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Reduced human disturbance increases diurnal activity in wolves, but not Eurasian lynx

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ABSTRACT

Wildlife in the Anthropocene is increasingly spatially and temporally constrained by lethal and non-lethal human disturbance. For large carnivores with extensive space requirements, like wolves and Eurasian lynx, avoiding human disturbance in European landscapes is challenging when sufficient space with low disturbance is rarely available. Consequently, investigating behavioural adjustments to human presence is critical to understanding the capacity to adapt to human disturbance. We hypothesised that under low human disturbance conditions, large carnivores would adjust their temporal behaviours to make use of daytime, and when daytime human disturbance is high, they would opt for nocturnality. Using camera trap data from nine European study sites along a gradient in human disturbance, we analysed wolf and Eurasian lynx activity patterns. Our data spanned multiple years, 2014 – 2022, and we focused our analysis on September until April, when most large carnivore monitoring takes place. For wolves, our analysis revealed i) increased nocturnal behaviour, ii) decreased diurnal overlap with increasing human activity, and iii) a significant association between a higher probability of nocturnal activity and

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increasing human disturbance. For Eurasian lynx, we found iv) consistently nocturnal behaviours across all study sites, regardless of human disturbance, and v) no association between human disturbance and increased probability of being active during the night. Our results show that wolves can adjust to diurnal or cathemeral behaviours under low human disturbance, but shift to nocturnality when human disturbance increases. Eurasian lynx, however, consistently maintain their nocturnal behaviour, which we attribute to their principal hunting strategy of stalk and ambush. If human disturbance constrains large carnivore activity to nighttime, it could influence their interactions with prey, leading to cascading effects in the ecosystem. On the other hand, maintaining nocturnal behaviours in human-dominated landscapes may benefit large carnivore conservation, by decreasing negative interactions with humans thereby contributing to a landscape of coexistence.

1. Introduction

Understanding the behavioural ecology of large carnivores is key to managing expectations, public attitudes, and their coexistence with humans in multiuse landscapes (Kuijper et al., 2019; Mech, 2017). Humans as the “super-predator” of all other species can induce fear effects and avoidance behaviour even in large carnivores (Bryan et al., 2015; Smith et al., 2017; Suraci et al., 2019; Ordiz et al., 2021), whereby large carnivores adjust their behaviour to avoid potentially risky interactions with humans. Consequently, Europe’s human-dominated landscapes form a matrix of risk that wildlife must navigate to minimise lethal and non-lethal human disturbances, such as hunting or recreational activities (e.g. Bonnot et al., 2020; Gehr et al., 2017; Ruiz-Villar et al., 2024). To balance risk avoidance and resource acquisition, wildlife in a human-induced landscape of fear wildlife is expected to allocate behaviours through spatio-temporal avoidance of risky times and places (Gaynor et al., 2019; Laundre et al., 2010; Laundreé et al., 2001; Lone et al., 2014; Palmer et al., 2022). One behavioural strategy to avoid risky interactions with humans is to be active at times when humans are not present, such as during the night (Hebblewhite and Merrill, 2007; Sunde et al., 2023).

Large carnivores, like other wildlife, may increase their nocturnality when their temporal niche is constrained by human disturbance during the day, while on the other hand, they become more diurnal with lower daytime disturbance (Bonnot et al., 2020; De Groeve et al., 2023; Gaynor et al., 2018; Mayer et al., 2023). However, large carnivores show differences in hunting modes, which may affect their preferred active times. For example, puma (*Puma concolor*) are ambush predators active during twilight and night to maximise their chances of successfully stalking their prey in low light conditions (Smith et al., 2019; Soria-Díaz et al., 2016). In contrast, African wild dogs (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) are mainly diurnal hunters using coursing or pursuit tactics to chase prey (Hayward and Somers, 2009; Makin et al., 2017). For prey, ambush predators may be more predictable in space, especially in heterogeneous landscapes, and therefore either more avoidable or elicit a stronger anti-predator response (Makin et al., 2017; Smith et al., 2019). Similarly, all predators whose hunting times are constrained (e.g. by human disturbance) could be more predictable in time, which has potential implications for predator-prey interactions (Palmer et al., 2022).

Previous studies have already sought to examine the activity patterns and nocturnality of wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*). Wolves are primarily cursorial hunters that also show cooperative hunting behaviours (Middleton et al., 2013; Van Beeck Calkoen et al., 2021; Woodruff et al., 2018). In Europe they are known to be principally nocturnal or crepuscular, such as wolves in Croatia (Blašković et al., 2022; Haswell et al., 2020; Kusak et al., 2005), Poland (Lazzeri et al., 2024; Theuerkauf et al., 2007), Denmark (Sunde et al., 2023), Italy (Ciucci et al., 1997; Mori et al., 2020; Rossa et al., 2021), and Spain (Jiménez et al., 2023). Lynx as stalking and ambush predators (Heurich et al., 2016; Van Beeck Calkoen et al., 2021) are also known to be nocturnal or crepuscular like wolves, shown by studies, from Poland (Schmidt, 1999), Croatia (Blašković et al., 2022), Germany, Czech Republic, Norway, and Sweden (Filla et al., 2017; Heurich et al., 2014). Some studies found an increased diurnal activity of these large carnivores and speculated that a lack of human disturbance is an important driving factor for this observation (Eggermann et al., 2009; Heurich et al., 2014; Martínez-Abraín et al., 2023; J. Theuerkauf et al., 2003). Also in North America, studies have observed diurnal tendencies in wolves (Frey et al., 2020; Kohl et al., 2018) and also shifts to nocturnal behaviours when human disturbance is high (Frey et al., 2022). Martínez-Abraín et al., (2023) point out that experimental conditions with human-exclusion which could allow researchers to test differences in large carnivore behaviour over the diel period are rare, especially at meaningful spatial and temporal scales,. However, the effect of human disturbance on the behaviour of large carnivores can be explored effectively by taking advantage of a gradient of human disturbance, including areas where humans are excluded.

Since both wolves and lynx have large home ranges (Linnell et al., 2021; Mysłajek et al., 2018; Ripari et al., 2022), it is apparent that nearly all large carnivores in Europe inhabit a matrix of quiet refugia (Martínez-Abraín et al., 2023; Smith et al., 2022), and areas of higher disturbance (Bubnicki et al., 2019; Ripari et al., 2022; Santini et al., 2016). Protected areas in Europe allow relatively little space for wildlife to exist undisturbed (Diserens et al., 2017), including national parks (Van Beeck Calkoen et al., 2020), which contrasts strongly with extensive protected areas in North America. European protected areas are generally small as well as being disturbed by forestry (Thorn et al., 2018), hunting (Van Beeck Calkoen et al., 2020), tourism and recreation (Belotti et al., 2018), or agriculture (Van Beeck Calkoen et al., 2020). On top of the risk of non-lethal disturbance is the human-induced mortality of large carnivores across their European range, through both legal and illegal killing (Heurich et al., 2018; Liberg et al., 2012; Musto et al., 2021; Nowak et al., 2021b).

Despite centuries of massive persecution in Europe, wolves and lynx are now making comebacks in distribution and abundance (Chapron et al., 2014; Cimatti et al., 2021). For both species, increased habitat and prey availability (Cimatti et al., 2021), as well as

