



Temporal activity patterns of bears, wolves and humans in the Cantabrian Mountains, northern Spain

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Abstract

Human-wildlife coexistence is important for a sustainable relationship between humans and the natural environment. However, human activities often act as a disturbance to wild animals, which may show behavioural shifts indicating human avoidance. For large carnivores, which are prone to conflict with many human interests, coexistence with humans can be particularly challenging. We used long-term camera trap data to evaluate seasonal and diel variations in activity of two large carnivores, the brown bear (*Ursus arctos*) and the grey wolf (*Canis lupus*), as well as humans in the Cantabrian Mountains, northern Spain. Brown bears were less active in winter than in summer; the opposite was observed for wolves, whereas there was limited seasonal variation in human activity. On a diel scale, both bears and wolves were mostly crepuscular during summer and had less distinct, but generally more nocturnal activity during winter. Humans were strictly diurnal during both seasons. We suggest that the diel activity of bears and wolves was partially caused by human avoidance, but that seasonal variations in both overall and diel activity were mainly caused by ecological and physiological factors. While we suggest that the observed similarity in diel activity of bears and wolves did not have caused strong competition between these two species, it may have influenced interactions with other predators and prey. Since such interactions are likely to be context dependent, we urge for further studies evaluating how humans influence the behaviour of large carnivores across different spatio-temporal scales.

Keywords Temporal niche use · Camera trapping · Human disturbance · Human-wildlife conflict · Large carnivores · Occupancy · Cantabria

Introduction

Conservation biology has seen several major paradigm shifts during the last centuries, with the current one being focused on the incorporation of humans within the biological and

geophysical environment (Mace 2014). Within this conservation paradigm, sustainable coexistence between humans and wildlife is of obvious importance (Frank and Glikman 2019). However, such coexistence is not without challenges. For instance, there are often intense conflicts between human

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activities and wildlife (Woodroffe et al. 2005; Leader-Williams et al. 2010; Redpath et al. 2013). Conflicts may arise when wildlife prey on livestock, destroy human properties, eat crops or attack people. These conflicts can also have socio-economic, cultural or political dimensions (Madden 2004; Dalerum 2021). Human-wildlife conflicts often result in persecution, which may have direct demographic effects on wildlife populations (Dalerum and Swanepoel 2017).

Human activities may also impact wildlife indirectly by acting as a disturbance, which may disrupt temporal and spatial patterns of activity (Frid and Dill 2002; Sutherland 2007). Avoidance of humans, in both space and time, is well documented across a wide range of taxa (Stankowich 2008; Larson et al. 2016; Pirodda et al. 2018; Suraci et al. 2019). In part, the strong behavioural responses to human disturbance may be attributed to humans' unique properties as predators (Darimont et al. 2015). Human persecution has driven directed and rapid selection of various phenotypic traits, including behaviour (Darimont et al. 2009). Disturbance may cause a displacement of animals into nocturnal temporal niches or into protected or inaccessible areas (Rode et al. 2006; Gaynor et al. 2018), but may also alter other aspects of animal behaviour, such as vigilance behaviour and movements (Jayakody et al. 2008; Doherty et al. 2021).

Large carnivores are particularly susceptible to causing conflicts with humans (Hovardas 2018). This is partly due to their predatory behaviour, which puts them in conflict with livestock owners and hunters (van Eeden et al. 2018), as well as other cultural and socio-economic factors (Dalerum 2021). In addition, the large area requirements of many large carnivores may lead to spatial overlaps with human activities, and also make them exposed to habitat degradation (Sunquist and Sunquist 2001; Finnegan et al. 2021). Furthermore, their relatively low natural mortality, low reproductive rates and low population densities make them demographically sensitive to human persecution and disturbance (Purvis et al. 2000). Hence, their biological properties make large carnivores both exposed to potential conflicts and also more sensitive to its possible consequences. However, despite the large amount of studies on the direct effects of human persecution and habitat degradation on carnivore population persistence (reviewed in Gittleman et al. 2001; Hovardas 2018), there are still limited studies on the effects of human activity on large carnivore behaviour.

