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Research Article

Recreational activities affect resting site selection and foraging time of Eurasian lynx (*Lynx lynx*)

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Abstract

Over the past decades, non-consumptive outdoor recreation has intensified, resulting in a more widespread and regular human presence in natural habitats, including protected areas. This has shown to negatively affect several animal species, and in some cases, cause their decline. Therefore, understanding the impacts of recreation on protected species is fundamental. In the Bohemian Forest Ecosystem, we GPS-monitored the Eurasian lynx (*Lynx lynx*), generally considered tolerant to human presence. We tested whether the local level of recreation influenced (a) time spent by lynx at killed prey, both in terms of number of hours each night and of number of nights at each killed prey (i.e. feeding behavior) and (b) selection of daytime resting sites. Furthermore, we checked whether each behavior was influenced by local habitat features ensuring low accessibility to people and high protective cover, and by the level of nature protection assigned to different parts of the study area, all of which likely influence perceived risk by lynx. Finally, we tested for seasonal (winter vs. summer) changes in these variables' effects. Throughout the year, the local intensity and recurrence of recreation was negatively correlated with the probability that lynx would use a given location for daytime resting and with the number of hours that lynx spent at a given killed prey each night. Furthermore, habitat features providing protective cover positively correlated with both behaviors, and the probability that lynx would use a given location for daytime resting was higher inside than outside protected areas. Finally, recreation negatively correlated with the number of nights lynx spent at killed prey only in winter (i.e. October-April). These findings can be applied when planning recreational activities, and generally highlight the need for a deeper understanding of the impacts of human activities across a range of species.

Introduction

Ecotourism (*sensu* Geffroy et al., 2015) and outdoor recreation (*sensu* Sun and Walsh, 1998) are a large and growing global industry, representing a key component of the tourism industry in several countries worldwide (Eagles, 2002; Balmford et al., 2009). During the past few decades, this has led to an increase of human presence in natural and semi-natural areas, that otherwise would be characterized by very low human densities (Gill and Sutherland, 2000). According to IUCN regulations, in national parks (*sensu* Dudley, 2008) recreation and ecotourism are as important as protection of species and natural processes, and delivering recreational benefits consistent with the other objectives of management should be an aim in protected areas of all categories, wherever possible (Dudley, 2008). Therefore, the development of non-consumptive recreation (i.e. dispersed, non-motorized activities such as hiking, biking, horseback riding, cross-country skiing -as defined by Reed and Merenlender (2008)), is generally encouraged inside national parks, as the resulting economic gain can be used to enhance conservation projects and increase acceptance of protection measures within local communities (Goodwin, 1996; Eagles, 2002; Buckley et al., 2016).

Nonetheless, an increasing number of studies indicate that even these apparently harmless human activities are not always compatible with conservation objectives, and can negatively impact a wide range of wildlife species (e.g. Amo et al., 1990; Thiel et al., 2008; Reed and Merenlender, 2008; Buckley et al., 2016). In fact, humans are the dominant predator across many systems (Darimont et al., 2015), and a large number of species continue to be directly persecuted by humans, including species which have been given legal protection but are still threatened by illegal hunting (e.g. Muller et al., 2014). Furthermore, in some cases, such as when people approach on foot, disturbance stimuli and true predatory stimuli can be indistinguishable from most animals' perspective (Frid and Dill, 2002). This implies that even non-consumptive recreation can produce similar effects as predation risk (risk-disturbance hypothesis - Frid and Dill, 2002): it can repeatedly evoke antipredator responses, diverting time from important activities, such as foraging or resting (e.g. Duchesne et al., 2000; Fernández-Juricic and Telleria, 2000), and it can modify spatial and temporal patterns of habitat use by several species (e.g. Fernández-Juricic and Telleria, 2000), potentially reducing the size of suitable areas for their conservation (Taylor and Knight, 2003; Rösner, 2014). This may induce similar adverse effects as habitat loss and fragmentation (Fahrig, 2003) and reduce individual fitness (Phillips and Alldredge, 2000; Frid and Dill, 2002; Beale and Monagan, 2004), all of which could impact pop-

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ulation abundance (Gill and Sutherland, 2000; Fernández-Juricic and Telleria, 2000).

