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Research Article

Hares, humans, and lynx activity rhythms: who avoids whom?

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Abstract

Predator-prey interactions and human presence are among the key factors shaping large mammal activity patterns. In human-dominated landscapes, large carnivores must balance their activity rhythms between optimizing feeding opportunities and avoiding encounters with humans. In northeastern Turkey, the Caucasian lynx (*Lynx lynx dinniki*), a threatened subspecies of the Eurasian lynx (*Lynx lynx*), occupies habitats that are heavily fragmented and dominated by human presence in the warm part of the year. Using camera traps and GPS-collar activity sensors, we investigated lynx circadian activity patterns across lunar phases and seasons. We compared the activity pattern of the lynx to the activity pattern of its primary prey, the European hare (*Lepus europaeus*), and humans. We found that during the warm season (May-October), lynx displayed a bimodal crepuscular activity pattern typical for this species and consistent with hare activity. During the cold season (November-April), both lynx and hares shifted to predominantly diurnal activity. During the full moon, hares reduced their activity due to the anti-predator behaviour, followed by a corresponding adjustment in lynx activity patterns. We conclude that lynx activity in our study area is an outcome of weather conditions, human presence and foraging behaviour. Our results also corroborate the suitability of camera trapping data in documenting multiple species' temporal activity patterns.

Introduction

Large carnivores are considered in conservation programs throughout the world since they often are recognized as keystone, flagship, and umbrella species that play essential roles in ecosystems (Linnell et al., 2000; Berger et al., 2001; Ripple et al., 2014). The conservation of these wide-ranging species and their habitats can facilitate the long-term persistence of many host ecosystems and co-occurrent species (Roberge and Angelstam, 2004).

Activity patterns of predators and their prey constitute crucial behavioural aspects that shape the interactions between species and their environment. In habitats where large carnivores coexist with humans, they often adjust their behaviour to anthropogenic presence in a similar way as prey respond to predation risk (Boydston et al., 2003; Ordiz et al., 2011; Corradini et al., 2021). Thus, in human-dominated landscapes, large carnivores may alter their behaviour to avoid encounters with humans, e.g., by shifting their activity towards night hours (Benítez-López, 2018; Gaynor et al., 2018; Nickel et al., 2020). Herbivores, on the other hand, must take into account both human and predation risk in their spatiotemporal decisions (e.g., Lone et al., 2014), though multiple factors related to physiology, optimization of foraging, competition, and niche partitioning, may come into play (McArthur et al., 2014; Sheremetev et al., 2014; Simon et al., 2019). Prey species may shift activity patterns (Nix et al., 2018; Wu et al., 2018; Bonnot et al., 2020), affecting the activity of their predators (Fenn and Macdonald, 1995; Harmsen et al., 2011). Shifts in circadian activity in both predator and prey species have potentially critical consequences for species ecology and ecosystems conservation (Kronfeld-Schor et al., 2017; Levy et al., 2018).

Eurasian lynx (*Lynx lynx*) is considered a roe deer (*Capreolus capreolus*) specialist in most of the species' range (Okarma et al., 1997; Molinari-Jobin et al., 2000). However, lagomorphs may also be an important in the lynx diet (Mengüllüoğlu et al., 2018; Soyumert et al., 2019). Previous studies on the activity patterns of several Eurasian lynx populations preying on roe deer have documented bimodal activity of the carnivore, with peaks during crepuscular hours driven mostly by the activity of its primary prey (Heurich et al., 2014). However, Kolbe and Squires (2007) found a more diurnal activity in Canada lynx *Lynx canadensis*, plausibly related to thermoregulatory and foraging strategies.