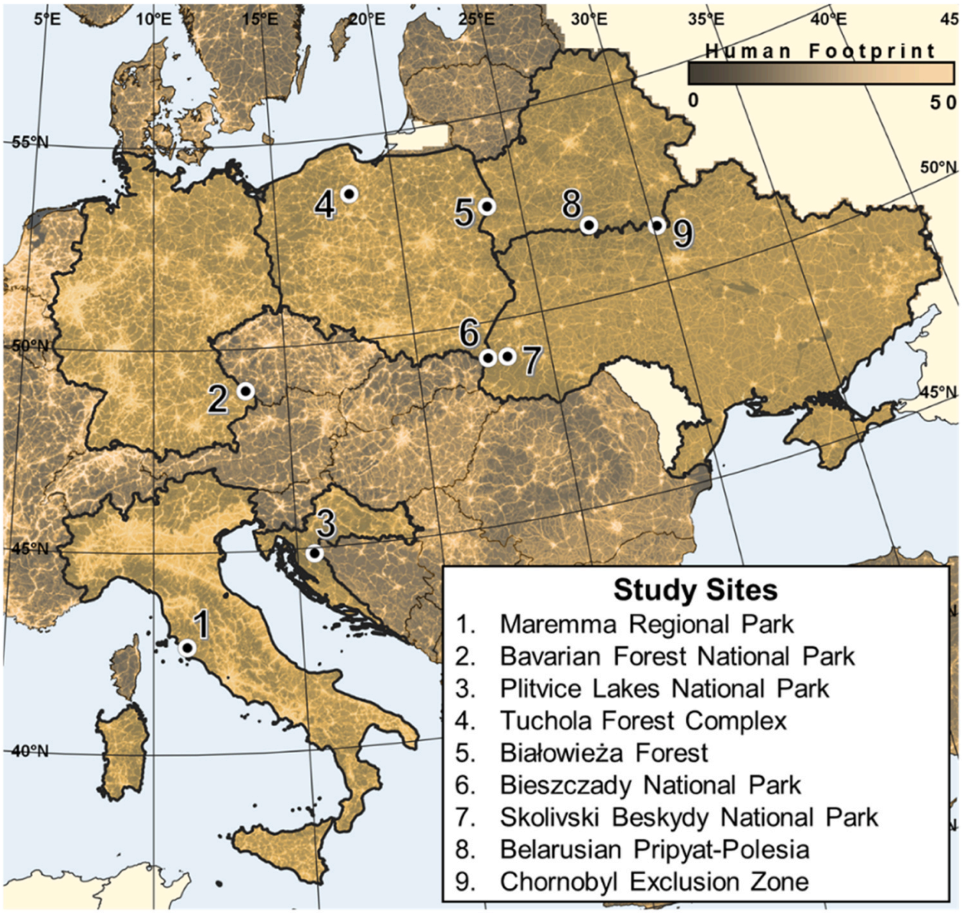

Fig. 1. : Study sites across Europe where camera trap data was collected. Highlighted countries indicate that study sites were present. Wolf data came from all sites except Bavarian Forest National Park (insufficient data). Eurasian lynx data came from all sites except Maremma Regional Park, Tuchola Forest Complex (not present), and Bieszczady National Park (insufficient data). The background layer depicts the Human Footprint Index (Venter et al., 2016).

proactive conservation action such as legal protection and reintroductions of lynx (Linnell et al., 2009; Skorupski et al., 2022) have aided their come back. However, the exact protective status, and the interpretation of this status, show high heterogeneity between the member states of the European Union (EU) and especially other European countries (Chapron et al., 2014; Trouwborst, 2010). Furthermore, the presence of these species in human-dominated landscapes over the last two decades has increasingly brought coexistence issues between humans and large carnivores. For example, when large carnivores kill livestock (Gervasi et al., 2021), and as humans increase their presence in wilder habitats (Mumme et al., 2023). As large carnivores continue to recolonise Europe, we are still unravelling their behavioural adaptations to the novel, human-dominated landscapes (Kuijper et al., 2024). If European landscapes force wolves and lynx to adapt their temporal niche it may increase the predictability of risk for prey (Palmer et al., 2022), thereby affecting the functional role large carnivores are expected to play in the ecosystem, such as asserting top-down control of prey populations and initiating trophic cascades (Kuijper et al., 2016).

To the best of our knowledge, no studies in Europe have examined wolf and lynx temporal behaviour along a human disturbance gradient from areas where humans are highly-restricted to areas of intense human disturbance. Based on previously mentioned studies, we developed two main hypotheses. Firstly, that i) the most diurnal behaviour of wolves and lynx would be apparent in the least human disturbed study sites, and ii) that the probability of being active during night would rise as human disturbance increased.

To address these hypotheses, we analysed camera trap data of wolves, Eurasian lynx, their main ungulate prey, and humans from nine study sites in Europe, and examined the carnivores' behaviour along a human disturbance gradient, including a large and minimally human disturbed baseline area, with decades of restricted human access (the Chornobyl Exclusion Zone in Ukraine). We quantified the probability of daytime and nighttime activity, assessed and compared the activity patterns of wolves and lynx between sites, and examined the relationships between nocturnal activity of wolves and lynx alongside various environmental and anthropogenic pressures. Since our study sites cover a broad gradient of human disturbances found in European landscapes, from protected areas without hunting but with substantial tourism pressure, to areas with hunting (for wolves), to areas where virtually all human activities have been excluded, it contributes important evidence about the behavioural patterns of these large carnivores.

Table 1
Study sites and camera trap information across Europe where camera trap observations of wolves, Eurasian lynx, and humans were gathered for analyses.

Study Site	Country	Wolf/ Lynx Data	Camera Trap Array (km^2)	Camera Trap Locations Used	Study Years	Main Human Disturbances	Mean Human Footprint Index	Main Habitats	Study Site Description/ Study Design
Maremma Regional Park	Italy	Wolf	55	55	2020	Tourism	16.8	Mediterranean pine forest and scrub	(Lazzeri et al., 2024)
Bavarian Forest National Park	Germany	Lynx	353	29	2019–2021	Tourism, forestry, hunting	10.2	Mixed-mountain beech-fir-spruce forest	(Palmero et al., 2021)
Plitvice Lakes National Park	Croatia	Both	189	54	2014–2017	Tourism	7.1	Mixed-mountain beech-fir forest	(Haswell et al., 2020)
Tuchola Forest Complex	Poland	Wolf	2930	48	2022	Tourism, forestry, hunting	14.9	Lowland deciduous forest	(Krawiec et al., 2022)*
Białowieża Forest	Poland	Both	671	103	2014–2015	Tourism, forestry	10.9	Lowland deciduous forest	(Bubnicki et al., 2019)
Bieszczady National Park	Poland	Wolf	236	15	2021–2022	Tourism	7.1	Mixed-mountain beech-fir-spruce forest	(Nowak et al., 2021a)*
Skolivski Beskydy National Park	Ukraine	Both	540	63	2020–2023	Tourism, forestry	8.8	Mixed-mountain beech-fir-spruce forest	(Palmero et al., 2023)
Belarusian Pripyat-Polesia	Belarus	Both	812	49	2020–2021	Tourism, foraging, forestry, hunting	6.8	Floodplain wetlands, pine forest	(Palmero et al., 2023)
Chornobyl Exclusion Zone	Ukraine	Both	792	65	2020–2021	Area protection	9.4	Floodplain wetlands, pine and oak forest	(Palmero et al., 2023)

* Asterix denote references where the study site was described but not the study design.

2. Materials and methods

2.1. Study sites

We deployed camera traps in nine study sites across six European countries (Fig. 1) with an expected gradient of human disturbance, described in Table 1. Since the Chornobyl Exclusion Zone (Ukraine) served as our baseline and reference site for wolf and lynx behaviour, we provide a more extensive description for context. Human activity inside the Chornobyl Exclusion Zone is low because of the long-term restriction on human access after the 1986 nuclear disaster. Nowadays, most human activity occurs in Chornobyl town (population ~ 1000) and the industrial zone of the Chornobyl Nuclear Power Plant. Human activity is limited to guard checkpoints, some forestry (also around electricity lines), villages (total population ~ 40), and scientific activities. Roads exist within the area, but travel is concentrated on the main road and is limited to daytime. The approximately 2600 km^2 Chornobyl Exclusion Zone in Ukraine is adjoined to the nearly 2200 km^2 Polesie (Palieski) State Radioecological Reserve in Belarus, with similarly strict regulations on human access. Hunting does not occur within the area, but anecdotal reports of poaching have arisen (Gashchak et al., 2022). The combination of size and protection creates some of the lowest human disturbance conditions in Europe, where large carnivore populations can develop with minimal human interference (Kudrenko et al., 2023; Palmero et al., 2023). Therefore, we expected the most natural wildlife behaviour possible in this human-restricted area compared to an otherwise human-dominated continent.

We also collected camera trap data in central Belarusian Pripyat-Polesia (southern Belarus), in Białowieża Primeval Forest (eastern Poland), the Tuchola Forest Complex (northern Poland), Bieszczady National Park (south-eastern Poland) and Skolivski Beskydy National Park (western Ukraine), Bavarian Forest National Park (south-eastern Germany), Plitvice Lakes National Park (central Croatia), and Maremma Regional Park (central-western Italy). Like most areas in Europe, our study sites (Fig. 1) host variable but often considerable human disturbances, generally from a mix of high tourism pressure, activities like forestry, and hunting for wildlife management (Table 1).