Brown bears (*Ursus arctos*, hereafter referred to as "bear" or "bears") and grey wolves (*Canis lupus*, hereafter referred to as "wolf" or "wolves") are two large carnivores that are frequently in conflict with humans (Breitenmoser 1998; Graham et al. 2005). In Europe, they both inhabit human-dominated landscapes, with the southernmost European populations occurring in northern and central Spain (Chapron et al. 2014). Both bears and wolves have historically been persecuted in Spain, mainly due to the damages caused to

livestock, crops and beehives (Blanco et al. 1992; Fernández-Gil et al. 2016). Currently, the brown bear is nationally listed as endangered, whereas the Spanish wolf is listed as a species requiring special protection (Ordiz et al. 2022). Spain is a relatively densely populated country, with approximately 20% of its close to 50 million inhabitants living in rural areas (World Bank 2022). Furthermore, livestock husbandry is common across the landscape (Delgado-Serrano and Hurtado-Matos 2018), and outdoor recreation is becoming increasingly popular (Rivera 2015). Hence, Spanish bears and wolves are likely to face frequent encounters with humans which may influence their behaviour in addition to the effects caused by direct persecution.

In this study, we used a long-term dataset of automated camera traps to assess the temporal activity patterns of brown bears, wolves and humans at seasonal and diel scales in a rural area of the Autonomous Region of Cantabria (hereafter referred to as "Cantabria"), northern Spain. Although brown bears in our study area may not necessarily hibernate (Nores et al. 2010; González-Bernardo et al. 2020), we anticipate them to display more seasonal variation in activity compared to wolves. Wolves, being primarily active hunters, are expected to maintain consistent activity levels throughout the seasons (Mech 1970). Since wolves have experienced the hardest persecution (Fernández-Gil et al. 2016; Quevedo et al. 2019), we expect lower overlap in diel activity between wolves and humans than between bears and humans. In addition, we expect the brown bear to show the biggest seasonal variation, both overall and in diel activity.

Material and methods

Study area

The study area covers approximately 1125 km² of the southwestern parts of the Autonomous Region of Cantabria, which extends approximately 130 km east to west and 70 km north to south along the south shore of the Bay of Biscaya in northern Spain (Fig. 1). The topography along the coast includes undulating hills and valleys, with the relief of the terrain becoming more pronounced inland closer to the Cantabrian Mountains. The elevation of the study area is highly variable, ranging from 400 to over 2000 m above sea level. The climate is atlantic, with a relatively small seasonal temperature oscillation (Peel et al. 2007). Winters are generally mild except for high alpine areas, with average temperatures of 9 °C, and summers only reaching moderate temperatures averaging 20 °C (Ancell Trueba and Célis Diaz 2012). Precipitation is abundant around the year, with an annual precipitation of approximately 1000 mm (Ancell Trueba and Célis Diaz 2012). Cantabria has a human population of 600,000,