However, the impact of non-consumptive recreation on wildlife likely depends on a number of factors, including local recreation intensity (i.e. number of people performing an activity in a given area at a given time), its spatial distribution (Blanc et al., 2006; Mallord et al., 2007), and the habitat structure within a given area (Knight and Temple, 1995; Fernández-Juricic et al., 2001). Furthermore, animal species seem to differ in their sensitivity to human disturbance (Frid and Dill, 2002; Taylor and Knight, 2003) and well planned mitigation measures have been shown to increase certain species' tolerance to disturbances (Fernández-Juricic and Telleria, 2000; Ordiz et al., 2011). This highlights the importance of understanding the effects of non-consumptive recreation under different environmental conditions across a variety of species, with particular regard to those endangered and playing key roles in ecosystem processes.

Most large carnivores worldwide are given legal protection and are considered particularly vulnerable to extinction due to their own ecological traits (Purvis et al., 2000; Ripple et al., 2014). Although these species are considered quite tolerant to human presence (e.g. Linnell et al., 2005), this is likely due to their ability to avoid people at a fine spatio-temporal scale (e.g. Theuerkauf et al., 2003; Ordiz et al., 2011; Carter et al., 2012). In fact, large carnivores may be able to persist in areas of high human presence, by modifying their behavioral state (Smith et al., 2015), and seeking less frequented areas for behaviors of fundamental importance, such as denning, resting or consuming a killed prey (Bouyer et al., 2015a). Thus, recreational activities may potentially affect these relatively tolerant species, by reducing the availability of undisturbed habitat patches that provide safety during daytime (Sunde et al., 1998).

To date, relatively few studies have investigated the impacts of non-consumptive recreation on carnivorous predators (e.g. White et al., 1999; Naves et al., 2001; Nevin and Gilbert, 2005; Muhly et al., 2011; Carter et al., 2012), including large carnivore species such as cougars (*Puma concolor*), wolves (*Canis lupus*) and brown bears (*Ursus arctos*). These studies indicate that recreational activities can affect these species' spatial and temporal activity patterns, for example displacing individuals when resting (Naves et al., 2001) or feeding (Nevin and Gilbert, 2005), increasing daily movements (Naves et al., 2001) or reducing energy intake (White et al., 1999).

The Eurasian lynx (*Lynx lynx*, hereafter: "lynx") is one of the most widespread large carnivores. However, most lynx populations inhabiting Europe are small, isolated and threatened with extinction (Chapron et al., 2014). These solitary, crepuscular felids (Heurich et al., 2014) mainly prey upon small ungulates (i.e. roe deer *Capreolus capreolus* in most areas where it coexists with lynx; Nowicki, 1997) and generally feed on a prey carcass for several nights (e.g. Belotti et al., 2015), which maximizes caloric yield and compensate for the high energetic costs of killing large prey (Williams et al., 2014).