2.2. Camera trap data collection methods

Camera traps were deployed on roads and trails, which are frequent landscape features large carnivores use to patrol their territories (Blašković et al., 2022; Iannarilli et al., 2021). Placing the camera traps on these features where animals are expected to walk minimises detection radius and efficiency problems (such as unidentifiable animals at far distances during nighttime; Palencia et al., 2022). Camera traps were used for monitoring wolves or lynx, or for lynx population monitoring with a paired camera trap design to distinguish individuals by their coat patterns in the Chornobyl Exclusion Zone, Belarusian Pripyat-Polesia, Skolivski Beskydy National Park, and Bavarian Forest National Park. Observations from the pair of camera traps were combined for that individual location. Data were generally not available during the summer, since most large carnivore monitoring using camera traps occurs in the autumn, winter, or spring, when juveniles are able to move around (Jedrzejewski et al., 2001; Weingarth et al., 2015; Zimmermann et al., 2014). We only used data from 1st September until 31st April to maximise the seasonal overlap between our study sites and reduce biases during the study period.

Camera traps were set to take photographs or videos at all times of the day (Appendix Table A1), and the data was stored and classified manually (Maremma Regional Park) or using the open-source software TRAPPER (Bubnicki et al., 2016) (Bieszczady National Park, Skolivski Beskydy National Park, Chornobyl Exclusion Zone, Belarusian Pripyat-Polesia, Białowieża Forest, Tuchola Forest Complex, Bavarian Forest National Park), or with Camelot (Hendry and Mann, 2018) (Plitvice Lakes National Park).

2.3. Data analysis

All data analyses were conducted in R statistical programming software (version 4.3.0, R Core Team, 2023), while GIS operations were conducted in QGIS (version 3.30; QGIS Association, 2023).

All species were classified to the lowest taxonomic resolution, and false-triggers and blank photographs were removed from the dataset before data analyses were conducted. We also excluded observations of other species that were not the focus of the study, and subset all camera trap observations of wolves, lynx, wild ungulate prey species, and humans from our camera trap datasets. Since the camera trapping data from our selected study sites did not always include information on types of human disturbance (e.g. tourists, staff, vehicles etc.), we could not differentiate among human disturbance classes in a comparable way. Therefore, we included all types of anthropogenic encounters as "humans" as general evidence of presence. We maintained temporal independence of these observations by using a 5-minute cut-off point from the first observation of our focal species at a camera trap location (Henrich et al., 2023; Kühl et al., 2023). We then calculated human encounter rate (i.e., relative abundance) for each study site by calculating the mean number of independent events per 100 days (O'Brien, 2011), to use later as an explanatory variable representing human disturbance in our modelling.

We defined night and day at each camera trap location based on the available light (Ensing et al., 2014; Hut et al., 2013), where day begins when the maximal change in sun light is observed at the start of civil twilight at dawn (sun at -6 degrees below the horizon) and the end of civil twilight at dusk (sun at -6 degrees below the horizon). Therefore, observations recorded during the brightest part of twilight were categorised as day, and observations during the darkest part of twilight were considered night. One advantage of this approach using brightness was that the availability of day and night are well balanced for this period of the year at our study sites (average night length from observations was 12.2 hours; Appendix Table A1). We then categorised each observation as night or day by calculating the sun angle using the *suncalc* package and added the instantaneous moments during the solar day (solar noon, day start,

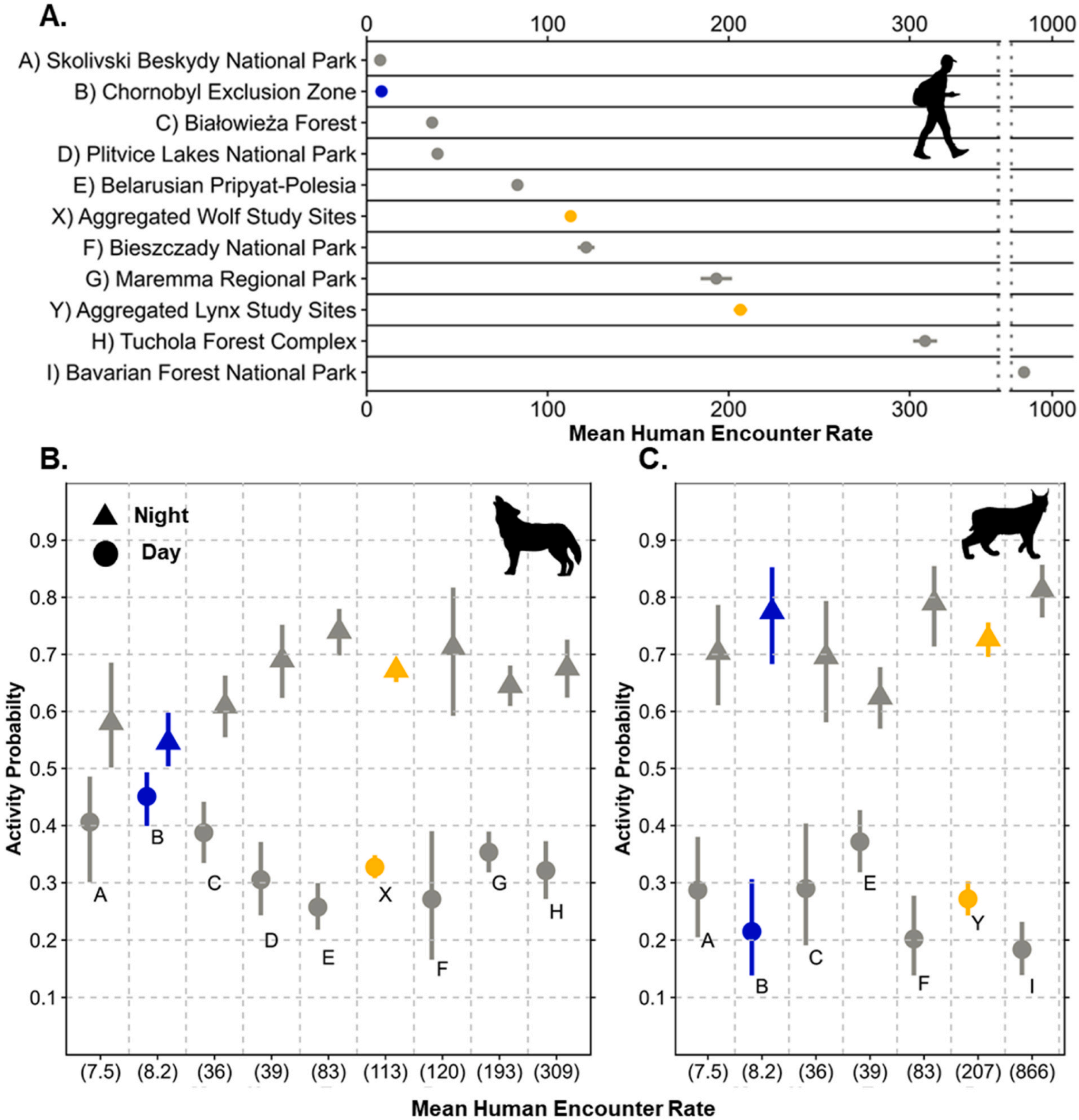

Fig. 2. **:** A. Mean human encounter rates for all at the camera trap for each study site (mean humans per day, including standard error). Activity probabilities with 95% confidence intervals for wolves (B.) and Eurasian lynx (C.), ordered according to human encounter rate. The Chornobyl Exclusion Zone as a human-restricted baseline is highlighted in blue, while the aggregated study sites, comprising all areas except the Chornobyl Exclusion Zone, are highlighted in yellow.

night start) to each camera trap observation based on its time, date, and coordinates.

2.3.1. Activity probabilities

We calculated activity probabilities for wolves and lynx in each study site separately, as well as all aggregated study sites (excluding the Chornobyl Exclusion Zone as our baseline) by using a Bayesian probabilistic multinomial modelling approach developed by Gerber et al., (2024), applied using the *Diel.Niche* package in R, which uses wrapper functions that implement modelling and estimation functions of the *multinomineq* package (Heck and Davis-Stober, 2019). Since we were strictly interested in night versus day activity based on our definition of these periods, we only used counts of day and night observations, and therefore the modified model parameters for the "maximising" hypothesis (result is either nocturnal or diurnal) implemented by the model became:

$$p(night) = 1 - p(day)$$

which allowed us to calculate the activity probability for each study area based on how much wolves or lynx use each diel period. More details can be found in the *Diel.Niche* documentation (Gerber et al., 2024).

