleret et al., 2019)). To investigate these aspects, we combine fine-scale satellite telemetry from wolves with environmental, management, and human-disturbance factors that quantify the importance of protected landscapes for wolves and wolf avoidance of humans in a European landscape.

2. Materials and methods

2.1. Study area

"National Park Belovezhskaya Pushcha" is an IUCN category II protected area covering around 1500km^2 across all zonations (Fig. 1). It is divided approximately north to south by the border fence between Poland and Belarus, and forms part of the greater Bialowieza Forest Complex, with central European forest and climate characteristics. The region is lowland and the main forest types are mixed, with pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) common, as well as sessile oak (*Quercus petraea*), hornbeam (*Carpinus betulus*), alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and birches (*Betula* spp.). The mean annual air temperature is 6.8 °C, with the warmest month being July (17.8°C) and the coldest month is January (−4.4°C). The average annual precipitation is 659 mm, with winter (December–March) snows (generally 10-50 cm deep) and spring frost. Outside the park territory there is arable farmland and commercial forests interspersed by rural settlements.

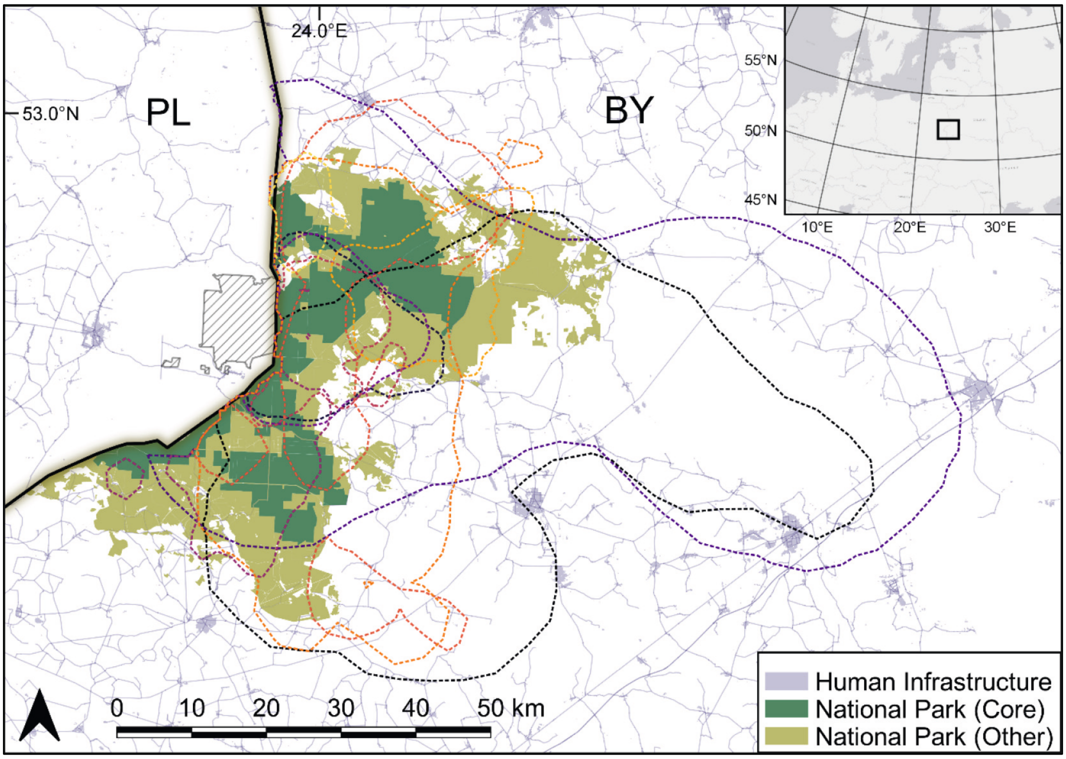

Fig. 1. Belovezhskaya Pushcha National Park in western Belarus and the surrounding area where data were collected showing the protected area zonation (dark green = core, light green = other zonations, white = outside the national park) as used in our analysis. The dotted lines denote the 99 % kernel utilisation density home ranges of the GPS collared wolves (*n* = 10). Note that a nearly impermeable border fence runs along the Belarusian-Polish border. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The area has been historically and ecological significant for wildlife, with a diverse mammal community. There are five ungulate species present; European Bison (*Bison bonasus*), Eurasian elk (*Alces alces*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*), which are common prey for wolves (Jędrzejewski et al., 2000). The national park core zone is strictly protected (only nature protection activities are allowed). The other parks zones comprise a sustainable use zone (some controlled hunting of ungulates, forestry, and tourism), an economic zone (hunting, forestry, and tourism are allowed), and a tourism zone (tourism). In the years before our study, wolf density was estimated at 2.5–3.2 animals per 100km^2, with 5–25 % of the wolves in the park shot through hunting annually (Fenchuk et al., 2017), but hunting did not occur during our study period. Apart from wolves, other permanently present carnivore species are Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), and European badger (*Meles meles*).