Although several studies throughout Europe have focused on how environmental characteristics, season, prey density, conspecific density, human population density and the level of anthropogenic habitat modification can affect lynx space use, habitat selection and hunting rates (e.g. Bunnefeld et al., 2006; Niedzialkowska, 2006; Nilsen et al., 2009; Belotti et al., 2013; Gervasi et al., 2014; Bouyer et al., 2015a,b; Filla et al., 2017), the potential effects of non-consumptive recreation on lynx still remain widely unknown (Filla et al., 2017). To our knowledge, these effects were only addressed in the Bohemian Forest Ecosystem, in Central Europe (Belotti et al., 2012; Filla et al., 2017). There, we found that during periods with access to killed ungulate prey, the distance from the site where the killed prey was located (hereafter: "kill site") and the corresponding lynx daytime resting sites was inversely correlated with the distance from the kill site to the closest tourist trail. In addition, even though the distribution of kill sites was not influenced by the distance to tourist trails (Belotti et al., 2012), lynx avoided the close proximity of tourist trails during daytime (Filla et al., 2017). This was interpreted as a behavioral response by lynx to human presence in the form of recreationists, which mainly use trails during light hours. Although mere behavioral reactions are not necessarily linked to negative impacts (*sensu* Beale, 2007), these findings suggest that intense and recurrent non-consumptive recreation may negatively affect lynx in the following ways. First, it may alter lynx resting site choice (as documented for other large carnivores, e.g. Ordiz et al., 2011), reducing their availability. In terms of lynx feeding activity, then, spending daytime hours far from the kill site may increase losses to scavengers (Krofel et al., 2012; Elbroch and Wittmer, 2013; Smith et al., 2015), thus reducing lynx energy intake. Furthermore, lynx traveling longer distances between a kill site and the corresponding daytime resting sites may compensate for the higher energy expenditure (Aldama et al., 1991; Karasov, 1992; Smith et al., 2015) by increasing foraging activity during each night spent at a killed prey, as suggested by Lima and Bednekoff (1999) predictions. Because night is when lynx feeding activity is concentrated (Podolski et al., 2013), and it is the period with lowest risk of human encounters (e.g. Ordiz et al., 2011), this may result in a longer time spent feeding on prey during single nights. Both circumstances may then lead to a lower number of nights spent at killed prey (i.e. shorter handling time, *sensu* Belotti et al., 2015), either accompanied by a decreased total energy intake per prey item (Kerley et al., 2002) or not.

In this study, we assessed whether the local intensity of non-consumptive recreation: (i) increased the time (i.e. the number of hours) that lynx spent at killed prey (i.e. roe deer, red deer *Cervus elaphus*, brown hare *Lepus europaeus*) during a single night (hypothesis 1); (ii) decreased the number of nights that lynx spent at a killed prey (hypothesis 2); (iii) reduced the probability that a given area will be used by lynx for daytime resting (hypothesis 3).

Finally, habitat features ensuring lower accessibility for humans and higher protective cover for lynx (namely high terrain ruggedness, steep slope, dense forest cover or understory layer) likely reduce the level of risk perceived by lynx and other carnivores (Sunde et al., 1998; Ordiz et al., 2011; Belotti et al., 2012). Furthermore, perceived risk is likely influenced by the local intensity of human activities other than recreation (e.g., forestry, hunting, farming; Bunnefeld et al., 2006; Bouyer et al., 2015a) and by the actual risk of illegal killing (Filla et al., 2017), both of which are higher outside protected areas compared to within protected areas (e.g. Muller et al., 2014). Therefore, in accordance with the predictions by the ecology of fear (Brown et al., 1999) and the risk-disturbance hypothesis (Frid and Dill, 2002), we also hypothesized that both measures of time spent at the killed prey and the probability that a given area will be used for daytime resting would be positively correlated with the presence of the habitat features described above (hypothesis 4) and would be higher inside protected areas compared to outside protected areas (hypothesis 5).

Materials and methods

Study area

The Bohemian Forest Ecosystem (hereafter: BFE) is a forested mountain range situated between 600 and 1456 m above sea level located along the Germany-Czech Republic border. This region encompasses the Šumava National Park (680 km^2) and a surrounding belt of Protected Landscape Area (hereafter: PLA, 990 km^2) on the Czech side, the Bavarian Forest National Park (Germany, 240 km^2) and the Bavarian Forest Nature Park (3,007 km^2) on the German side. This area is subject to different levels of nature protection, and the main human activities are hiking, biking, horse-back riding, cross-country skiing and mushroom and berry picking (hereafter collectively referred to as: "recreational activity"). These activities are mostly performed during light hours (Seibold and Shao, 2014) and in the first and core zones of the National Parks they are only allowed on-trail. To a lesser extent, forest management also takes place inside all protected areas, outside the non–intervention zones of the National Parks. The foothills around the entire system of protected areas (10 km belt) are characterized by a denser net of paved roads, several small human settlements and a stronger influence of forestry and agricultural activities. Recreational activity is much less intense in the foothills, except for a few renowned localities close to the main towns and except for mushroom and berry picking, which is widespread throughout the study area (apart from first zones of both National Parks and PLA Šumava). Human population density varies from 1.9 ind./ km^2 in the central parts to approximately 30 ind./ km^2 at the margins on the Czech side and 70 ind./km^2 at the margins on the German side (Podolski et al., 2013).Throughout the region, the mean annual precipitation varies between 830 and 2230 mm. Snow cover persists for 7-8 months at the higher elevations and for 5–6 months in the valleys. The forest cover of the entire mountain range is approximately 60% but reaches 90% in the two National Parks (Wölfl et al., 2001).