The activity of prey species, and consequently their predators, may also be influenced by moonlight. During intense moonlight, small mammals, such as rodents (Daly et al., 1992; Bouskila, 1995; Hemami et al., 2011) and lagomorphs (Prugh and Golden, 2014) reduce their activity to avoid predation (Daly et al., 1992; Hughes and Ward, 1993; Bouskila, 1995; Naderi et al., 2011). In a case where Eurasian lynx were primarily feeding on ungulates, Heurich et al. (2014) repor-

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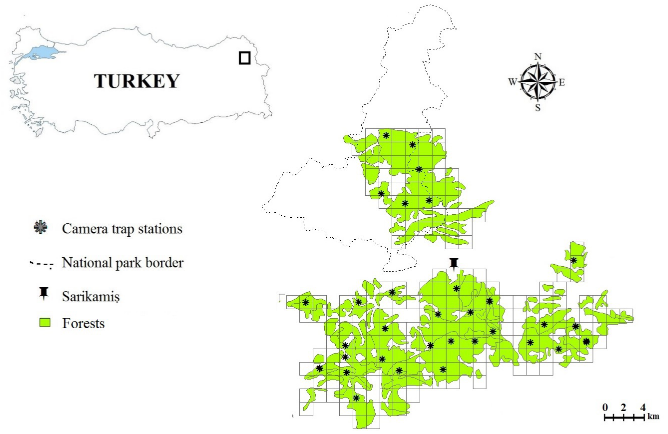

Figure 1 – The study area in the Kars province of north-eastern Turkey (black square). The points indicate the locations of camera stations used from 2015 to 2019 in 2 km^2 grids.

ted that moon phases had no meaningful influence on the activity patterns of lynx, likely because moonlight did not influence the activity of roe deer. However, moonlight may affect the activity of lynx which feed primarily on small mammals. For example, Iberian lynx (*Lynx pardinus*) showed reduced movements during the full moon (Penteriani et al., 2013), while bobcats (*Lynx rufus*) increased their movement rates during night time when lunar illumination was high (Rockhill et al., 2013).

We still lack a clear understanding of the ecology of the Caucasian lynx (*L. l. dinniki*), a subspecies of Eurasian lynx with a small population inhabiting highly fragmented forests at the intersection of the Caucasus and Anatolian global biodiversity hotspots in north-eastern Turkey (Chynoweth et al., 2015; Kitchener et al., 2017). European hares (*Lepus europaeus*) comprise the main prey of lynx in this region (Mengüllüoğlu et al., 2018), especially because roe deer is scarce due to poaching (Chynoweth et al., 2015). Apart from habitat fragmentation and prey scarcity, this lynx population is severely impacted by vehicle collisions, poaching, and livestock guarding dogs (Chynoweth et al., 2015). There is little information regarding the interdependence of lynx-hare behavioural interactions, including activity rhythms, in this area.

In this study, we analysed the activity patterns of lynx and hares in an area dominated by human activity in north-eastern Turkey. We used camera traps and GPS-collar activity sensors to understand if lynx activity rhythms were related to the circadian activity patterns of European hares and humans across seasons and lunar phases. We addressed the following questions and hypotheses:

1) Do lynx circadian activity patterns follow the activity of hares? If true, we expect a high degree of overlap between lynx and hare circadian activity patterns across seasons;
2) Does moonlight affect the activity of both species? If true, we expect a corresponding variation in activity rhythms of lynx and hares among moon phases;
3) Does human presence affect lynx activity with respect to the circadian and seasonal cycles? If true, we expect the lynx to display a nocturnal and crepuscular activity during the warm season, and to shift to more diurnal activity during the cold season, when human presence is negligible.

Materials and methods

Study area

The study site was in Kars province in north-eastern Turkey, near the town of Sarıkamış (40°11′ to 40°27′ N, 42°24′ to 42°49′ E, Fig. 1). The study area consisted of four forest patches with a total area of 338.5 km^2. The three southern patches are logged commercially and the northern fragment has been mostly protected and is in the Sarıkamış Forest-Allahuekber Mountains National Park (Fig. 1).