2.2. Animal capture

Capture, tagging, and monitoring protocols were approved and permitted by the Hunting Department of the Belarusian Nature Protection Institution "National Park Belovezhskaya Pushcha", who licence the use of traps and handling of game species within the park boundaries. Wolves were live-captured using foot-hold traps (Minnesota Brand, Minnesota Trapline Products, MN, USA). We chemically immobilised trapped animals with a 0.1 % solution of medetomidine (Apicenna LLC, Moscow, Russia) at 1 ml per 10 kg of animal weight, with a 0.5 % atipamezole (Apicenna LLC, Moscow, Russia) solution as an antidote. Trap-related cuts were sprayed with antiseptic and bandaged, and animals given a broad spectrum antibiotic (amoxicillin, Nita-Farm, Saratov, Russia). We fit each animal with GPS Plus GPS-GSM collars (VECTRONIC Aerospace GmbH, Berlin, Germany). Wolves were collared during September–December 2015 (*n* = 5; 3-h fixes) and October–November 2017 (n = 5; 1-h fixes). For further information see Table 1.

2.3. Data preparation

Data handling and analyses were conducted in the R programming language (Version 4.0.2, R Core Team, 2020). We prepared the data to use a used/available resource selection function approach to examine wolf habitat selection at the third order (within individual home ranges; Manly, 2010).

We removed the obvious dispersal movements from two animals in the study area to avoid any associated bias (Dondina et al., 2022), and then used the GPS locations for each individual to delineate home ranges using 99 % kernel density estimates with the *adehabitatHR* package (Calenge, 2006). We then randomly distributed available locations within the individual home ranges using the *sf* package (Pebesma, 2018), and assigned them a corresponding time and date from our used locations. With used/available designs, a key consideration is the proportion of available locations to use to best depict available resources (Brivio et al., 2019; Ciuti et al., 2018). We ran a sensitivity analysis (Roberts et al., 2017) to determine the number of used to available locations using a simplified model with high-resolution spatial predictors (tree cover and distance to public roads, see below for predictor details). To do so, we ran 10 models for each proportion, while gradually increasing the number of available points until we saw consistent average model estimates. Some available locations fell within Poland, and as such on the opposite side of the border security fence which divides the Bialowieza forest complex. Although wolves can dig under or use holes in the fence to cross the border, we visualised from the GPS locations that the animals' movements are indeed restricted by it, and the Polish side of the fence was not truly available to the collared animals (Fig. 1). Accordingly, we removed available locations that fell on the Polish-side of the border fence before building our resource selection

Table 1
Information on collared wolves (n = 10) used for habitat selection analysis. Utilised ranges for the analysis were calculated using 99 % kernel utilisation density estimates from GPS fixes.

Wolf ID	Sex	Year birth	Exact year of birth?	Pack status	Begin	End	Utilised range (km^2)	GPS fixes	End reason
100	Male	2013	No	Solitary	Sep-2015	Nov-2015	3257	644	Shot, hunted outside PA
101	Female	2013	No	Unknown	Nov-2015	Apr-2016	420	1345	Intra-specific kill
102	Male	2010	Yes	Solitary then joined pack	Nov-2015	Dec-2016	4465	1578	Battery/drop-off
103	Female	2013	Yes	Solitary then joined pack	Nov-2015	Jan-2016	404	396	Battery/drop-off
104	Female	2014	No	In pack	Dec-2015	Jan-2017	407	2611	Battery/drop-off
106	Male	2016	No	In pack	Oct-2017	Apr-2018	288	4435	Battery/drop-off
107	Male	2013	No	Solitary then joined pack	Oct-2017	Nov-2017	1013	1484	Shot, hunted outside PA
108	Male	2014	No	Solitary	Nov-2017	Aug-2018	1921	5239	Battery/drop-off
109	Female	2016	Yes	In pack	Nov-2017	Aug-2018	409	5991	Battery/drop-off
110	Male	2014	No	Solitary	Nov-2017	Jan-2018	107	1364	Battery/drop-off

model.

We extracted environmental predictors (Normalised Differential Vegetation Index - NDVI, Digital Elevation Model - DEM, tree cover, landcover) from the Google Earth Engine platform (Gorelick et al., 2017), and used spatio-temporal joins to attach these predictors at their highest resolution to our used/available data (e.g. a position in a given month were matched with the NDVI value of that position for that month and year; Table 2). Anthropogenic predictors were taken from OpenStreetMap data (OpenStreetMap contributors, 2021), namely buildings - which were merged into a "settlements" polygon - and traffic roads (both paved and unpaved) into the category road (Table 2; for all road categories we used see Table S1). National park zonation boundaries were provided by the park administration.