The Eurasian lynx was reintroduced into the Bavarian Forest and Šumava National Parks in the 1970s and 1980s, respectively (Wölfl et al., 2001). Since then, it has been the only large carnivore permanently inhabiting the region[1] (Anděra et al., 1994), with estimated densities ranging from 0.4 to 0.9 independent lynx/100 km^2 for the core area (Weingarth et al., 2012). The most abundant carnivore is the red fox (*Vulpes vulpes*, Anděra et al., 1994), while the primary species of wild ungulate are roe deer, red deer and wild boar (*Sus scrofa*). Roe and red deer represent more than 90% of lynx kills (Belotti et al., 2015). Outside the National Parks both deer species are hunted by local hunters during specific seasons (and, in the PLA Šumava, in compliance with this area's management plan prepared by the Šumava National Park Administration), while wild boar is hunted year-round. Inside both Parks, characterized by the strictest level of protection, roe deer hunting has been prohibited for the past decade, while red deer and wild boar hunting is still partially allowed and is performed by National Parks' employees, to control species abundance (Heurich et al., 2015).

For the current research, we focused on an area of about 1400 km^2, resulting from the sum of 100%-Minimum Convex Polygon home ranges of GPS-monitored lynx (see below). Each of these home ranges included both protected and unprotected areas. The entire study area is permanently occupied by lynx on a coarse scale (Magg et al., 2015) and is located at the core of this lynx population's distribution (Muller et al., 2014).

Lynx data

Between 2005 and 2012, 10 lynx (6 males and four females) were live-trapped (see Belotti et al., 2012), fitted with GPS/GSM-collars (Vectronics Aerospace, Berlin) and monitored for periods ranging from 101 to 870 days (mean=466 days, SD=229 days). Individuals collared during the first two winters (one male and one female) were monitored for nocturnal activity (three GPS positions per night recorded). All other collars registered one GPS-position at midday, when lynx is generally resting (Podolski et al., 2013; Heurich et al., 2014), and one at midnight, when lynx is mainly active, hunting or moving through its territory (Podolski et al., 2013; Heurich et al., 2014). Furthermore, during one month per each of the four seasons of the year, collars recorded two additional GPS-positions per day, at dawn and evening twilight, in order to enhance the probability to identify all large prey killed by each collared lynx during that time period. Finally, once every 14 days collars recorded one GPS-position per hour from 3.00 PM to 7.00 AM (UTC time) of the following day (intensive monitoring periods).

Because climatic conditions, vegetation structure and density, prey distribution and lynx foraging strategy and diet composition in the study area vary noticeably from winter to summer (Mayer et al., 2012; Belotti et al., 2013, 2015), we divided the study period into 6-month seasons, hereafter referred to as summer (from 15th April to 14th October) and winter (from 15th October to 14th April). All lynx data were classified as summer or winter sites according to the date of recording.

We visualized lynx GPS positions using ArcGIS 9.2 (Esri, 2009); the locations of putative kill sites were identified (see Podolski et al., 2013) and subsequently verified in the field. To prevent any influence on lynx behavior, we searched for killed prey only after lynx had likely abandoned them. For each verified kill site, we also recorded the date of killing, the prey's species, and the sex and reproductive status of the lynx which made the kill. Additional information about prey age and sex could be determined only for about 60% of killed prey found, implying that prey items could not be further categorized into size classes. However, about 67% of killed roe deer for which age and sex could be determined were adults, and almost 90% of killed red deer were juveniles (see Heurich et al., 2016 for details). Thus, we are confident that the classification of killed prey according to prey species sufficiently reflected differences in prey size.