To enhance further analysis aimed at explaining diel activity of large carnivores, we also calculated an activity probability for their main ungulate prey species in each study area. For wolves, the main prey species were red deer (*Cervus elaphus*), European roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), Eurasian elk (i.e. moose; *Alces alces*), and Eurasian wild boar (*Sus scrofa*). We combined the observations of wolf prey species to get a single probability of prey activity for each study site. For lynx, we only calculated the activity probability for roe deer as the preferred main prey (Khorozyan and Heurich, 2023).

2.3.2. Activity curves

We transformed the observation timestamps to "solar time" in radians anchored to sunrise and sunset at each camera trap location to account for some differences in day length from the start to the end of the season, as well as latitudinal differences (Vazquez et al., 2019). Average-anchoring time transformations before analysis provides approximately unbiased estimates of activity level comparable between the season or latitude of observations from our study areas (Vazquez et al., 2019). Using the timestamps, we created activity density curves to visualise the diel activity patterns of wolves and lynx in each study site and all aggregated study sites (excluding the Chornobyl Exclusion Zone) to compare diel activity. We calculated activity curves using the *fitact* function from the *activity* package (Rowcliffe et al., 2014), which creates circular kernel density distributions using our observation data with average-anchored times. We resampled the data using 100 bootstraps to estimate uncertainty around our activity density distributions.

We computed overlap between large carnivore populations in the Chornobyl Exclusion Zone versus each of the other study areas, and then the Chornobyl Exclusion Zone versus the other study areas aggregated, using the *compareCkern* function. We subsampled the overlap coefficient between the activity distributions using 1000 bootstraps to calculate uncertainty using the bootstrapping functions in the *overlap* package. We compared the percentage change in overlap between large carnivores and humans in each study site, and all

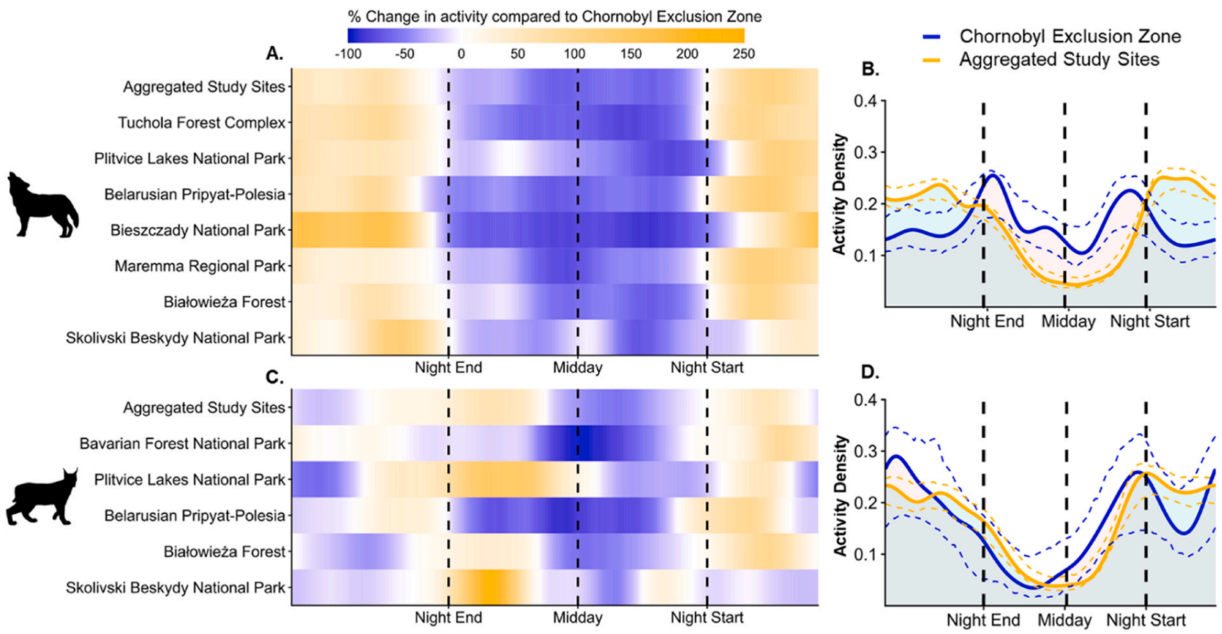

Fig. 3. : Changes in activity across the diel period and activity patterns for wolves (A. and B.) and Eurasian lynx (C. and D.) compared to their conspecifics in the Chornobyl Exclusion Zone as the human-restricted baseline. The aggregated study sites comprise all study sites except the Chornobyl Exclusion Zone. Wolf overlap between the aggregated study sites and the Chornobyl Exclusion Zone was 0.74±0.05, and Eurasian lynx overlap between the aggregated study sites and the Chornobyl Exclusion Zone was 0.88±0.07.

aggregated sites, versus our baseline estimates for the Chornobyl Exclusion Zone.

2.3.3. Regression models

Finally, we used generalised linear regression to model the night activity probabilities from our Bayesian probabilistic multinomial models above for wolves and lynx. Each model was assigned a quasibinomial family to best account for overdispersion and the data structure arising from probability (0 – 1) as a response variable. Our explanatory variables were the human encounter rate (log transformed to account for large differences between study sites; min = 7.5, max = 866), the probability of prey to be nocturnal (0 – 1), and the average conditions covering both environmental and human disturbance variables at the study site level, with one model per explanatory variable. Specifically, we extracted road density (Meijer et al., 2018), human population density (CIESIN, 2018), terrain ruggedness (Danielson and Gesch, 2011), human footprint (index of agriculture, population, and infrastructure; Venter et al., 2016), latitude, and tree cover (Sexton et al., 2013). Before extracting these variables, we created convex polygons of the camera trap arrays, and added a 10 km buffer around them, in order to best represent conditions at the landscape in and around our study sites at a scale meaningful for large carnivore home ranges (i.e. > 100 km^2; Mancinelli et al., 2018; Ripari et al., 2022). For Maremma Regional Park, this buffer ended at the Mediterranean Sea, and for Białowieża Forest, this buffer excluded the area on the Belarusian side of the Polish-Belarusian border, due to the extensive border fence which restricts wildlife movement (Fenchuk et al., 2017; Smith et al., 2022). We extracted the mean value of various environmental variables within the buffer for each study site and checked correlations between each variable ensure there was no collinearity (correlation coefficient < 0.7; Dormann et al., 2013).

3. Results

Our final dataset consisted of 71,357 independent encounters. Of these, 2430 were of wolves, 934 were of lynx, 8585 were prey species, and 59,408 were human encounters. The highest human encounter rate based on camera trap effort was in Bavarian Forest National Park (866 humans per day; Fig. 2), while the lowest was in Skolivski Beskydy National Park (7.5 humans per day; Fig. 2), followed by the Chornobyl Exclusion Zone (8.2 humans per day; Fig. 2). There were not enough independent events of wolves in Bavarian Forest National Park (n = 10; low wolf density at this time), and not enough events of lynx in Bieszczady National Park (n = 1; short survey effort) to produce robust results, hence we excluded them from the respective species analysis.

3.1. Wolves

According to our diel niche models, wolves in all our study sites were always more nocturnal than diurnal. As expected, wolves in our baseline study area in the Chornobyl Exclusion Zone showed the highest levels of diurnal activity (Fig. 2), with a daytime activity probability of 0.451 (CI = [0.397 – 0.494]). Skolivski Beskydy National Park and Białowieża National Park and Forest wolves were the next most diurnal (day probability of 0.408, CI = [0.304 – 0.488]; and 0.388, CI = [0.334 – 0.442] respectively; Fig. 2) while Belarusian Pripyat-Polesia wolves were the most nocturnal (day probability of 0.257, CI = [0.221 – 0.299]).