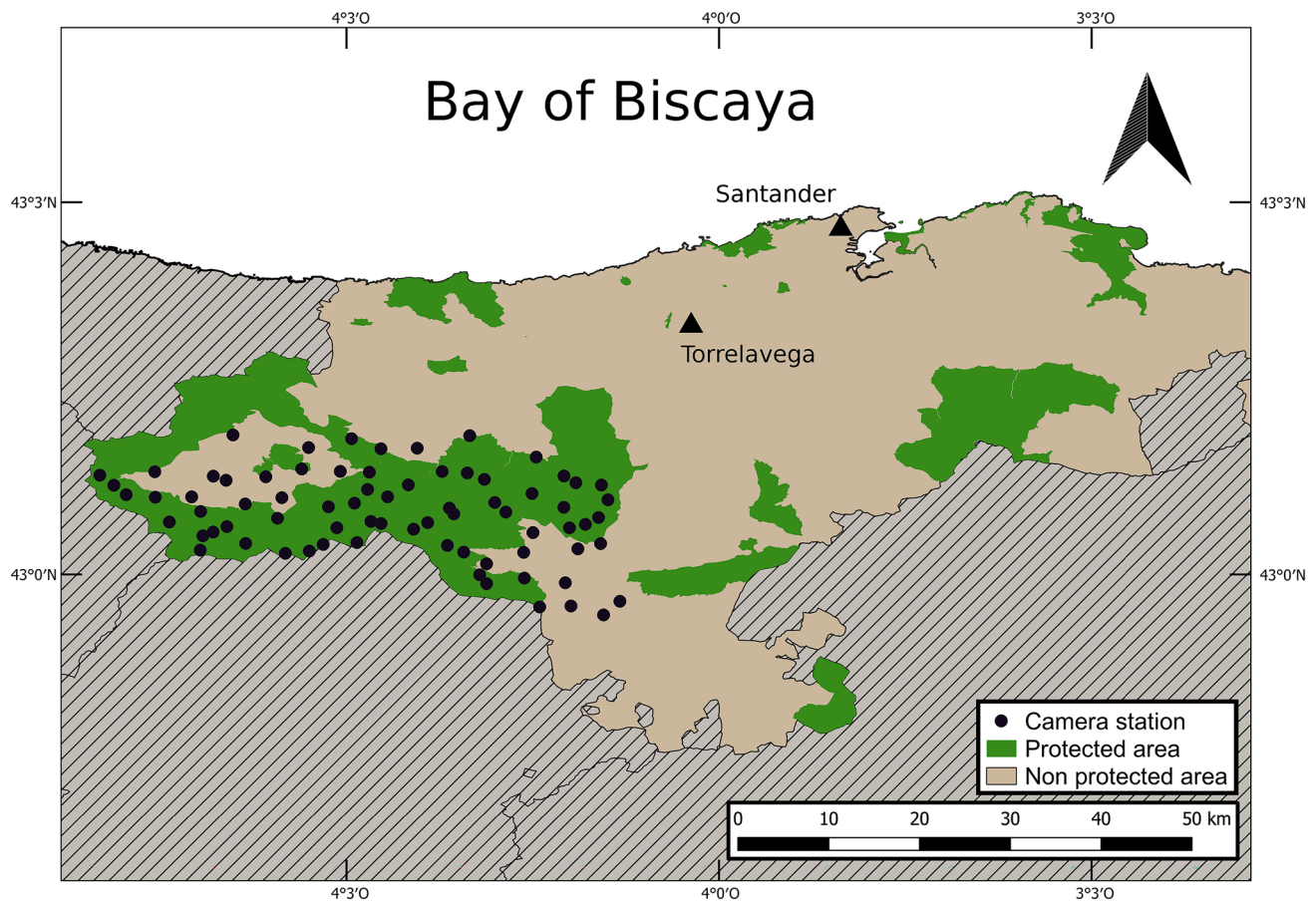


Fig. 1 Location of the Autonomous Region of Cantabria in northern Spain as well as the locations of the trap camera stations within the province

which gives an average human density of 109 humans/km² (Instituto Nacional de Estadística, <https://www.ine.es>). Most people are distributed in and around the two main cities of Santander (approximately 180,000 inhabitants) and Torrelavega (approximately 60,000 inhabitants), and human population density generally declines from the coast towards the inland. Important economic activities in rural areas include livestock farming, mostly cattle, but mining, tourism and mountain sports, hunting, agriculture and timber harvesting are also of local importance.

Much of former forest has been transformed into pasture and brushwood, but vegetation and land use vary with altitude. The most common vegetation types in the study area are different types of deciduous forests, comprised of species such as beech (*Fagus sylvatica*), oak (*Quercus* sp.), holly (*Ilex aquifolium*) and birch (*Betula* sp.), as well as chestnut (*Castanea sativa*) and hazel (*Corylus avellana*) (Durán-Gómez 2014). The mammal community consists of two large carnivores, the bear and the wolf, a number of mesocarnivores, large herbivores such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus*

scrofa) and chamoix (*Rupicabra rupicabra*), as well as smaller mammals (Palomo et al. 2007).