Estimations of time at the prey

Based on lynx GPS positions, we obtained two estimates of the time that lynx fed at kill sites. First, we used the data from the intensive monitoring periods to calculate the number of hours that lynx spent at the prey during a single night. Following Nystrand (2012) and Falk (2009) work on lynx, and Smith et al. (2015) work on pumas (*Puma concolor*), we considered "at the prey" all lynx positions that were located within 100 m from the corresponding kill site. After excluding all cases in which the series of GPS positions were not complete, the number of hours at the prey during a single night (hereafter: "hours at the prey") could be calculated for 56 kill sites.

Furthermore, we used data from the entire monitoring period of each lynx to calculate the number of nights during which lynx fed at each prey. Because approximately 75% of the tracking period collars recorded only a single GPS position per night, we had to consider the possibility that these positions could have been taken while the lynx was traveling to or from the kill site. In order to help identify whether GPS positions represented lynx still visiting the kill site, we created buffers around kill sites. To establish buffer size, we considered that, both in winter and in summer, male lynx had up to 4 times larger day- and night-ranges (Filla et al., 2017), they traveled faster, more directly and up to twice as long distances (Jedrzejewski et al., 2002; Belotti et al., 2012), and they walked approximately twice as far from their kill sites between revisits compared to females (Nystrand, 2012). Furthermore, the mean distance between consecutive kill sites attributed to male lynx was approximately twice as large as that between consecutive kill sites attributed to females (see Fig. S1). Therefore, based on the mean values indicated by Nystrand (2012), on Ersson (2011) and Krofel et al. (2013) work and on our field experience, we classified as a visit to the kill site all night GPS positions within 500 m and 250 m from the kill site in the case of male and female lynx, respectively. After excluding all cases in which the series of GPS positions were not complete, the number of nights during which lynx fed at the prey (hereafter: "nights at the prey") was calculated for 188 kill sites.

Daytime resting sites and lynx space usage

Based on the distribution of midday lynx GPS-positions ($n = 4122$ in winter; $n = 3355$ in summer), we also obtained a measure of the probability that a given area will be used for daytime resting (see below for details). Data from the two lynx whose collars only recorded night positions were excluded from these analyses.

For comparison, we also evaluated lynx space use during nights when they likely were not consuming any killed prey (hereafter: "nights with no prey") using non-clustered midnight GPS-positions ($n = 3948$ in winter; $n = 3294$ in summer).

Recreational activity

To estimate the spatial variation in the intensity and regularity of recreational activity, the study area was divided into 50-hectare grid cells ($n = 2790$ and 2795 for summer and winter, respectively). After excluding those cells whose surface was covered by more than 50% of permanently inhabited human settlements (n=14), we applied the expert evaluation method from Rösner (2014): for each grid cell included in the home ranges of monitored lynx, national park rangers, foresters, hunters, naturalists, and other local experts (i.e. people that were very familiar with a portion of the study area and had several years of field experience), all referred to as "experts" hereafter, were required to evaluate the intensity and recurrence of recreational activity inside the cells

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[1] Regarding the wolf (*Canis lupus*)'s presence, the situation has been changing quickly during the last years. During the entire study period and earlier, only single migrants occurred sporadically in the BFE, but since 2015-2016, wolves established first as single individuals and then as a wolf pack.