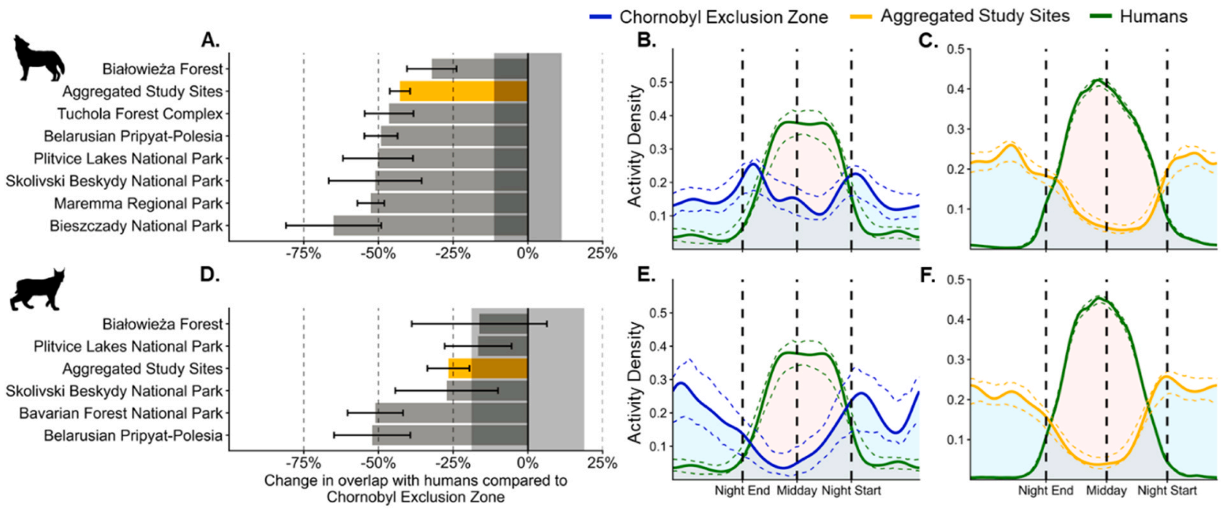

Fig. 4. : Change in activity overlaps between humans and large carnivores in study sites across Europe compared to the overlap in the Chornobyl Exclusion Zone as a human-restricted baseline (A. and D.). The shaded area of the bar plots denotes the 95% confidence interval of the overlap coefficient of the Chornobyl Exclusion Zone. (A. and D.) Error bars for each study site that overlap the confidence interval are not significantly different from the overlap in the baseline area. The data of the aggregated study sites comprise all study sites except the Chornobyl Exclusion Zone, and are highlighted in yellow. Overlap between the activity curves of wolves and humans in the Chornobyl Exclusion Zone was 0.56±0.06 (B.), between wolves and humans in the aggregated study sites was 0.32±0.02 (C.). Overlap between the activity curves of Eurasian lynx and humans in the Chornobyl Exclusion Zone was 0.39±0.07 (E.), and 0.29±0.03. for the aggregated study sites (F.).

Wolf activity overlaps between other study sites and the Chornobyl Exclusion Zone were the highest with Skolivski Beskydy National Park (overlap = 0.79±0.09), and lowest with Bieszczady National Park (overlap = 0.55±0.11). Wolves from the aggregated study sites had an average overlap of 0.74±0.05 with the Chornobyl Exclusion Zone (Fig. 3). Wolves showed substantial increases in nighttime activity (often 50 – 100% or higher) in all study areas when compared to the Chornobyl Exclusion Zone. Comparatively lower wolf activity during the day was observed in Bieszczady National Park (Fig. 3).

Following our prediction, wolves were most day active, and showing the most overlap with human activity, in the study site with the least overall human disturbance, in the Chornobyl Exclusion Zone (overlap = 0.56±0.06; Fig. 4). All other study areas had statistically significant reductions in overlap between wolves and humans compared to the Chornobyl Exclusion Zone (Fig. 4), with the highest overlap reduction in Bieszczady National Park of 65.0±15.9%, where the overlap between wolf and human activity was only 0.19±0.09 (Appendix Fig. A1). The lowest reduction in overlap compared to the Chornobyl Exclusion Zone was found for Białowieża Forest (32.2±8.3%). The aggregated study sites had an average a 42.8±3.4% lower wolf activity overlap with humans of compared to the Chornobyl Exclusion Zone (Fig. 4). Human activity patterns in all study areas were characterised by strong peaks during the middle of the day.

3.2. Eurasian lynx

Similar to wolves, our diel niche models for Eurasian lynx highlighted consistently nocturnal behaviour across all study sites. However, lynx in the Chornobyl Exclusion Zone did not have the highest observation probability during the day (0.214, CI = [0.140 – 0.306]). Instead, Plitvice Lakes National Park lynx had the highest probability of observation during the day (0.371, CI = [0.317 – 0.428]), while lynx in Bavarian Forest National Park were the most nocturnal (day probability of 0.183, CI = [0.141 – 0.236]).

Lynx activity in the Chornobyl Exclusion Zone overlapped most with lynx activity in Skolivski Beskydy National Park (overlap = 0.87±0.08), and lowest in Plitvice Lakes National Park (overlap = 0.78±0.09; Fig. 3). Lynx activity for the aggregated study sites had an average overlap of 0.88±0.07 with lynx in the Chornobyl Exclusion Zone (Fig. 3). Lynx in both Skolivski Beskydy National Park and Plitvice Lakes National Park had increased activity in the morning when compared to the Chornobyl Exclusion Zone. In contrast, their daytime activity in Belarusian Pripyat-Polesia and Bavarian Forest National Park decreased by nearly 100% when compared to the baseline (Fig. 3).

The strong activity peaks of humans during the day were contrasted with crepuscular or nocturnal activity patterns in lynx (Fig. 4). Similar to wolves, lynx in the Chornobyl Exclusion Zone showed the largest overlap with humans (overlap = 0.39±0.07). When compared to the Chornobyl Exclusion Zone, lynx had a significantly lower their overlap with humans in Bavarian Forest National Park and Belarusian Pripyat-Polesia, where overlap was lower by 51.1±9.3% and 52.1±12.7% respectively. The aggregated study areas showed an average decrease in overlap between lynx and humans of 26.6±7.0% compared to the Chornobyl Exclusion Zone.

3.3. Regression models

The probability of wolf activity at nighttime increased significantly with the log mean human encounter rate ($P = 0.011$), but this was not the case for lynx ($P = 0.324$). Our regression analysis showed that the probability of wolf nocturnal activity increased by 15.4% as the log human encounter rate increased by 1. No significant relationships ($P < 0.05$) were detected between the probability of nocturnal activity of wolves or lynx and any other predictors at the study site level (Appendix Table A1; Appendix Fig A2).

4. Discussion

Our results provided unique insights into large carnivore behaviour by showing contrasting diel activity responses of wolves and Eurasian lynx along a gradient of human disturbance in Europe's human-dominated landscapes. In accordance with our initial hypothesis, our analysis revealed increases in wolf nocturnal activity with increasing human disturbance. As expected, wolves were most active during day in our minimally disturbed baseline area (the Chornobyl Exclusion Zone), but we also saw that in the study site with the least human encounters on camera traps, Skolivski Beskydy National Park, wolf behaviour most closely matched the expected baseline. In contrast to our hypothesis, our analysis revealed only smaller changes in diel activity for Eurasian lynx, with consistently nocturnal patterns of behaviour, regardless of the study site and despite variation in human disturbance. Our results also showed significant decreases in overlap with human activity for wolves and lynx compared to the Chornobyl Exclusion Zone.

Increasing human disturbance along our reported gradient shifts wolves to more nocturnal activity and encounters are implicated in this pattern, whereby the intensity of human presence during daytime in the landscape has consequences for wolf behaviour. While we did not examine the mortality causes of large carnivores, both species are under protection in all our study sites except for wolves in Belarusian Pripyat-Polesia (where they can be legally hunted), which adds to the overall human disturbance. Since we report the most nocturnal behaviours from this study site, this conforms to the expectation that general disturbance combined with the roles that humans may play in the landscape (e.g. as hunters, or as tourists) contributes to shifts to nocturnal behaviour. Illegal killing of wolves and lynx can occur but are difficult to assess (e.g. Eurasian lynx in Germany, Heurich et al., 2018; wolves in Poland, Nowak et al., 2021b; wolves in Italy, Ciucci, 2015). In some areas, a significant proportion of large carnivores are still persecuted and many studies have published numbers of illegal killings e.g. in Italy (Musto et al., 2021) and Poland (Nowak et al., 2021). But even if we do not always know the exact numbers for our study sites, the baseline for detected events is already high. Despite wolves being legally hunted in Ukraine, but not within our study sites (Cherepanyn et al., 2023; Kudrenko et al., 2023; Shkvyria and Vishnevskiy, 2012)., animals in the Chornobyl Exclusion Zone and Skolivski Beskydy National Park were the least nocturnal, implying their size and strict protection allow them to act as refugia which permit wolves to be more active during the day (Smith et al., 2022). Existing studies also suggest direct mortality risk from human hunting may influence the temporal landscape of fear for large carnivores in some places (Frey et al., 2022) and the variation across the diel period lends itself to dynamic landscape of fear effects (Palmer et al., 2022) induced by humans. Sources of human-induced mortality and disturbance that remain undetected by camera traps may shape the behaviour of large carnivores regardless of their protection status or the protection at our study sites. Other human influences, like roads and settlements, ultimately play a part in creating lethal and non-lethal disturbance and shaping temporal avoidance (Carricondo-Sanchez et al., 2020; Dennehy et al., 2021; Smith et al., 2022; Theuerkauf, 2009).