Camera trapping

Camera trapping took place between 2016 and 2022 using a total of 85 camera stations (Fig. 1). To maintain distance between the stations, a grid with a cell size of 5 × 5 km was superimposed across the study area. The Cantabrian Mountains are highly heterogeneous and complex both topographically and in land cover (Grilo et al. 2019; Ávlarez García 2007). This grid size therefore represents spatially independent sample units. From 2016 to 2018, one station was placed within each of 36 cells, with a minimum distance of 3.5 km between two stations. From 2019 to 2022, the survey was expanded so that one station was placed within each of 45 cells, with the same minimum distance. Of these 45 stations, 15 were kept in the same locations as the earlier period. In addition, from 2018 to 2022, an additional 2–9 extra cameras were placed within the grid every year. The number of active stations at any

given time therefore varied from 36 to 54. The number of active days for each station varied from 21 to 660 (mean of 325 days \pm SD 171 days).

Each station consisted of a single motion triggered digital camera (Bushnell Trophy Cam Aggressor No Glow, Bushnell, Corp., Overland Park, Kansas, USA) placed on a tree trunk approximately 1 m above the ground. Each station was baited with a fish scent placed approximately 7 m in front of the camera. This bait was placed to attract animals into an appropriate position in front of the camera. Since the bait was used in a consistent manner during the full duration of the survey and for all stations, we argue that it did not influence our estimates of either seasonal or diel variations in animal activity. The angle of detection of each camera was 43.9°, and the angle of view was 35°. Each camera had a trigger speed of 0.6 s and was configured to take one photo as well as one 30-s video in daylight and one photo and one 15-s video at night. After each set of a photo and video, there was a period of 6 s until the camera could be triggered again. Maximum distance of detection was 25 m in daylight and 20 m at night. Each station was visited on a monthly basis to change batteries, download images and reapply the bait (Government of Cantabria 2021).

Although the camera trapping program was ongoing during the whole period, we focused only on data recorded during June and July, reflecting late spring and early summer (referred to as “summer”) and December and January, reflecting late fall and early winter (referred to as “winter”), except for the summer period in 2020. These two periods represent the months with most (summer) and least (winter) daylight hours in our study area (<https://gml.noaa.gov/grad/solcalc/>). We opted to define our sample periods based on light regimes due to their strong effects on animal activity across different temporal scales (Wetterberg 1994). We excluded observations from June and July in 2020 due to possibly confounding effects of Covid-19-related restrictions of human movements (Rutz et al. 2020). We used all observations of bears, wolves, humans and domestic dogs, except shepherd dogs, made at different stations or at the same stations at least 30 min apart for our data analyses. Since there are no feral dogs in our area, we assumed that all dogs except shepherd dogs were accompanied by a person and hence reflected human activity. Shepherd dogs are frequently left unattended for days in the area, and can thus not be used as indicators of human activity.

Data analyses

We estimated seasonal levels of activity from the single season occupancy model initially proposed by MacKenzie et al. (2003). For each species, we fitted separate models for winter and summer. Each model was fitted on data pooled

across all years, using a whole sampling period (i.e. December and January for winter and June and July for summer) as our smallest independent observation unit. We fitted number of days active as a station-level covariate for each sampling period. Fitting the models on data pooled in this way prevented the fitting of models on zero-inflated data, which may hamper the model-fitting process (MacKenzie et al. 2006). We recognize that there may not be much seasonal difference in the occupancy of neither bears, wolves nor humans in our study area, i.e. we do not expect that either of these species would leave or enter the study area on a seasonal basis. However, we believe that occupancy estimates provide a useful heuristic measurement of overall activity that accounts for imperfect detection.