to which they were assigned. Their evaluation was based on (daily) direct observations of recreationists on and off trails, and (in winter) of snow tracks. Although most of these experts probably have a better overview of recreationists' diurnal movements (i.e. from early morning to evening), we are confident that their evaluations should not be biased, as the number of recreationists visiting the study area at night is very low (Čihař, 2008; Seibold and Shao, 2014). Because summer and winter recreational activity is not always concentrated in the same areas, the intensity and regularity of summer and winter recreation was evaluated separately. This was done by marking every grid cell with two values (one per season) on the following ordinal scale: 0 (=no or minimal activity); 1 (=slight activity); 2 (=mid-level activity); 3 (=intense, recurrent activity) (see Rösner, 2014 for details). Recreational activity within individual grid cells was estimated by a total of 15 (winter) and 16 (summer) experts (mean number of evaluators per cell = 2.03). Subsequently, we normalized recreational activity scores separately for individual experts and for winter and summer seasons using z-score transformation. Agreement between individual experts (after z-score transformation), assessed as the intraclass correlation coefficient (one way random model -i.e. Shrout and Fleiss, 1979), was 0.72 and 0.73 for winter and summer dataset, respectively. Finally, we computed cell-specific means of recreational activity z-scores separately for both seasons and used these values as an index of the local intensity and regularity of recreational activity (hereafter: "recreational activity index") for further statistical analyses.

Environmental variables

In this study, we focused on the potential effects of the three environmental variables that were most likely to affect both lynx space use and the behavior of lynx at kill sites, by influencing the level of "human-related" risk perceived by lynx: forest cover, slope and level of legal protection (see Supplemental Material S2 for a detailed rationale behind the choice of these variables). For each grid cell, percentage of forest cover and mean slope were calculated according to specific GIS layers (Sources: Český Úřad Zeměměřický a Katastrální - ČUZK, Praha; ATKIS - Data Bayerisches Landesamtfür Geoinformation). Furthermore, we classified each cell as "protected" (i.e. located in the Bavarian Forest, Šumava National Parks, or in the Šumava Protected Landscape Area) or "unprotected" (i.e. located in the unprotected surroundings or in the Bavarian Forest Nature Park —where the level of nature protection is much lower than in the other protected areas of the Bohemian Forest Ecosystem— Underwood, 2014).

Statistical analysis

We used generalized linear mixed effect models (GLMMs) assuming Poisson error distribution to explore the effects of each explanatory variable on the nights at the prey and the hours at the prey (in a single night). Lynx identity was included in the models as random intercept, to account for data non-independence. GLMMs were fitted using package `lme4` (Bates et al., 2012) running in R 2.13.1 (R Core Team, 2012).

For both estimates of time spent at the prey, we tested for effects of: (1) prey type (hare vs. red deer vs. roe deer); (2) lynx sex and reproductive status; (3) season (winter vs. summer); (4) recreational activity index; (5) forest cover; (6) slope and (7) level of protection (protected vs. unprotected). Two-ways interactions of season with all other explanatory variables were only considered in the models regarding the nights at the prey, as sample size for models focused on the hours at the prey was too small. Finally, the analyses focusing on the hours at the prey were adjusted for the effect of time (i.e. how many nights) passed since the prey had been killed (hereafter: "time since kill event").

To test if lynx presence/absence within individual grid cells during daytime (midday) and nights with no prey (midnight) was affected by the explanatory variables described above, excluding variables (1) and (2), we used spatially-explicit Generalized Additive Models (GAM, e.g. Bivand et al., 2008) fitted using the R package `mcgv` (Wood, 2011). Specifically, to account for spatial autocorrelation, residual spatial variation was modelled by a nonparametric spatial smooth function, while the relationships between response and other explanatory variables were modelled using a parametric logit-link function. The two-way interactions of season with all other explanatory variables were also considered. Backward elimination of the non-significant terms in the GLMM was used to select the best minimal adequate model (MAM), i.e. the most parsimonious model with all effects being significant (Crawley, 2007). There was no indication of overdispersion in the fitted models, thus we assumed a χ^2 distribution of the difference in deviances (Crawley, 2007). We assessed the adequacy of the MAMs based on standard diagnostic plots.

Estimates of variance inflation factor were always < 2, indicating that our analyses were not inflated from multicollinearity (Belsley et al., 1980). Continuous variables were z-score transformed prior to computation, in order to allow for more straightforward comparison of the resulting effect sizes.

Results

A representation of the spatial variation of the recreational activity index in the study area is shown in Fig. S3A (summer) and S3B (winter).