We log-transformed our distances to roads and settlements and then scaled all continuous predictors [(x - mean)/SD] before running models to improve model convergence. We checked our environmental predictors for collinearity with pairwise Pearson correlation coefficients (collinearity when $|r_p| \geq 0.7$; Dormann et al., 2013) and calculated the variance inflation factors (multicollinearity when VIF > 3; Zuur et al., 2009). Landcover (cultivated vegetation, herbaceous vegetation, open forest, closed forest) and tree cover were highly correlated ($r_p = 0.84$, Fig. S1), and we proceeded with the latter as it was higher resolution and more continuous. As our coarse-scale temporal predictor, we divided a year into four categorical "seasons" corresponding to wolf behaviours and ecology. We created a factorial variable for season starting with late winter and mating (middle of January to the middle of April), for denning and pupping (middle of April to the middle of July), for the rendezvous period when food is provided to other pack members (middle of July to the middle of October, (Zimmermann et al., 2014)), and for early winter period (middle of October to the middle of January). Similarly, we chose to use the sun angle (degrees above or below the horizon) as our continuous, fine-scale temporal predictor rather than clock time to best understand how wolves perceive human-risk and allow more appropriate comparisons within a day by corresponding wolf behaviour to the times at which we knew humans were most active (Unpublished camera trap data, Fig. S2). As sun angle was highly correlated with the period of the day (i.e. dawn, day, dusk, night; $r_p = -0.78$), we excluded the period of the day in favour of sun angle, as this predictor had a higher temporal resolution. We also excluded elevation as the range of possible values (136–260 m) did not offer any real insight for this lowland study area.

2.4. Statistical analysis

We built a model of wolf habitat selection to test our a priori hypotheses on the relative probability of selection for environmental and anthropogenic predictors (Table 2). We fit this to a binomial (used/available) generalised linear mixed effect model using the *glmer* function in the *lme4* package (Bates et al., 2015) with the response variable being used (1) versus available (0), with a binomial error distribution and a logit link function, that allows the quantification of releative selection probability for each resource based on the availability of the resources within the landscape (Boyce, 2006). We included the individual wolf ID (Table 1) as a random intercept to account for dependence structures between GPS points of each individual animal, and successfully verified the normality of the random intercepts using the *ranef* function from the *lme4* package (Bates et al., 2015). The ages of most of the animals were not known exactly, and as the pack status, monitored by tracking and camera traps, changed at unknown times (Table 1), we opted to exclude age and pack status from further analysis, and instead proceeded with more exact data and tolerate more general interpretability from our results. To relax the assumption that available points can be used by the animals, we extracted the coefficients of the model and inserted them into the exponential form of the resource selection function (Boyce et al., 2002; Brivio et al., 2019).

We tested for spatial and temporal autocorrelation in our model residuals by creating a variagram (Roberts et al., 2017) and the Durbin-Watson test in the package *DHARMa* to a random subset of the data

Table 2
Predictor variables used in the habitat selection model. The level of measurement, range within the dataset, and reason for inclusion are also given.

Predictor	Resolution	Range	Reasoning	Source
Distance to public roads	1 m	0–6541 m	Disturbance from road traffic, human access	(OpenStreetMap contributors, 2021)
Distance to settlements	1 m	0–10,370 m	Disturbance from continuous human presence	(OpenStreetMap contributors, 2021)
NDVI	250 m/ monthly	−0.2–1	Proxy for food abundance of prey	(MODIS; Kamel, 2015)
Tree cover	30 m/every 5 years	0–95 %	Refuge for resting or avoiding disturbance, proxy for food abundance of prey	(GFCC: Sexton et al., 2013)
National park zonation	3 levels	Core Zone, Other Zone, Outside Park	Proxy for disturbance from tourism, hunting, forestry, and level of protection	National Park Belovezhskaya Pushcha (official GIS data of administrative borders)
Sun angle	Nearest degree	−60–60°	Daily scale wolf perception of risk of human encounters	*sunangle* function in the package *oce* (Kelley and Richards, 2022)
Season	4 levels	Annual	Seasonal scale wolf behavioural states and perception of risk of human encounters	
Year	4 levels	2016–2018	Year the GPS fix was taken	

(Hartig, 2022). As habitat selection models using used/available data are not true presence/absence data, we ran a five-fold cross validation of the model by building five models on 80 % of the data and testing it on the remaining portion to test the models predictive power (Boyce et al., 2002). To do so, we computed Spearman rank correlations between frequencies of cross-validation locations (area-adjusted), and then calculated a rank for each cross-validated model. We expected better predictive performance would be indicated by a strongly positive correlation, because more used locations (area-adjusted) would score higher (Boyce et al., 2002; Brivio et al., 2019).

In order to visualise model results, we predicted model outputs focusing on the different variables which would test our a priori hypotheses. Unless we specifically visualised them, we set environmental variables to their median values, with season set to "late winter and mating", sex set to "male", park zonation set to "core zone," and the year set to "2018."

3. Results

Our sensitivity analysis indicated that equal proportions of used/available locations were enough to achieve stable model parameter estimates for our dataset (Fig. S3). Since we could afford the time and computational power required, we decided to run our model using a ratio of 1:30 locations. There was no evidence of spatial autocorrelation in the dataset from our resulting variograms (Fig. S4) and no evidence of temporal autocorrelation from our applied Durbin-Watson test (non-significant, $p = 0.766$; Fig. S5). Our 5-fold cross-validation demonstrated our habitat selection model had a high predictive performance on withheld data (mean Spearman correlation: $\rho = 0.939$; Fig. S6).