The study area has a semi-continental climate (Cozzi et al., 2016) mostly affected by the Caucasian climatic regime. August is the warmest month (mean temperature = 15.6 °C), and January is the coldest (mean temperature = −8.1 °C). Snowfall usually starts in October, and the mean depth of the snow cover typically exceeds 53 cm from January to March. The study area is usually covered by snow for more than 200 days every year (Sarıkamış Weather and Snow Trends, 2020). The altitude ranges from 2100 to 3120 m a.s.l. Due to relatively intensive agrarian activities in the area, including livestock grazing and logging for fuel or other usages, the landscape has been occupied for a very long time and has an extended history of human influence, including decreases in tree canopy cover, forest continuity, and to some extent, changes in the overall composition of regional flora (Cozzi et al., 2016).

Vegetation growth season in the study area lasts approximately 150 days (*pers. obs.*). All forest patches are heavily fragmented, and the forest is dominated by Scots pine (*Pinus sylvestris* var. *hamata*), European aspen (*Populus tremula* L.), ash (*Fraxinus* spp.), and sessile oak (*Quercus petraea*) (Atalay, 1983). Forest understory vegetation varies from almost none to a dense undergrowth of various members of the *Rubus* genus. Brown bears (*Ursus arctos*), gray wolves (*Canis lupus*) and Caucasian lynx constitute the community of large carnivores in the study area (Chynoweth et al., 2015; Capitani et al., 2016), and there is a high degree of large-carnivore-related human-wildlife conflict (Chynoweth et al., 2016). Medium- and small-sized carnivores occur in very low densities, even lower than large carnivores (KuzeyDoga, unpublished data; Karataş, *pers. comm.*, 2021). The small mammal community consists primarily of European hares, red squirrels (*Sciurus vulgaris*), Caucasian squirrels (*Sciurus anomalus*), Williams' jerboa (*Allactaga williamsi*), and several species of Muridae (mainly *Apodemus* spp. and *Microtus* spp., Kryštufek and Vohralík, 2001). Wild boar (*Sus scrofa*) is the only commonly occurring wild ungulate species, and there are very few records of roe deer in the area (Chynoweth et al., 2015). Formerly present red deer (*Cervus elaphus*) is now locally extinct (Chynoweth et al., 2015). Around 85% of the study area, especially the three southern forest patches, is affected by regular seasonal logging activities (mainly in late spring and summer). Illegal tree cutting is widespread everywhere, including in the national park (Şekercioğlu, 2012). Outside the winter season, human activities involve livestock herding, recreation (picnicking), and wild herb and mushroom collecting (Cozzi et al., 2016).

Camera trapping

Data collection took place as part of the large carnivore study by KuzeyDoğa, a nature conservation organization that works in north-eastern Turkey. This region is located at the confluence of the Caucasus and Irano-Anatolian biodiversity hotspots and it is known for its high biodiversity and threatened ecosystems (Akküçük and Şekercioğlu, 2016). We installed cameras (Reconyx Ultrafire XR6 and Reconyx PC900) at the intersections of minor forest roads and wildlife trails. The cameras were moved to new locations every summer from 2015 to 2021, except for summer 2017 (no data were collected during 2017 season due to funding issues). We used a 2 km^2 grid (generated in ArcGIS software ver. 10.3.1, ESRI, Redlands, CA) as the basis for the uniform-random distribution (Luo et al., 2020, Fig. 1) of camera trap stations, following study designs for lynx monitoring and based on Eurasian lynx average home range size (Zimmermann et al., 2013; Fležar et al., 2019). We systematically relocated some of the cameras to cover as much of the study area as possible (Fig. 1). The total number of cameras varied from 28 to 42 throughout the study period due to equipment theft and destruction. We did not use any bait or attractant at the camera trap stations. To ensure no missing events, cameras were set for continuous activity, a series of five photos per trigger with no delay, medium sensitivity, and a 30-second sensor break between series (Kays et al., 2009). All cameras were set to record the date, time, ambient temperature, and location. We checked camera stations routinely, approximately every three months, to change batteries and download photos.