Nights at the prey

We found highly significant support for the effect of prey type, season and the interaction between season and recreational activity index on the number of nights at the prey (Tab. 1, S1; Fig. 1). Lynx spent more nights at larger prey: 5.3 ± 0.4 (mean±S.E.) nights at killed red deer; 3.4 ± 0.1 nights at killed roe deer and 2.0 ± 0.3 nights at killed hares. Furthermore, lynx spent more nights at prey killed in summer than in winter (Tab. 1, S4). While there was no significant correlation between nights at the prey and recreational activity index during summer, lynx spent significantly more nights at the prey when the kill site was in areas characterized by lower recreational activity index in winter (Tab. 1; Fig. 1). Other variables were far from significant, with the exception of forest cover (Tab. S3), that was marginally non-significant and tended to be positively associated with the nights at the prey (coefficient ± S.E.=0.081 ± 0.044).

Hours at the prey (in a single night)

Hours at the prey decreased with increasing time since kill event, and increased with slope (Tab. 2). Lynx also spent more hours at the prey during winter than during summer. Recreational activity index was negatively related to hours at prey (Tab. 2, Fig. 2). All other predictors included in the initial model had no significant effect on hours at the prey (Tab. S3).

Choice of resting sites and space use

Grid cells including at least one lynx midday GPS-position (i.e. daytime resting site) were characterized by higher forest cover, steeper slope and lower recreational activity index (Tab. 3; Fig. 4) than grid cells where lynx positions were not recorded. Also, grid cell occupancy was higher in protected areas compared to unprotected surroundings (Tab. 3), and in summer compared to winter (Tab. 3). In addition, a marginal significance of the interaction between season and level of protection (Tab. S4) indicated that the contrast between protected and unprotected areas may exhibit seasonal variation. Particu-

Table 1 – Parameter estimates for the minimal adequate model on the nights that lynx spent at killed prey. Standard errors (S.E.), test statistics (z-value) and associated probabilities (p-value) are shown for each predictor.

	Estimate	S.E.	z-value	p-value
(Intercept)	1.801	0.094	19.12	0.001
Prey type (roe deer vs. red deer)	−0.491	0.095	−5.144	0.001
Prey type (hare vs. red deer)	−1.049	0.327	−3.208	0.001
Season (winter vs. summer)	−0.203	0.08	−2.525	0.012
Recreational activity index	0.054	0.051	1.053	0.292
Season (winter vs. summer): Recreational activity index	−0.212	0.075	−2.814	0.005

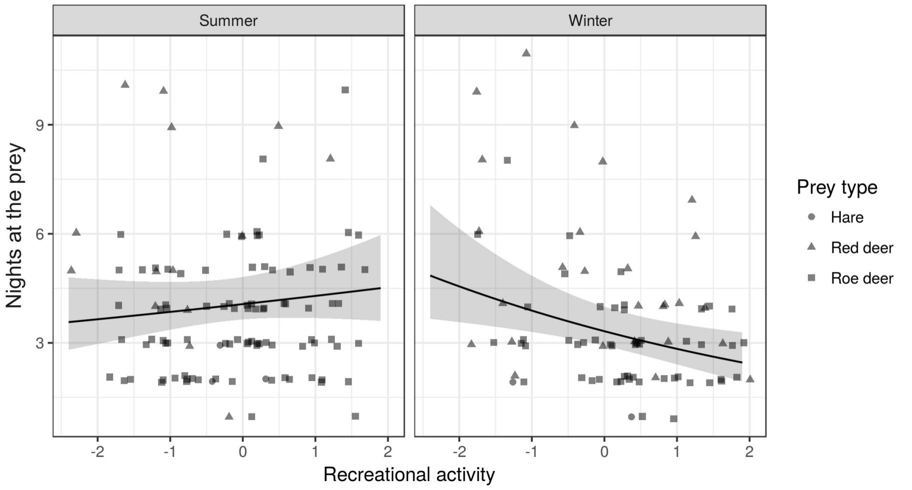

Figure 1 – Relationship between the nights that lynx spent at killed prey and the recreational activity index. Summer and winter data are presented in different facets. Prey species is indicated by the shape of plotting symbols. Lines correspond to generalized linear mixed effect model predictions and 95% confidence intervals.