Our habitat selection model results demonstrated fine-scale spatio-temporal avoidance patterns of anthropogenic disturbance within the wolf home ranges. Most of the environmental predictors in our model had clear significant effects on the relative probability of habitat selection, including interactive effects (Table 2).

Wolves in Belovezhskaya Pushcha National Park selected for zones in the PA that are under higher levels of protection, preferring the core zone of the national park to other park zones, and other zones over areas outside of the park (Fig. 2a). Our results showed higher values of selection for areas of greater protection where wolves were likely to encounter less disturbance. Wolves selected for distances far from roads in the core zone of the park, but showed no strong selection outside of the core zone and the protected area (Fig. 2b).

Wolves were highly avoidant of public roads during the peak of day (brighter colours in Figs. 3, 4a–c), but towards twilight (medium brightness in Figs. 3, 4a–c) and night (darker colours in Figs. 3, 4a–c) they were less avoidant (Fig. 3). As tree cover increased, wolves generally avoided areas near roads. During winter months, wolves were selective for areas near roads when tree cover was lower (Fig. 3a), but avoidant when it was higher (Fig. 3b–c). During summer months, wolves were always avoidant of roads, with the strongest avoidance occurring at higher levels of tree cover (Fig. 3e–f). Seasonally, wolves in Belovezhskaya Pushcha showed strong avoidance of public roads (Fig. 4a). Both male and female wolves avoided roads similarly at all distances, with only weak differences between the sexes in their avoidance or selection of distances to public roads (Fig. 4d; Table 3).

Wolves avoided being close to settlements overall (Fig. 4b). However, wolves avoided settlements less during night and twilight than during daylight. Female wolves expressing stronger avoidance than males, but both sexes avoided areas up to 7500 m from settlements (Fig. 4e).

Considering tree cover alone, wolves selected strongly for low levels of tree cover during night (Fig. 4c). During twilight hours, this selection became weaker, and during the day wolves opted for higher levels of tree cover. Selection for higher values of tree cover (>75 %) was higher during the day than during the night. Wolves also selected for areas where vegetation productivity, measured by NDVI, was higher (Fig. 4f).

4. Discussion

Our approach revealed that wolves are able to adapt their fine-scale spatial and temporal behaviour to the landscape of risk stemming from human disturbance. They selected areas of higher protection in the core zone of the national park over less strictly protected zones and areas outside the park's boundaries. Moreover, they adjusted their habitat selection towards human infrastructure according to their perception of human risk. During the day when humans are active, wolves selected to be farther from roads and villages regardless of tree cover and sex, while during the night they were less avoidant. Wolves also selected for more open areas during night. Building on the growing body of evidence surrounding wolf habitat selection in relation to human disturbance

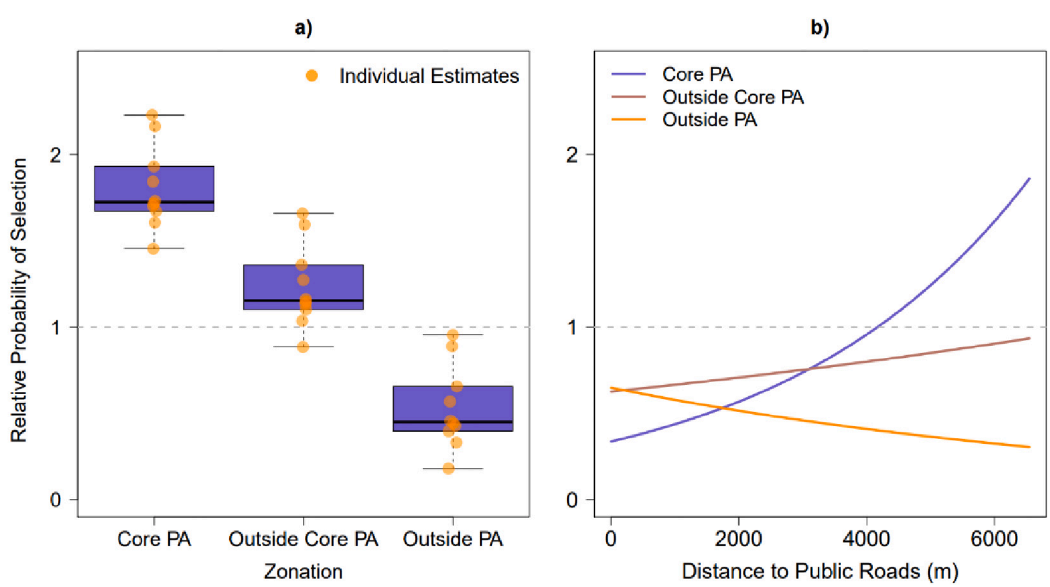

Fig. 2. Distribution of the relative probability of selection by individual wolves for protection zones inside Belovezhskaya Pushcha National Park (core and other zones) and areas outside the PA (a) and selection for distances to public roads for each zonation (b). Dashed horizontal lines denote selection ratios (used/available = 1).