Table 1 – Data on the GPS-tracked lynx in north-eastern Turkey.

No.	Sex	Tracking period Start	Tracking period Finish	No. of activity readings
1	M	04/06/2014	14/03/2015	80538
2	F	20/06/2018	24/01/2019	61913
3	F	10/07/2018	08/07/2019	103337
4	F	03/06/2019	31/05/2020	104737
5	M	22/07/2019	19/07/2020	104754
6	F	27/06/2020	26/06/2021	104773
7	M	11/08/2020	01/08/2021	102305
8	F	20/08/2020	24/07/2021	97217

GPS-collar activity sensors

To investigate the year-round lynx activity patterns, we captured and fitted eight individuals with telemetry collars in 2014–2020 (Tab. 1). We used box traps equipped with GSM alarms set along plausible lynx travel routes, mostly along the forest roads. Captured animals were tranquilized with a combination of ketamine and medetomidine (Kreeger and Arnemo, 2012), examined, measured, sampled, and equipped with Vectronic Aerospace GPS-GSM/Iridium collars (Vectronic Aerospace GmbH, Berlin, Germany) with two-axis activity sensors which continuously recorded the acceleration and stored the values within a range of 0–255 in five-minute intervals.

Data analyses

Two consecutive photo series were considered as belonging to two different events when they were taken more than one hour apart (Rovero and Zimmermann, 2016). All recorded events of lynx, hares, humans, and roe deer were classified based on date, time, and location. The whole period in which cameras were active was considered as the total trapping effort (Jackson et al., 2006). To investigate the relationships between activity patterns of lynx, hares and humans, the number of events captured per camera trap day was estimated as the relative abundance index (RAI). For each target species, we calculated RAI as the total number of events per station multiplied by 100, and then divided by the number of camera trap days for the corresponding station (O'Brien and Kinnaird, 2013; Cusack et al., 2015).

All camera-trapping events were categorized into periods of the day: twilight, i.e. dusk and dawn (one hour before and after sunset and sunrise), daytime (from dawn to dusk), and night-time (from dusk to dawn) based on databases available online (https://www.timeanddate.com/). Since the duration of each period is different, the number of recorded events in each period was weighted to allow for comparison of activity levels among periods of the day: the numbers of events were divided by the total number of hours for the corresponding period, and then recalculated as relative percentages. We defined two seasons: warm (May-October) and cold (November-April) based on weather conditions to differentiate the warm vegetation season from the rest of the year (Turkey Weather Atlas, https://www.weather-atlas.com/en/turkey-climate). Based on the minimum number of required events (Otis et al., 1978), our camera-trapping dataset had enough statistical power for reliable interpretations only for the warm season. However, despite the lower number of events for winter period, we performed analogical statistical analysis for that period in order to compare them with the activity data of eight collared lynx. Therefore, the findings for hares' activity during the cold season should be interpreted with precaution.

We distinguished two lunar phases: the new moon (first and last quarter) and the full moon (second and third quarter) for the centre of the study area (https://www.timeanddate.com). The duration of full- and new-moon phases was homogeneously distributed among warm and cold seasons. We used linear regression to test the correlation between the lynx and hare RAIs at different camera stations. To compare lynx and hare RAIs between the moon phases at the same stations, we used the Wilcoxon signed-rank test and included only the nocturnal data sets.

To investigate the activity pattern overlap between lynx, hares, and humans, we adopted kernel density estimation (Lashley et al., 2018) after converting time format data to radians using `astroFns` package in R (R Core Team, 2019). We used the nonparametric Δ_4 coefficient of overlap, ranging from 0 to 1 (Ridout and Linkie, 2009). We also calculated 1000 smoothed bootstrap resamples to check the bootstrap bias and produce confidence intervals at 95% (Monterroso et al., 2014). To compare the RAIs of lynx, hares, and humans among camera stations, we used the Wilcoxon signed ranks test.