We estimated diel activity patterns using a kernel-based density estimator based on the time stamp of camera trap observations, converted to radians (Ridout and Linkie 2009). We made separate activity estimations for each species and each season. We used a non-parametric estimation of the common area under the estimated probability density curves as an index of temporal overlap both between seasons for bears, wolves and humans separately, as well as between each pair of species within each season. The estimator ranges from 0 (no overlap) to 1 (overlap), and was calculated using the following equation:

$$\Delta 1 = \frac{\sum_i^T \min \{f(t_i), \hat{g}(t_i)\}}{T}$$

where T is a large number of equally spaced values between 0 and 2π , which in our case was set to 128, and $f(t_i)$ and $\hat{g}(t_i)$ are the two estimated density distributions reflecting activity at time t (Schmid and Schmidt 2006). Since we were interested in describing differences in activity rather than overlap, we have presented the results as the additive inverse of the overlap index (Greco et al. 2021). We used permutation tests to evaluate if the observed values of overlap deviated from random expectations for each contrast, i.e. winter versus summer for each species and each species pair within each season. These tests were based on 1000 permuted datasets where the time stamps were randomly re-assigned to each observation. We evaluated the likelihood of the observed overlap using Z score conversion but adjusted the corresponding two-tailed p values for multiple comparisons using a method controlling the false discovery rate (Benjamini and Hochberg 1995).

Results

Our observations were based on 27,731 individual camera trap nights, 15,185 during winter and 12,546 during summer. We obtained 44 independent observations of bears

during winter and 79 during summer, 215 and 82 observations of wolves during winter and summer, respectively, and 238 observations of humans during winter and 108 during summer. These observations were recorded at 16 and 38 stations for bears during winter and summer, 61 and 29 stations for wolves and 60 and 41 stations for humans.

Bears had substantially lower activity in winter (mean occupancy \pm SE = 0.33 ± 0.10) than in summer (0.84 ± 0.14), whereas the opposite was observed for wolves (winter 0.99 ± 0.08 ; summer 0.71 ± 0.16 , Fig. 2). Humans, in contrast, showed limited seasonal variation in activity (winter 0.89 ± 0.06 ; summer 0.85 ± 0.12) (Fig. 2).

Brown bears and wolves had less pronounced diel variation in activity in winter than in summer, with both species showing distinct crepuscular activity during summer (Fig. 3a, c) and mainly nocturnal activity in winter (Fig. 3b, d). Humans were strictly diurnal during both summer (Fig. 3e) and winter (Fig. 3f). There were significant differences in diel activity between summer and winter for both bears ($Z = 3.45$, $p_{adj} = 0.001$) and wolves ($Z = 4.74$, $p_{adj} < 0.001$), but not for humans ($Z = 0.50$, $p_{adj} = 0.615$). There were also significant differences in diel activity between both bears and wolves in winter ($Z = 2.41$, $p_{adj} = 0.020$), but not in summer ($Z = 1.97$; $p_{adj} = 0.06$). Diel activity of humans differed from both bears and wolves during winter (bears: $Z = 10.54$, $p_{adj} < 0.001$; wolves: $Z = 21.31$, $p_{adj} < 0.001$) as well as during summer (bears: $Z = 9.59$, $p_{adj} < 0.001$; wolves: $Z = 8.00$; $p_{adj} < 0.001$) (Table 1).