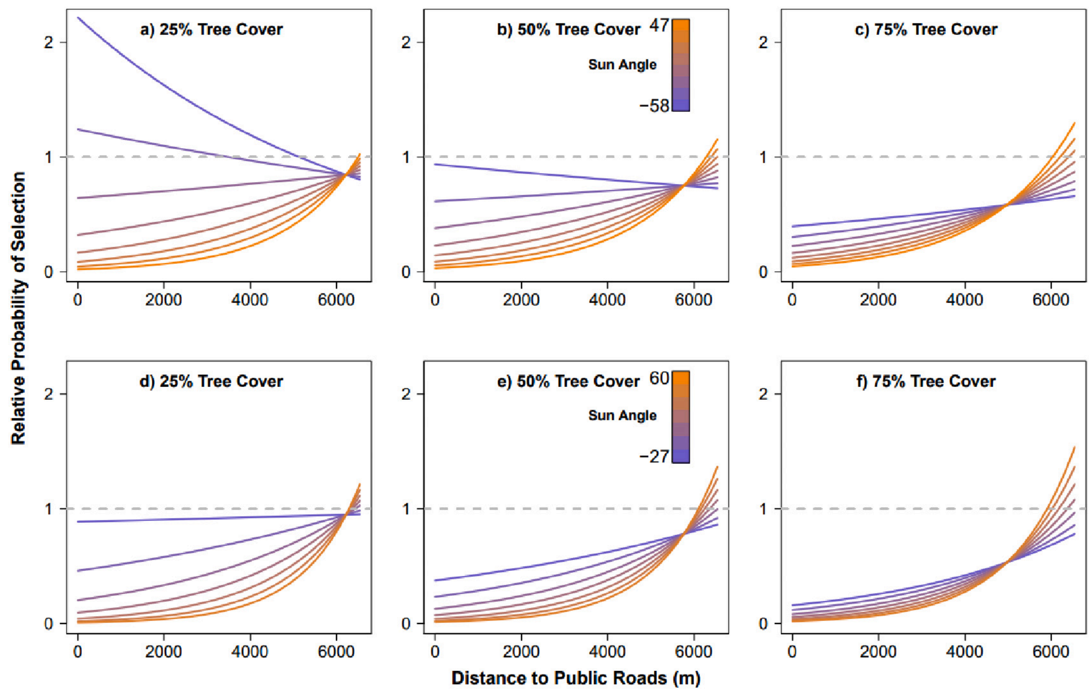

Fig. 3. Relative probability of wolf selection in Belovezhskaya Pushcha National Park for distance to public roads under differing conditions of sun angle and tree cover during late winter/mating season (middle of January to middle of April; a–c) and denning/pupping season (middle of April to middle of July; d–f). Wolves avoided roads at nearly all times of the day and across seasons. Dashed horizontal lines denote selection ratios (used/available = 1).