We separately analysed lynx activity data obtained from GPS-collar activity sensors to make a more robust inference of lynx activity in warm and cold seasons. Similar to camera-trapping data, we used kernel density estimation. To distinguish between active and inactive states, we followed an individual-based procedure developed by Gervasi et al. (2006) analysed separately for warm and cold season as recommended by Brivio et al. (2021). The threshold values of accelerometer's readings summed for X and Y axes ranged from 40 to 100, and differed among the seasons in four out of eight individuals.

Results

Camera trapping effort totalled 6845 trap days, 4156 during the warm season, and 2689 during the cold season. Cameras recorded a total of 1753 events of lynx, hares, and humans, of which 1626 events were recorded during the warm season and 127 events during the cold season. The number of recorded events of humans, lynx, and hares during the warm season was 1329 (RAI=39.08), 87 (RAI=3.91), and 210 (RAI=6.31) respectively, while during the cold season there were 75 (RAI=2.25), 14 (RAI=0.49) and 38 (RAI=2.01) events respectively. During the warm season, hares were mostly active at night (89% of events), while in the cold season, 73% of events were recorded during the day. Humans were rarely recorded at night (4.6% of events). Only three roe deer events were recorded during the whole study period, all in the Sarıkamış Forest-Allahuekber Mountains National Park, during the day and in the warm season.

Lynx circadian activity rhythms based on camera trap data

Two clear activity peaks of lynx were documented for the warm season, between 02:00 and 06:00 (N=43, 49.0%) and between 19:00 and 22:00 (N=39, 44.0%). After accounting for the length of the periods, the events were 30 times more likely to occur during twilight, and 6.4 times more likely to occur during the night, than during the daytime. Density plots of the lynx and hare activity times indicated a high overlap for warm season (Δ_4=0.77, bootstrap bias=0.13) and cold season (Δ_4=0.95, bootstrap bias=0.12). The overlap between lynx and human activity times was lower during the warm season (Δ_4=0.39, bootstrap bias=0.14) (Fig. 2) than during the cold season (Δ_4=0.93, bootstrap bias=0.11).

The linear regression showed a positive correlation between the RAIs of lynx and hares at the camera trap stations (r=0.84, SE=4.15). Wilcoxon signed ranks test indicated that the median RAIs of lynx and hares were significantly different during the new and full moon periods. Both lynx and hare activity were reduced during the full moon phase (Zlynx=-3.35, p<0.01, Zhares=-1.92, p<0.05) (Fig. 3). There was a significant negative correlation between RAI of lynx - humans and lynx - hares, based on RAIs at the same stations (Zlynx-human=-3.24, p<0.01, Zlynx-hares=-2.52, p<0.05).

Activity pattern of lynx based on acceleration sensor data from GPS collars

Activity data received from the collared individuals during the warm season confirmed that lynx were 3.15 times more likely to be active during twilight than during daytime and nighttime, and the number of activity events during day did not differ from the night time. During the cold season, about two-thirds of the lynx activity shifted mostly to daytime (Fig. 4).