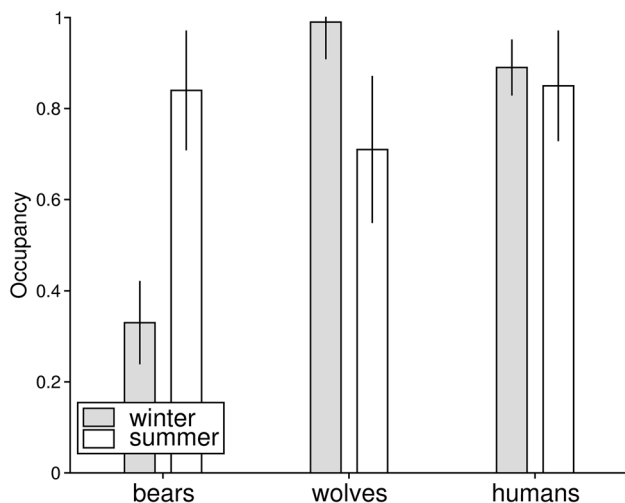


Fig. 2 Occupancy estimates for winter (December and January) and summer (June and July) for bears, wolves and humans in the Autonomous Region of Cantabria, northern Spain. Occupancy estimates were derived from occupancy models and based on camera trap data collected between 2016 and 2022, and should be interpreted as a relative index of seasonal activity within each species

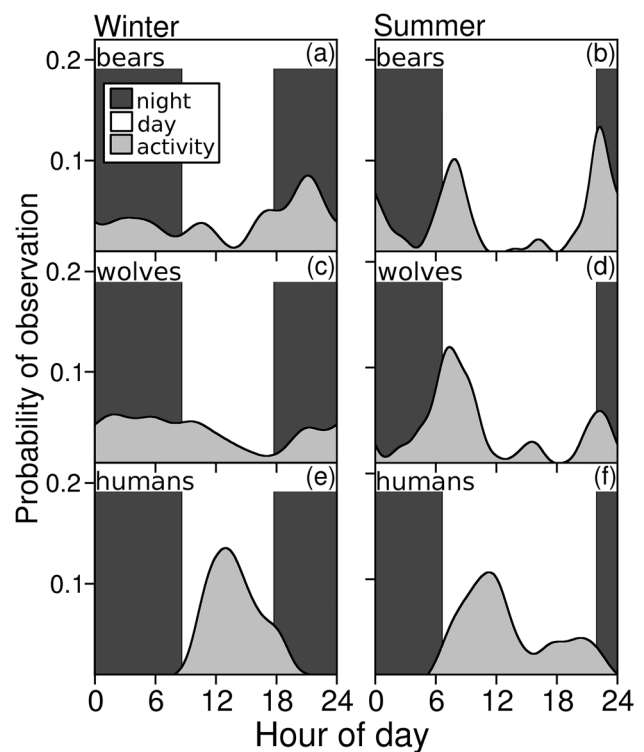


Fig. 3 Probability distributions describing temporal activity of bears in winter (a) and summer (b), wolves in winter (c) and summer (d) and humans in winter (e) and summer (f). The probability distributions were estimated from camera trap observations made from 2016 to 2022 in the Autonomous Region of Cantabria, northern Spain

Discussion

We noted clear distinctions in the diel activity patterns of both bears and wolves when compared to humans. The two carnivores exhibited predominantly crepuscular or nocturnal activity, whereas humans displayed strictly diurnal activity. We suggest that these results indicate temporal avoidance of humans on a diel timescale. Such avoidance is likely a consequence of past or present persecution (Blanco et al. 1992; Fernández-Gil et al. 2016). The observed bear and wolf diel activity in Cantabria generally agrees with previous observations of these species (Theuerkauf et al. 2003; Ordiz et al. 2011; Støen et al. 2015), and our interpretation of these results lends further support to general suggestions of an increased nocturnality in animals due to human disturbance (Gaynor et al. 2018; Nix et al. 2018). However, the observed seasonal variation in activity of bears and wolves did not seem to be linked to similar seasonal variation in human activity. Therefore, the activity patterns in these two large carnivores appear to be dictated by a combination of human avoidance as well as other factors linked to energetic constraints and prey activity (e.g. Capellini et al. 2008; Vallejo-Vargas et al. 2022). Our study therefore points to the complexities

Table 1 Results from pairwise tests for differences between winter and summer in diel activity of brown bears, wolves and humans in the Autonomous Region of Cantabria, northern Spain, as well as differences in diel activity between each pair of species during winter and summer. Observed differences were calculated as the additive inverse of a temporal overlap index calculated on the time of camera trap observations and represent the proportional pooled activity between two areas that do not overlap. The expected differences were calculated from 1000 random permutations of the observation times from each pair of areas. Deviations from random expectations were evaluated by Z score conversion, and the associated two-tailed *p* values were adjusted for multiple comparisons controlling for the false discovery rate