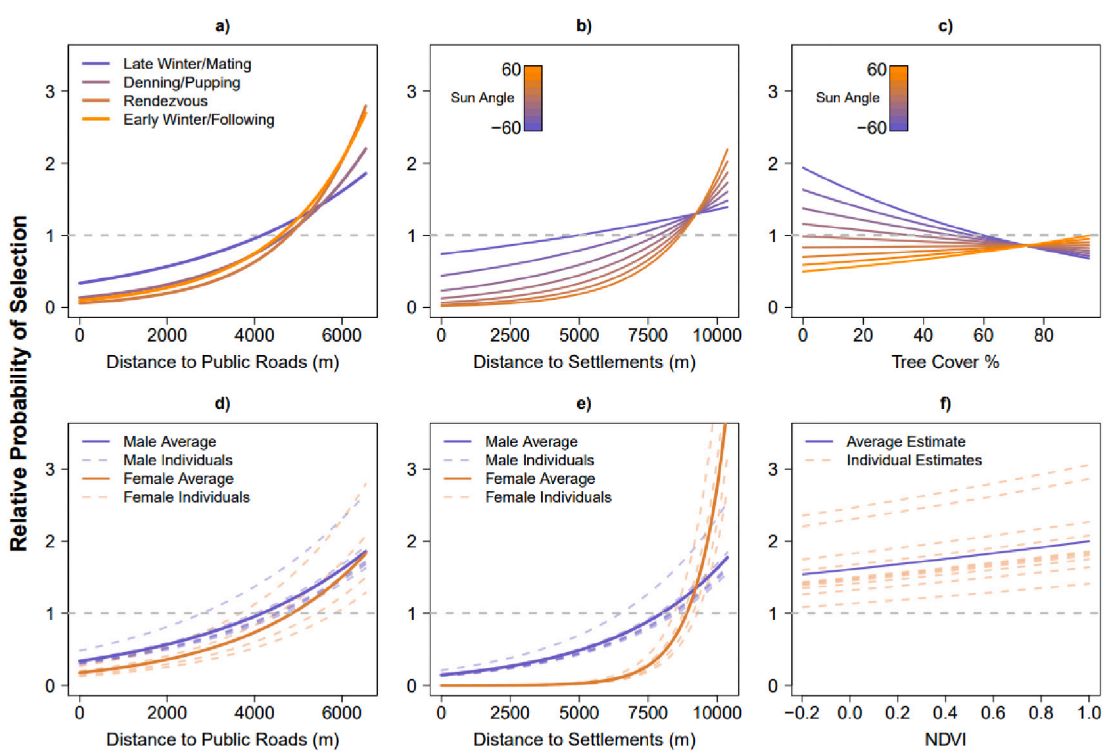

Fig. 4. Relative probability of wolf habitat selection for a) distance to public roads across seasons, b) distance to human settlements over the diel period, c) tree cover density over the diedl period, d) distance to public roads for each sex, e) distance to settlements for each sex, f) productivity indicated by NDVI. Wolves avoided being close to roads across seasons. Wolves of both sexes avoided areas up to 7500 m from settlements, with females expressing stronger avoidance than males. Wolves selected areas of lower tree cover at night and slightly more productive areas of the landscape. Dashed horizontal lines denote selection ratios (used/available = 1).

(Carricondo-Sanchez et al., 2020b; Ciucci et al., 2018; Mancinelli et al., 2019; Zimmermann et al., 2014), we used even finer scales to examine wolf avoidance of humans and the importance of PAs for wolves in Europe, highlighting the importance of providing such areas for large carnivores, which we show allow them to escape human pressure.

Table 3
β estimates of the wolf habitat selection model with standard errors and statistical significance.

Predictors	β	SE	*Z*-value	p	
Fixed effects					
(Intercept)	−3.322	0.117	−28.288	<0.001	***
Park zonation [other zonation]	−0.344	0.018	−19.077	<0.001	***
Park zonation [outside park]	−1.159	0.027	−43.408	<0.001	***
Sun angle	−0.117	0.009	−12.878	<0.001	***
Sun angle^2	−0.032	0.007	−4.447	<0.001	***
Tree cover	1.010	0.049	20.453	<0.001	***
Tree cover^2	−1.063	0.047	−22.642	<0.001	***
Distance to public roads	0.573	0.061	9.330	<0.001	***
Distance to public roads^2	−0.376	0.053	−7.113	<0.001	***
Distance to settlements	1.290	0.107	12.107	<0.001	***
Distance to settlements^2	−0.481	0.095	−5.065	<0.001	***
Season[pupping/denning]	−0.117	0.026	−4.413	<0.001	***
Season[rendezvous]	−0.149	0.030	−4.908	<0.001	***
Season[early winter/ following]	−0.045	0.017	−2.678	<0.01	**
Sex [female]	0.339	0.150	2.262	0.024	*
NDVI	0.054	0.009	6.193	<0.001	***
Interacted effects					
Distance to public roads * park zonation [other zonation]	−0.179	0.020	−9.130	<0.001	***
Distance to public roads * park zonation [outside park]	−0.336	0.025	−13.564	<0.001	***
Tree cover * distance to public roads * sun angle	−0.042	0.008	−5.316	<0.001	***
Tree cover * distance to public roads	0.049	0.010	4.792	<0.001	***
Tree cover * sun angle	0.144	0.008	17.475	<0.001	***
Distance to public roads * sun angle	0.123	0.009	14.056	<0.001	***
Distance to settlements * sun angle	0.101	0.010	10.077	<0.001	***
Distance to public roads * season[pupping/denning]	0.148	0.025	6.033	<0.001	***
Distance to public roads * season[rendezvous]	0.289	0.028	10.240	<0.001	***
Distance to public roads * season[early winter/ following]	0.217	0.017	13.095	<0.001	***
Distance to public roads * sex [female]	−0.087	0.017	−5.177	<0.001	***
Distance to settlements * sex [female]	−0.725	0.022	−32.880	<0.001	***
Random effects	Var.	SD		Groups	
Animal ID	0.054	0.233		10	
Year	<0.001	<0.001		4	

* $p < .01$.
** $p < 0.01$.
*** $p < 0.001$.

4.1. Importance of protected areas for wolves

Our results demonstrated that wolves in Belovezhskaya Pushcha National Park preferentially choose areas of higher levels of protection, preferring the core zone of the national park to other zones, and other zones over unprotected areas outside of the national park. Since no hunting, forestry, and limited tourism takes place in the core zone of the national park, wolves can use this space to escape most human disturbance. Other zones have associated disturbance which have been shown to affect wolves such as tourism (Malcolm et al., 2020), forestry operations (Bojarska et al., 2021; Lesmerises et al., 2012), and hunting (Bryan et al., 2015). However, historic hunting may still have hangover effects on the behaviour or physiology (Bryan et al., 2015) of wolves in our study. To our knowledge, there was no evidence of illegal wolf poaching inside Belovezhskaya Puscha National Park during our study period. In Belarus, wolves can be hunted legally outside of protected areas but were not hunted within it during this study, which explains the strong preference for areas within the national park. Since all areas within the park are regarded as nature protected, wolves still prefer these zones to being outside the park boundaries, where regular and more intense human disturbance stems from towns and villages, main roads, hunting, forestry, and agriculture.