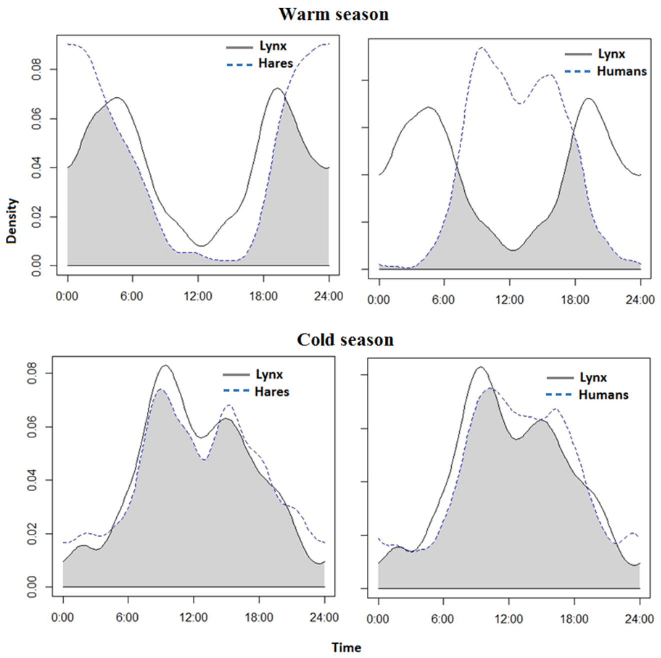

Figure 2 – Smoothed kernel density overlaps of lynx-hare and lynx-human activity periods during warm and cold seasons based on camera trap records in north-eastern Turkey in 2015–2019. The number of observations in the warm season: lynx: 87, hares: 210, humans: 1329 in the cold season: lynx: 14, hares: 38, humans: 75.

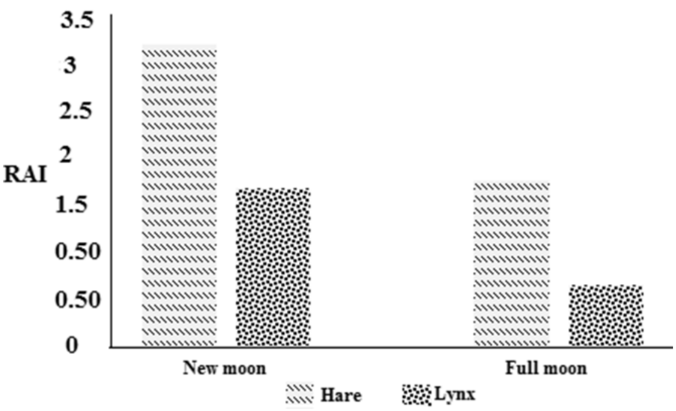

Figure 3 – Hare and lynx relative abundance (RAI indices) during new and full moon periods in north-eastern Turkey in 2015–2021.

Discussion

This study reveals several potential factors that shape the activity patterns of lynx in north-eastern Turkey. Our results indicate that lynx activity is correlated to the interactions between the seasonal and daily variations in the activity of hares, moonlight, weather conditions, and human presence. Lynx activity, revealed by both camera traps and GPS-collar activity sensors, followed a clear bimodal pattern during the warm season, with peaks during the twilight periods and higher activity levels at night compared to daytime. A similar crepuscular activity pattern was found in several Eurasian lynx populations and is considered an adaptation to hunting prey (Podolski et al., 2013; Heurich et al., 2014; Soyumert et al., 2019). The bimodal activity pattern of lynx partially followed the activity of its main prey, the European hare, consistent with our first hypothesis. However, hares seemed more nocturnal than lynx during the warm season, indicating other potential factors are involved in shaping lynx circadian activity rhythms.

Bimodal, crepuscular activity of Eurasian lynx feeding on ungulates has often been considered an intrinsic behaviour (e.g. Soyumert et al., 2019). However, the results of our study suggest that this may not be the case in north-eastern Turkey. During the cold season, lynx in our study area shifted to a predominantly daily activity pattern, clearly documented by data obtained both from camera-trapping and GPS-collar activity sensors. This shift might be caused by a combination of factors, including a similar shift in hare activity, low temperatures and snow cover, and less intensive human presence. A relatively low number of records of hares in the cold season prevents us from drawing strong conclusions regarding the relationship between lynx and hare activity.