Contrast	Observed difference	Expected difference	Z	<i>p</i> _{adj}
Between seasons				
Bears	0.35	0.18	3.45	<0.001
Wolves	0.26	0.11	4.74	<0.001
Humans	0.08	0.10	0.50	0.615
Between species, winter				
Bears-wolves	0.24	0.14	2.41	0.020
Bears-humans	0.55	0.14	10.54	<0.001
Wolves-humans	0.59	0.09	21.31	<0.001
Between species, summer				
Bears-wolves	0.24	0.17	1.97	0.060
Bears-humans	0.49	0.13	9.59	<0.001
Wolves-humans	0.40	0.12	8.00	<0.001

involved with the regulation of animal activity across different timescales (Halsey et al. 2018).

We suggest several possible ecological processes that could have been influenced by the observed patterns of temporal activity in bears and wolves. First, a similar diel activity of bears and wolves might lead to an intensification of intra- and inter-specific competition. However, even if carnivore competition can be severe (Polis et al. 1989; Palomares and Caro 1999; Donadio and Burskik 2006), we suggest that competition is unlikely in our area. We base this suggestion on the different resource utilization of the two species, with Cantabrian bears generally being omnivores and scavengers (Clevenger et al. 1992; Naves et al. 2006; Rodríguez et al. 2007) whereas wolves are hyper-predatory (Lagos and Bárcena 2018; Janeiro-Otero et al. 2022). While both bears and wolves were primarily crepuscular or nocturnal, they did separate their diel temporal niches, especially during winter. There is also the possibility of spatial rather than temporal avoidance among the two species (e.g. Ordiz et al. 2015). However, if the diel activity patterns were caused by human avoidance, so that animals were forced into similar temporal niches, it could influence intra-specific competition. This may be particularly relevant for the bears, which may suffer from human-induced increased infanticide risk in our study area (Penteriani et al. 2020). Altered activity

patterns in response to humans could also cause changes in predation patterns, mainly in the hyper-predatory wolf.

Bears showed a very marked seasonal pattern in overall activity, with lower activity in winter than in summer. While this observation agrees with the ecology of this species, which is largely dormant during winter across the majority of its range (Pasitschniak-Arts 1993), it provides further evidence for a lack of extended dormancy in this southern population (Nores et al. 2010; González-Bernardo et al. 2020). However, we suggest that the lower activity of bears during winter still highlights the energetic constraints experienced during colder periods (Capellini et al. 2008). We observed a largely crepuscular diel pattern in bear activity during summer, and a more nocturnal activity during winter. In northern Europe, where bears are hunted, bears become even more nocturnal when hunting season starts (Ordiz et al. 2012), as well as after encounters with people in the forest (Ordiz et al. 2013). Since there were less overall human activity during winter than during summer, and strict diurnal activity of humans during both seasons, bear seasonal shifts in diel activity might be prevalently caused by factors other than human avoidance.

Similar to the bears, the wolves exhibited mainly crepuscular diel activity during the summer, but this variation was less pronounced during winter, though they remained primarily active at night. Interestingly, the wolves showed increased activity in winter compared to summer. This lower summer activity could be attributed, in part, to restricted movements near breeding sites and broader territorial movements during non-breeding seasons to avoid prey depletion and conduct territorial surveillance (Jędrzejewski et al. 2001). On a diel timescale, lack of daytime activity in wolves has been mainly explained by temperature regulation, particularly during summer (Mech 1970), the need to hunt during times when prey are active (Torretta et al. 2017) and human avoidance (Ciucci et al. 1997; Frey et al. 2022). While we do not regard temperature regulation to be a particularly likely explanation in the Cantabrian Mountains, we recognize that we cannot distinguish between the effects of prey activity and direct human avoidance on wolf diel activity. However, as humans may influence the activity of many of the main prey species of wolves as well, we suggest that humans may influence wolf activity both directly, through avoidance behaviour, and indirectly by shifting the diel activity of prey (Monk et al. 2018). Such a shift in diel activity may influence wolf predation success, with possible demographic consequences both for the wolves and their prey (Wilson et al. 2020).