On a macro-European-level, there is a good understanding of wolf and other large carnivore distributions (Cimatti et al., 2021; Cretois et al., 2021). However, a substantial knowledge gap on the importance of protected areas for wolves exists in Europe, compared to long-term research from North America e.g. Isle Royale and Yellowstone ecosystems (Nelson et al., 2011; Peterson et al., 2014). The interesting interplay between recolonising wolves settling in German military training areas versus PAs further demonstrates the adaptability of wolves to optimise their territory placement in the landscape to avoid disturbance and mortality risk (Reinhardt et al., 2019). Playback experiments to locate wolf use areas in central Italy most often located them in PAs (Bassi et al., 2015). However, PAs in Europe, such as national parks, are small and heavily used for recreation, requiring large carnivores to adapt to these disturbance regimes (Belotti et al., 2018). In the EU, the Habitats Directive requires the use and creation of Natura 2000 protected areas to protect the core habitats of wolves and other large carnivores (Diserens et al., 2017). Diserens et al. (2017) points out that Natura 2000 PA network designed prior to the continued expansion of the wolf in Europe possibly leaves much to be desired in terms of fulfilling the goals of the Habitats Directive, such as size or connectivity. Our results may indicate that, with size and lower disturbance regimes, the Natura 2000 network can substantially reduce human pressures on wild wolves, which could boost conviviality. We do not know to what extent wolf ecological function is capped by the need to adapt to human disturbance spatially and temporally, and our study does not demonstrate any reduction of the carrying capacity of wolves in the area. In principle, a release from disturbance may allow wolves to maximise hunting opportunities and reproduction success in the landscape and best fulfil their role as predators. In Belarus, there are a number of PAs, such as Braslavskie Ozera (714.9km^2) and Paleski State Radio-Ecological Reserve (2162 km^2; UNEP-WCMC, 2022), that have ample room for multiple wolf or other large carnivore home ranges, and whose size relieves pressure on large carnivores in a landscape of fear, and also on wolf management and conservation efforts, even if territories only partially exist within these PAs.

4.2. Wolves avoid public roads

Roads are increasingly identified as important landscape features influencing wolf movement behaviour (Basille et al., 2013; Dennehy et al., 2021; Iliopoulos et al., 2014; Llaneza et al., 2016; Mattisson et al., 2013; Zimmermann et al., 2014). Wolves in Belovezhskaya Pushcha National Park avoided roads in nearly all cases, with the strongest avoidance during the day. They selected to be far from roads inside the core zone of the park, where roads are sparse. Wolf-road relationships are complex with gravel or forest roads often playing a part in assisting wolves in moving further, faster - with lower energy costs (Eriksen et al., 2009; Gurarie et al., 2011; Mattisson et al., 2013; Zimmermann et al., 2014). Some gravel and forest roads in Belovezhskaya Pushcha National Park can not be passed or are driven sporadically by staff, and these types of roads can be unconvincing metrics for sustained human disturbance in forest landscapes (Mattisson et al., 2013) and are excluded from public mapping data. However, this is not necessarily the case outside the park where they are often used. Theuerkauf et al. (2003a, 2003b) concluded that wolves in Bialowieza (Poland) showed avoidance of roads yet demonstrably shown through our study and highlighted in others in Scandinavia is selection and avoidance of public roads by wolves shifting over the course of a day (Milleret et al., 2018; Zimmermann et al., 2014).

Wolves showed stronger avoidance of roads during the summer months (i.e. pupping and denning season (middle of April to the middle of July) than during the late winter and mating season (middle of January to the middle of April). We explain this stronger summer avoidance of roads by probable den establishment and higher risk of human encounters across a greater proportion of the day. In Bialowieza Forest (Poland), wolves move shorter distances during summer, when pups are born and being raised (Jedrzejewski et al., 2001). Wolf habitat selection studies and behaviour of an individual animal often elucidates space use for others in their social unit - especially relevant to breeding (Bassi et al., 2015; Llaneza et al., 2018; Sazatornil et al., 2016) and rendezvous site selection (Bojarska et al., 2021; Ciucci et al., 2018; Iliopoulos et al., 2014). Since we did not know when some animals shifted their pack status (e.g. pack member to solitary) we were unable to use this information effectively in our analysis. However, we still see from our seasonal results that at more sensitive times (i.e. pupping and denning season), spatio-temporal avoidance of roads by wolves is maintained and increased. Separate analysis of males and females may offer better resolution here. For example, solitary males and pack females could be expected to behave differently during the pupping period. High snow cover may also make travelling on cleared public roads attractive for wolves, but the unknown times and places where it occurs in rural landscapes makes it quite unpredictable as a movement strategy, and hard to test empirically.