Our results showed no relationship between average terrain ruggedness, tree cover, latitude, or prey activity and the probability that large carnivores are more nocturnal. We also found no significant relationship between the study sites' average road density, human population density, or human footprint and the probability of large carnivores being nocturnal. Even in protected landscapes, roads have been shown to influence large carnivores behaviour over the diel period (Ciucci et al., 2018; Filla et al., 2017; Smith et al., 2022; Zimmermann et al., 2014). It is possible that road density, population density, and human footprint at the landscape level combined with the low spatial resolution of camera trap arrays in our study do not capture finer-scale adaptability of large carnivore diel activity. Also, human footprint as a landscape index might not equate to represent actual human presence (Nickel et al., 2020), which in our case, relates strongly to the fluctuating patterns of tourism and forestry that vary daily and seasonally. Tourism is highly relevant to our study, since six of our nine areas encompass national or regional parks (Table 1), where tourism-related disturbance dominates. Tourists are often seasonal and heterogenous in both space and their mode of visitation or transportation (motorised, bicycle tourism, ski tourism, horse-back tourism, by foot, etc.), which may have different individual or cumulative non-lethal disturbance effects on wildlife (Corradini et al., 2021; Morales-González et al., 2020), but makes quantifying their effects difficult. In Belarusian Pripyat-Polesia, where the probability of wolf activity during day was lowest, human disturbance arises from forestry activities, as well as intensive berry and mushroom picking activities (Palmero et al., 2023), which over-shadow tourism pressure, but are in turn over-shadowed by hunting pressure on wolves.

We saw increased nocturnality and decreases in temporal overlap between wolves and humans owing to high human encounter rates at the study site level stemming from activities like tourism, and also by comparing activity probability and activity patterns to the Chornobyl Exclusion Zone. In Skolivski Beskydy National Park, the area with the lowest human encounter rate, tourism is concentrated in certain areas and is even restricted where some camera traps were located, which likely facilitates wolf activity during daytime. Tourism has been specifically shown to affect large carnivores (Belotti et al., 2018; Fennell et al., 2023; Granados et al., 2023; Ladle et al., 2018; Malcolm et al., 2020; Morales-González et al., 2020). Therefore, we expect that the combination of human activity patterns and average human encounter rates provides an overall indicator of temporal disturbance allowing a comparison of our study sites.

There were contrasting patterns in activity and shifts to nocturnality between wolves and lynx in our analyses, which are probably explained best by the combination of their different predation ecology and their overall tolerance to human disturbances. Wolves, predominantly cursorial predators, rely heavily on extended pursuit tactics to hunt (Van Beeck Calkoen et al., 2021; Woodruff et al., 2018). However, they can also adopt stalk and ambush strategies depending on their choice of prey (e.g. beavers; Gable et al., 2024), which is likely to be associated with low light conditions at nighttime and cover that favours their concealment. Wolf hunting success is reported as being greatest during twilight, to which their sense of sight is well adapted (Kohl et al., 2018; Theuerkauf et al., 2003). It could be expected, that wolves displaying more daytime activity under less human disturbance have improved hunting success during daytime and twilight. In Yellowstone National Park, the lowest frequencies of wapiti elk (*Cervus canadensis*) movements ending in risky locations were during the day, when wolf activity was high, corresponding to the highest predation risk (Kohl et al., 2018). However, since protected areas of this size are rare in Europe (Van Beeck Calkoen et al., 2020), the reproducibility and comparability of these findings is expected to be limited, but could be tested in an area such as the Chornobyl Exclusion Zone.

Time of day may be a potential factor in the prey choice and hunting strategy for wolves, with social dynamics and cohesiveness also affect hunting behaviours (Metz et al., 2011; Nordli et al., 2023). Lone wolves or smaller wolf packs may be less conspicuous, allowing activity throughout the day. Wolf group sizes can vary greatly both within and between years (Chapron et al., 2016), but an average wolf pack (winter) in Europe is 2.6 – 6.0 individuals (references in Llaneza et al., 2023), which overlaps with the ranges we expect in our study sites where data exists. For example, in Tuchola Forest, an average pack consisted of ~5 individuals, but packs of 8 – 11 were also recorded (K. Kasper, *pers. comm.*), while similar winter averages of 4 – 5 with a maximum of 12 wolves were reported for Skolivski Beskydy National Park (A.T. Bashta, *pers. comm.*). For Białowieża Forest, winter packs were 3 – 8 individuals (Jędrzejewski et al., 2007), and in the Chornobyl Exclusion Zone an overall average of 5 – 7 wolves per pack was reported (Shkvyria and Vishnevskiy, 2012). We had little further evidence to account the differences in activity between study sites based on sociality, since pack sizes were all relatively similar to each other and the European average.

As predominantly solitary, ambush predators of ungulates and medium-sized mammals (Khorozyan and Heurich, 2023), lynx fit well into the nocturnal-crepuscular niche because darkness lends itself much better to stalking and ambushing (Heurich et al., 2016; Hočevar et al., 2021; Schmidt, 1999). Wolves and lynx co-occur in seven of our nine study sites and while both species have dietary overlaps, specialisation for preferred prey species has been noted as the most likely adaptation to overall coexistence between the two species (Schmidt et al., 2009; Wikenros et al., 2010). However, negative interactions like interspecific killings and kleptoparasitism of kills, have been reported before in Belarus (Sidorovich, 2022).

Public discourse related to large carnivores in Europe often focuses on their top-down effects on prey populations and behaviour, resulting in more complex ecological interactions and trophic cascades (Hayward et al., 2019; Kuijper et al., 2013; Van Beeck Calkoen et al., 2023). However, human disturbance constraining the active periods of large carnivores to night might mediate the effects on prey by creating a "temporal refuge" during day (Palmer et al., 2022; Smith et al., 2019), but this will likely be influenced by the stronger fear effects from humans – especially if hunting is also occurring (Bonnot et al., 2020; Lone et al., 2014). In contrast, one might expect that predators that achieve "temporal release" (activity possible throughout the diel period) create an unpredictable risk landscape for prey, resulting in correspondingly impactful anti-predator responses. As noted by Kohl et al., (2018) spatiotemporal patterns of predation risk caused by multiple, asynchronous predators (e.g. more diurnal wolves and consistently nocturnal lynx in the Chornobyl Exclusion Zone) probably require prey to respond to one predator over the other, at the expense of increasing their risk. The complication in disentangling the dynamics between humans, predators, and prey is that human disturbances that impact large carnivores are also likely to affect prey species (Dorresteijn et al., 2015; Ordiz et al., 2021, 2013). Indeed, human hunters in Europe have been shown to have even stronger effects than natural predators (Van Beeck Calkoen et al., 2023). While we do not focus on prey activity here, they may be expected to react in line with our hypothesis for large carnivores and the trend of increased nocturnality in the Anthropocene due to human disturbance (Gaynor et al., 2018). Since the Chornobyl nuclear disaster created "accidental rewilding" conditions after decades of reduced human influence (Deryabina et al., 2015; Dombrovski et al., 2022; Hostert et al., 2011), further experimental comparisons of large mammal behaviour and trophic effects may be possible there, which we demonstrate here may have real value in understanding wildlife behaviours.

5. Conclusions and limitations

Using camera trap data from multiple study sites across Europe, we concluded that increased nocturnal behaviour in wolves was linked to increasing human disturbance, while the nocturnal behaviour of lynx was not. For wolves, this fits the trend of increasingly nocturnal wildlife behaviour driven by human disturbance in the Anthropocene (Gaynor et al., 2018; but see Frey et al., 2020). Apart from human encounter rate and wolf nighttime activity, no human disturbance factors, such as human population or road density, at the landscape level explained higher activity at nighttime well. Comparing and contrasting the strength and patterns of these behaviours demonstrates the behavioural plasticity of wolves and the consistency of lynx activity across Europe. The relatively diurnal behaviour of wolves in the Chornobyl Exclusion Zone demonstrates facultative diurnal and cathemeral activity is possible and even natural for wolves under reduced human disturbance conditions. Combining different methods and new study areas confirms that previously reported patterns are consistent. Also, as activity patterns, human encounter rates, and landscape variables we used are concatenated at the study site level, extremely fine-scale avoidance behaviour (i.e. per individual camera trap location) might be overlooked due to limitations of the data resolution. Our data comes from camera traps on forest roads and trails, which are preferred not only by large carnivores but also by humans. In some places, large carnivores may be more diurnal away from these linear features, which could be examined by future studies embracing camera traps in more random locations and/or with fine-scale telemetry data to look at spatial avoidance. We also lack data from even more disturbed landscapes, like peri-urban or agricultural areas, where large carnivores are expanding their ranges (Fechter and Storch, 2014; Kuijper et al., 2019). Further work should consider if there are costs to increased nocturnality in wolves and how this relates to predator-prey interactions. Another consideration is the specific relationship to the crepuscularity of wolves and lynx, which may also help them trade-off human disturbance with opportunities to hunt.