Humans, in contrast to bears and wolves, had a strictly diurnal diel activity but limited seasonal variation, both in overall activity and at a diel scale. A strictly diurnal human activity agrees with previous findings across the globe, and has frequently been suggested to cause

increased nocturnality in wildlife as a way of avoiding disturbance (Gaynor et al. 2018; Shamoon et al. 2018; Gallo et al. 2022), although animals already occupying nocturnal niches may be less affected by human activity (Reilly et al. 2017; Khatiwada et al. 2023). The lack of seasonal variation in human activity was slightly surprising, considering the strong pulse of tourist into the region in summer (Insitudo Nacional de Estadística 2023), as well as a documented shift in human diel activity when people are not working (Green et al. 2023). The observed lack of seasonal variations point suggests that the observed activity primarily consisted of local and regional residents, and also to some extent of professional activities such as animal husbandry or forestry.

Despite our study being based on a robust set of data collected during 6 consecutive years, we do recognize some limitations with our analyses. First, we have also only evaluated the activity of bears, wolves and humans along temporal scales. We recognise that behavioural responses to human activity might also include context-dependent spatio-temporal responses that were not captured in our analyses (e.g. Catford et al. 2022; Palmer et al. 2022), for instance related to the effects of density and distribution of human infrastructure or roads (e.g. González-Bernardo et al. 2023). Second, to achieve appropriate sample sizes for each season, we ran our analyses on pooled data across the whole study period. This was necessary, as the number of observations within individual seasons was too low for meaningful analyses, particularly for bears. Hence, we cannot rule out that our temporally pooled analyses could have masked changes in seasonal or diel variation in activity during the study period. Third, we based our study periods strictly on light regimes, and not on climate-based seasonal definitions or on biologically important periods for bears and wolves, e.g. during reproduction. While we recognize that other definitions of the study periods might have caused slight variations in the results, we justify our choice by the strong effects light regimes have on animal activity. Hence, we believe that our choice was appropriate for our analyses since it should generate strong seasonal contrast in activity. Finally, we assumed that seasonal differences in occupancy reflected seasonal differences in activity. Under the assumption that neither species differed in abundance across seasons, seasonal differences in occupancy could only be attributed to seasonal changes in activity or to seasonally altered space use. Altered activity would result in different number of observations whereas altered space use, given equal activity, would result in different number of camera stations with observations. Since we observed both, i.e. both different number of observations as well as different number of stations with observations, we believe that the observed seasonal differences in occupancy reflected actual variation in activity.

To conclude, we have highlighted important differences in the activity of two large carnivores, the brown bear and the wolf, and humans, during both summer and winter in a human-modified landscape. We suggest that these results were at least partly caused by a temporal avoidance of humans on a diel scale, which in the case of wolves may also have been a consequence of human avoidance by wolf prey. However, we also observed seasonal variation in overall activity and diel activity patterns of both bears and wolves that appeared to have been less linked to human presence, but rather to energetic constraints on movements for bears and to reproductive events for wolves. The complexity of the interactions of factors regulating large carnivore activity asks for further studies evaluating how humans influence the behaviour of large carnivores across different spatial and temporal scales.

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Author contributions TV and FD conceptualized the study, conducted data analyses and wrote the first draft of the manuscript, CM and VP assisted with data interpretation and manuscript preparation, and JG, MÁL, EM, PG, AC, BC, MJV and EÁ contributed with field data designed and carried out the field data collection. All authors commented on previous versions of the manuscript and have read and approved the final manuscript.

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Availability of data The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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