Public roads are key causes of human-induced mortality for wolves owing to vehicle collision risk (Dennehy et al., 2021; Sunde et al., 2021), persecution (Suutarinen and Kojola, 2018), or both (Zimmermann et al., 2014). We assume based on the strong avoidance of roads during the day that wolves perceive a risk of human disturbance on an even finer temporal scale than shown in previous studies. Our analysis employed a fine time-scale (sun angle) that demonstrated the attuned avoidance behaviours wolves apply based on their shifting perception of human-induced risk in European landscapes.

4.3. Selection for forest cover changes throughout the day

Forest-cover is an important habitat consideration for predators like wolves (Bojarska et al., 2021) and lynx (Ripari et al., 2022), to balance hunting opportunities and avoid human disturbance. Bojarska et al. (2021) demonstrated the visibility associated with forest resting sites was important for avoiding daytime human disturbance, reproduced in our results highlighting avoidance of roads during the day. We also attribute this to finding suitable resting locations, as selection for resting site cover can be strong even compared to human infrastructure (Llaneza et al., 2016). Wolf pack territories on a landscape-scale opt for high tree cover, but often utilise open areas within those territories (Ciucci et al., 2018). Our results revealed the selection for more open areas is greatest during twilight and night to avoid the greater human disturbance from roads while simultaneously providing ample hunting opportunities in areas where ungulates preferentially feed (Kuijper et al., 2009) at times they are active. However, disturbance may restrict wolf hunting opportunities temporally. While Theuerkauf et al. (2003a, 2003b) concluded that wolves in Bialowieza Forest (Poland) completely avoided arable areas (highly open), this was investigated with low resolution VHF telemetry. With higher resolution data our analysis builds on this work, revealing that large carnivores may be more dynamic in their requirements for tree cover, which should be considered in conservation planning. It also demonstrates the adaptability of wolves in Europe to coexistence on a finer temporal scale by utilising more open areas only at times they perceive as less risky.

4.4. Wolves avoid settlements

As highlighted by our results, wolves avoid human settlements in a similar way to roads. In the wolf-percieved landscape of fear, roads carry a somewhat more unpredictable risk as traffic may pass at any given time (daily or seasonally). Conversely, settlements are more likely to be associated with a constant, predictable association to human risk in the landscape (Zimmermann et al., 2014). As animals forage for resources in the landscape, they must trade off risks with opportunities for these resources. According to the risk allocation hypothesis (Lima and Bednekoff, 1999b), unpredictable risks (roads) should have a stronger impact on wolf foraging than predictable risks (settlements). Settlements may provide wolves simultaneous opportunities to predate (e.g. dogs, livestock; Sidorovich et al., 2003) or scavenge from anthropogenic sources rather than natural ones. We show wolves avoided distances close to settlements during day, but less so during night, possibly to utilise greater food resources for prey that can be found near settlements (Dupke et al., 2017). More generally, settlements are avoided by both Eurasian lynx (Ripari et al., 2022) and wolves in other study areas (human density - Ciucci et al., 2018; Kaartinen et al., 2005; Milleret et al., 2018; Zimmermann et al., 2014). Furthermore, our results revealed an interesting relationship between avoidance of settlements and sex, with females being more avoidant than males. However, we urge caution on the interpretation of this result, as i) the sample size when split between males and females is small, and ii) most of the male wolves were solitary while the females were pack-living. We also do not know when wolves switched pack status. Solitary wolves might be more exploratory and bolder in their movements while searching for mates and prey than individuals living in packs. Accounting for more dynamic individual variation by using random slopes is also an opportunity for further advancement, and is a potential limitation of our work.

4.5. Outlook and conclusions

Our results reveal how wolves adjust fine-scale movement behaviours temporally to reduce their risk of encountering human disturbance helping to explain the continued perseverance of wolves in the Anthropocene's shared landscapes. For wolves, it demonstrates an anti-predator strategy against the human "super predator."

With their large territories and ability to disperse over long distances (Byrne et al., 2018), wolves will undoubtedly intersect human economic and social interests. Luckily, management options exist to foster coexistence further (Kuijper et al., 2019). Fine-scale wolf adaptation to human-risk requires constantly updating our knowledge of wolf behaviours and, in turn, updating finely-tuned wolf management and conservation strategies in the future. As highlighted by our results here, the "first preference" of wolves is avoidance of human disturbance if given the opportunity. In European land-sharing environments, areas of lower disturbance are vital for minimising negative interactions. Careful examination of wolf behaviour can help policy and management implement the best landscape and local changes to further foster coexistence with wolves, or predict and understand scenarios where behaviours of wolves are unexpected or lead to conflicts. Since wolf behaviour shows clear avoidance of human disturbance, it could be considered their ecology is a natural fit to fostering coexistence.

CRediT authorship contribution statement

Adam F. Smith: Formal analysis, Writing - Original Draft.
Simone Ciuti: Writing- Reviewing and Editing, Supervision.
Dimitri Shamovich: Resources, Fieldwork.
Viktar Fenchuk: Conceptualisation, Project administration.
Barbara Zimmermann: Writing- Reviewing and Editing, Supervision.
Marco Heurich: Writing- Reviewing and Editing, Supervision.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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