Since restricting human access to large areas in Europe is unlikely, we believe that expanding large carnivore populations in Europe will continue to display principally nocturnal behaviours when humans are present in the landscape. However, this behaviour also allows a landscape of coexistence (Gehr et al., 2017; Oriol-Cotterill et al., 2015), where both large carnivores and humans can share the environment, facilitated by a segregation of temporal activity patterns. While this may not avert coexistence issues entirely, it may reduce interactions leading to fear in humans, but will still require management measures for the prevention of livestock depredations. A solid understanding of the diel activity behaviours of large carnivores lends is crucial to the implementation of management actions aiming at preventing and/or mitigating human-carnivore conflicts.

CRediT authorship contribution statement

Adam F. Smith: Writing – original draft, Formal analysis, Data curation, Conceptualization. **Katharina Kasper**: Writing – review & editing, Resources, Data curation, Conceptualization. **Lorenzo Lazzeri**: Writing – review & editing, Resources, Data curation. **Michael Schulte**: Writing – review & editing, Resources, Data curation. **Svitlana Kudrenko**: Writing – review & editing, Resources, Project administration, Methodology, Data curation. **Elise Say-Sallaz**: Writing – review & editing, Resources, Data curation. **Marcin Churski**: Writing – review & editing, Resources, Data curation. **Dmitry Shamovich**: Writing – review & editing, Resources, Methodology, Data curation. **Serhii Obrizan**: Resources. Serhii Domashevsky: Resources. **Kateryna Korepanova**: Resources. **Andriy-Taras Bashta**: Writing – review & editing, Resources. **Rostyslav Zhuravchak**: Writing – review & editing, Resources, Project administration, Conceptualization. **Martin Gahbauer**: Resources. **Bartosz Pirga**: Writing – review & editing, Resources, Data curation. **Viktar Fenchuk**: Writing – review & editing, Resources, Project administration. **Josip Kusak**: Writing – review & editing, Resources, Project administration, Data curation. **Francesco Ferretti**: Writing – review & editing, Resources, Project administration, Data curation. **Dries P.J. Kuijper**: Writing – review & editing, Resources, Project administration, Data curation. **Krzysztof Schmidt**: Writing – review & editing, Resources, Project administration, Data curation. **Marco Heurich**: Writing – review & editing, Supervision, Resources, Project administration, Conceptualization.

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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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Appendices

Table A1
Extra study site information including camera trap models, media, and the average length of night during the study based on the night length of each observation from that study site.

Study Site	Camera Trap Models	Media Type	Mean Night Length (hours)
Maremma Regional Park	Ir-plus 100 – HD; Ir-plus HD2 – BF; Scout SG-2060X; Comitel Guard – 1; Comitel Guard - Z2	Video	11.5
Bavarian Forest National Park	Cuddeback Attack; Cuddeback Ambush; Cuddeback C-series.	Photo	12.4
Plitvice Lakes National Park	Cuddeback C-series; Acorn LTL Acorn	Photo	11.8
Tuchola Forest Complex	Browning Spec Ops Elite HP5	Photo	11.8
Białowieża Forest	Ecotone SGN-5210A	Both	11.7
Bieszczady National Park	Browning Recon Force Elite HP4	Photo	13.1
Skolivski Beskydy National Park	Cuddeback C-series	Photo	13.2
Belarusian Pripyat-Polesia	Cuddeback G-series	Photo	13.0
Chornobyl Exclusion Zone	Cuddeback G-series; Cuddeback C-series	Photo	13.4

Table A2
Proportions of the wild ungulate prey species of wolves from camera traps for study sites which provided this information.

Study Site	% Red Deer	% Roe Deer	% Fallow Deer	% Moose	% Wild Boar
Maremma Regional Park	NA	6.2	88.1	NA	5.7
Plitvice Lakes National Park	28.8	48.1	NA	NA	23.1
Białowieża Forest	34.0	2.7	NA	2.0	61.3
Bieszczady National Park	33.3	63.3	NA	NA	3.3
Skolivski Beskydy National Park	72.2	15.6	NA	0.0	12.2
Belarusian Pripyat-Polesia	0.0	68.3	NA	13.4	18.3
Chornobyl Exclusion Zone	37.2	16.2	NA	38.7	7.9

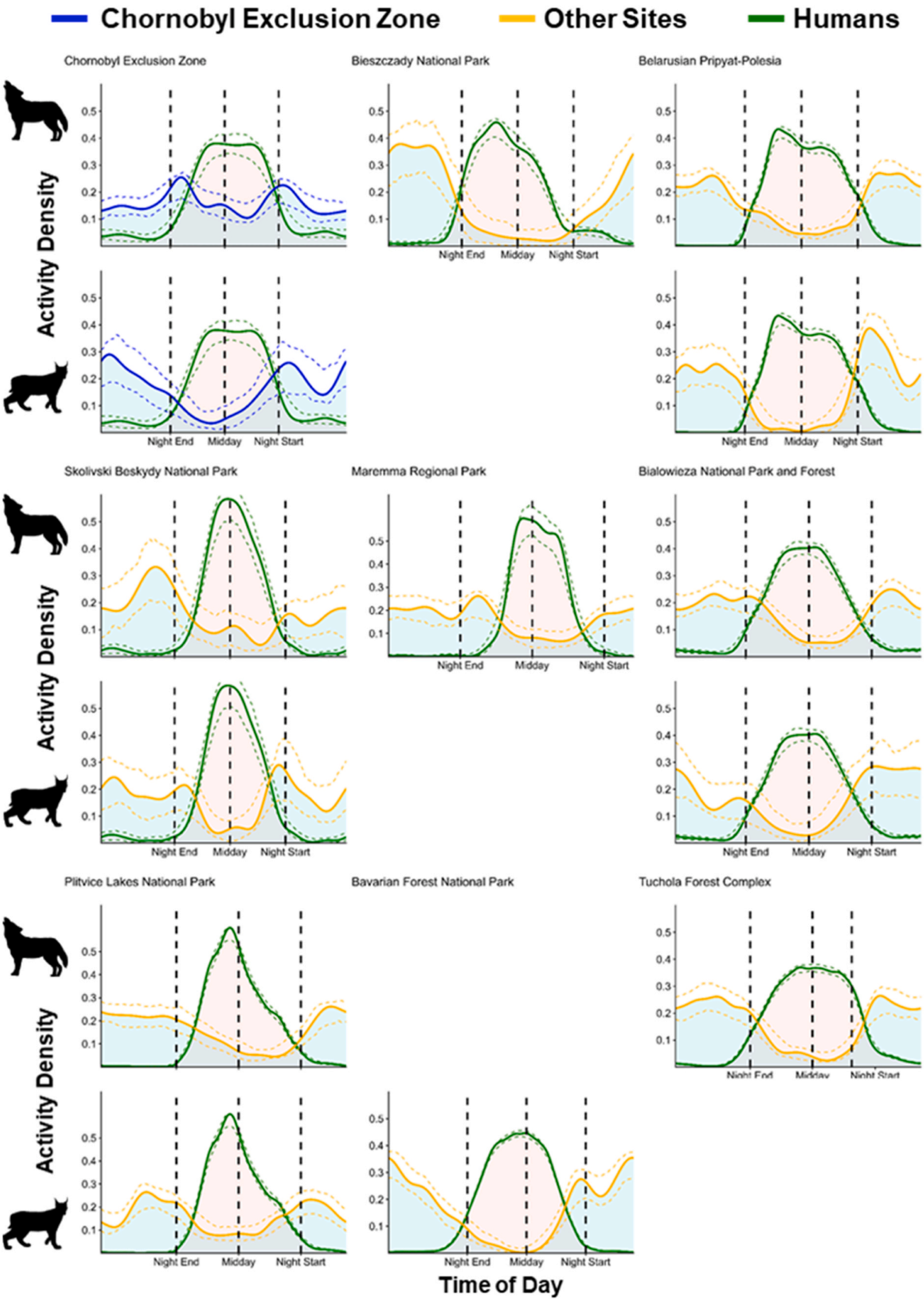
Table A1Study SiteCamera Trap ModelsMedia TypeMean Night Length (hours)Maremma Regional ParkIr-plus 100 – HD; Ir-plus HD2 – BF; Scout SG-2060X; Comitel Guard – 1; Comitel Guard - Z2Video9.9Bavarian Forest National ParkCuddeback Attack; Cuddeback Ambush; Cuddeback C-series.Photo12.4Plitvice Lakes National ParkCuddeback C-series; Acorn LTL AcornPhoto11.8Tuchola Forest ComplexBrowning Spec Ops Elite HP5Photo11.8Białowieża ForestEcotone SGN-5210ABoth11.7Bieszczady National ParkBrowning Recon Force Elite HP4Photo13.1Skolivski Beskydy National ParkCuddeback C-seriesPhoto13.2Belarusian Pripyat-PolesiaCuddeback G-seriesPhoto13.0Chornobyl Exclusion ZoneCuddeback G-series; Cuddeback C-seriesPhoto13.4