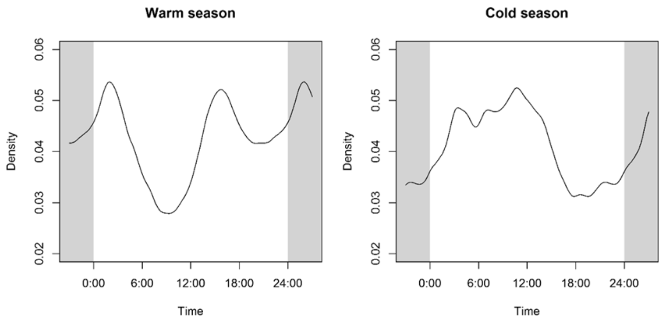

Figure 4 – Smoothed kernel density plots of lynx activity derived from collar acceleration sensors of eight individuals for the warm season (left) and cold season (right) in north-eastern Turkey in 2014–2020.

In turn, weather conditions and human presence were probably the main factors affecting the circadian activity patterns of hares. As the warm season coincides with a 17-fold increase in human activity in the lynx habitat during the day, both hares' and lynx's crepuscular and nocturnal activity was likely a strategy to avoid humans. Similar temporal avoidance of humans was observed in several large carnivore species (e.g., Kusak et al., 2005; Kaczensky et al., 2006; Odden et al., 2008; Bojarska et al., 2020). Moreover, hares and lynx possibly seek shelter from the hot weather during summer days, and from freezing weather during winter nights (Eriksen et al., 2011).

The low number of lynx and hare recordings during the cold season may have several explanations. One of them may be a local migration to areas with thinner snow cover, i.e. to south-facing slopes outside the forested area, which we have observed in wild boars (Kusak, *pers. comm.*, 2021). Moreover, forest roads typically have deeper and longer-lasting snow cover than their surrounding landscapes which may prevent the wildlife from using them in the cold season. Finally, some of the cameras during the initial years of the study were periodically covered with snow due to their low location on the tree trunks.

Hare activity was much lower during the full moon periods, which indicated their preference to reduce foraging and movement and/or stay hidden in denser microhabitats (Longland and Price, 1991; Hughes and Ward, 1993; Hemami et al., 2011). This corroborates earlier findings on the role of moonlight as an essential factor shaping the anti-predator behaviour of small mammals (Longland and Price, 1991; Vásquez et al., 1994; Bouskila, 1995; Hemami et al., 2011; Khalatbari and Naderi, 2018). We found that the lynx activity pattern was closely tied to hare activity levels at night and across the lunar phases, thus corroborating our second hypothesis. Therefore, lunar phases affect the lynx activity pattern indirectly by reducing the activity of its main small mammal prey, unlike where lynx feed on large herbivore prey (Heurich et al., 2014). This is the first study documenting a variation in activity across moon phases in the Eurasian lynx. A similar behavioural response to moonlight has been observed only in Iberian lynx, whose activity was reduced during the full moon period, following a decline in the activity of their primary prey (European rabbit *Oryctolagus cuniculus*; Penteriani et al., 2013).

Our data suggest that lynx activity patterns throughout the year were shaped directly by prey activity and to lesser extent are indirectly influenced by human presence, partly corroborating our third hypothesis. During periods with low human disturbance and in severe winter weather conditions, lynx may display diurnal activity synchronized with their prey. At night, when humans were not active, lynx activity rhythms also tracked hare activity across lunar phases. Lynx spatial behaviour may be shaped by humans during the day and by prey activity during the night (Filla et al., 2017). Since our cameras were placed on forest roads that humans use, the effect of human disturbance on lynx and hare activity in the summer may be even more pronounced due to avoidance of the roads during the day. This corroborates the hypothesis that humans drive an increase in nocturnal activity in wildlife (Gaynor et al., 2018). Our results also align with the general concept of the human role as diurnal "super predators", who interfere with predator-prey relationships at multiple levels and contexts (Clinchy et al., 2016; Haswell et al., 2017). Shifts in activity patterns help lynx and hares to avoid encounters with humans and, as such, may facilitate their survival in human-dominated landscapes. However, the consequences of these behavioural modifications for individual fitness and the long-term persistence of populations remain unknown.

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