Table A2Proportions of the wild ungulate prey species of wolves from camera traps for study sites which provided this information. Table A2Study Site% Red Deer% Roe Deer% Fallow Deer% Moose% Wild BoarMaremma Regional ParkNA10.045.8NA44.2Plitvice Lakes National Park28.848.1NANA23.1Białowieża Forest34.02.7NA2.061.3Bieszczady National Park33.363.3NANA3.3Skolivski Beskydy National Park72.215.6NA0.012.2Belarusian Pripyat-Polesia0.068.3NA13.418.3Chornobyl Exclusion Zone37.216.2NA38.77.9

Table A3
Model estimates from individual generalised linear regression between nighttime activity probabilities and the environmental variables for study sites with wolves (n = 8) and Eurasian lynx (n = 6). For prey nightime activity for wolves, we had data for n = 7 study sites.

Wolf			
Model	Odds Ratios	CI	p-value
Road density	1.00	1.00 – 1.00	0.954
Population density	1.00	0.99 – 1.01	0.946
Terrain ruggedness	1.00	0.98 – 1.02	0.852
Human footprint	0.98	0.92 – 1.05	0.586
Latitude	0.99	0.93 – 1.06	0.829
Tree cover %	1.00	0.99 – 1.02	0.834
Log human encounter rate	1.21	1.04 – 1.31	**0.011**
Prey nighttime activity	0.29	0.05 – 1.73	0.173
Eurasian Lynx			
Model	Odds Ratios	CI	p-value
Road density	1.00	1.00 – 1.00	0.392
Population density	1.01	0.99 – 1.02	0.441
Terrain ruggedness	0.99	0.96 – 1.01	0.396
Human footprint	1.05	0.85 – 1.29	0.650
Latitude	1.07	0.97 – 1.18	0.191
Tree cover %	0.99	0.95 – 1.02	0.481
Log human encounter rate	1.10	0.91 – 1.34	0.325
Prey nighttime activity	3.63	0.04 – 456.15	0.590

Figure A1Wolf and Eurasian lynx activity curves for study sites where data was available (Maremma Regional Park and Plitvice Lakes National Park) during summer (1st May – 31st August). Observations during summer had a mean night length of 7.9hours in Maremma Regional Park and 8.0hours in Plitvice Lakes Regional Park.Figure A1 Figure A2Activity curves showing camera trap activity density for wolves and humans (top rows) and Eurasian lynx and humans (bottom rows) for each study site.Figure A2 Figure A3Simple linear regressions between night activity probability and study site level human disturbance and environmental factors for wolves (left plots) and Eurasian lynx (right plots). Blue points on the regression plots indicate the values for the Chornobyl Exclusion Zone as a human-restricted baseline. Only human encounter rate (log-transformed) for wolves significantly increased nighttime activity probability. Figure A3



(caption on next page)

Figure A1. Activity curves showing camera trap activity density for wolves and humans (top rows) and Eurasian lynx and humans (bottom rows) for each study site.

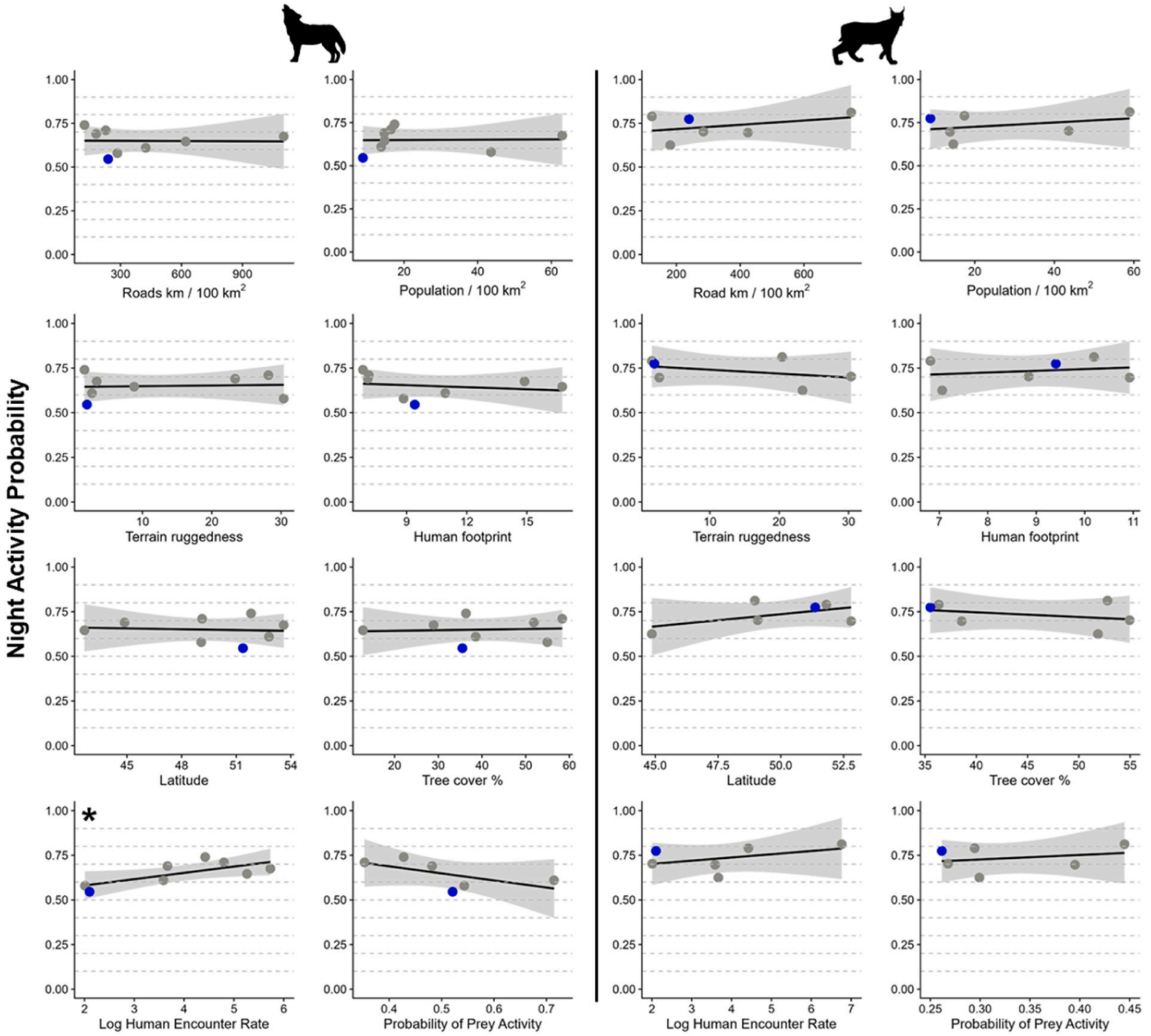


Figure A2. Simple linear regressions between night activity probability and study site level human disturbance and environmental factors for wolves (left plots) and Eurasian lynx (right plots). Blue points on the regression plots indicate the values for the Chornobyl Exclusion Zone as a human-restricted baseline. Only human encounter rate (log-transformed) for wolves significantly increased nighttime activity probability.

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