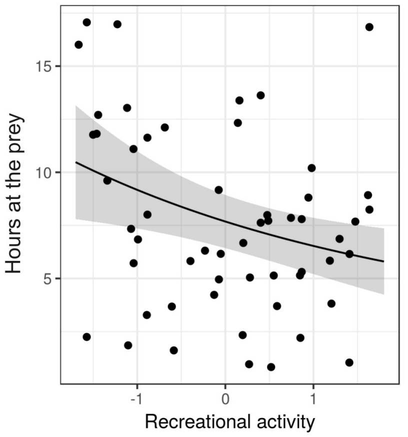

Figure 2 – Relationship between the hours that lynx spent at each killed prey (during a single night) and the recreational activity index. Lines correspond to generalized linear mixed effect model predictions and 95% confidence intervals. Predictions account for all variables included in the minimal adequate model.

Table 2 – Parameter estimates for the minimal adequate model on the hours that lynx spent at each killed prey (during a single night). Standard errors (S.E.), test statistics (z-value) and associated probabilities (p-value) are shown for each predictor.

	Estimate	S.E.	z-value	p-value
(Intercept)	2.139	0.12	17.802	0.001
Time since kill event	−0.104	0.048	−2.173	0.03
Season (winter vs. summer)	0.243	0.117	2.074	0.038
Slope	0.146	0.054	2.709	0.007
Recreational activity index	−0.167	0.063	−2.683	0.007

Table 3 – Parameter estimates for the minimal adequate model on presence/absence of lynx A) midday and B) midnight GPS-positions in each of the 50-hectare grid cells included in the study area. Standard errors (S.E.), test statistics (z-value) and associated probabilities (p-value) are shown for each predictor.

	Estimate	S.E.	z-value	p-value
A) Midday positions				
(Intercept)	−2.246	0.092	−24.409	0.001
Season (winter vs. summer)	−0.282	0.092	−3.066	0.002
Level of protection (unprotected vs. protected)	−0.618	0.237	−2.606	0.009
Slope	0.202	0.056	3.597	0.001
Forest cover	0.682	0.082	8.291	0.001
Recreational activity index	−0.244	0.053	−4.625	< 0.001
B) Midnight positions				
(Intercept)	−2.095	0.085	−24.709	< 0.001
Season (winter vs. summer)	−0.231	0.097	−2.391	0.017
Level of protection (unprotected vs. protected)	−0.796	0.246	−3.236	0.001
Season (winter vs. summer) : Level of protection (unprotected vs. protected)	0.934	0.248	3.766	0.001

larly, our data showed a lower number of daytime-occupied cells inside protected areas in winter (proportion of daytime-occupied cells ± S.E.=0.133 ± 0.007) compared to summer season (0.186 ± 0.009), whereas the opposite pattern was observed in the case of unprotected areas (proportion of daytime-occupied cells ± S.E.=0.122 ± 0.017 during winter and 0.106 ± 0.019 during summer).

For comparison, when analysing the presence/absence of lynx midnight GPS-positions (recorded during nights with no prey), only season, level of protection and their interaction had significant effects (Table 3). Consistent with the analysis of lynx midday positions, lynx space usage during nights with no prey showed a decrease of grid cell occupancy from summer to winter (proportion of occupied cells = 0.160 ± 0.008 vs. 0.128 ± 0.007) in protected areas and a corresponding increase in unprotected areas (0.090 ± 0.013 vs. 0.114 ± 0.013). The effects of all other variables, including recreational activity index, were non-significant (Fig. 4; Tab. S4).

Discussion

Our results fully supported our initial hypotheses that recreational activity would influence the choice of lynx resting sites and that habitat features related to high protective cover and low human accessibility would positively correlate with the presence of resting sites and with the time lynx spent at each prey. In partial accordance with our expectations, the recreational activity index was negatively correlated with the nights at the prey, but only during winter. In addition, the recreational activity index indeed correlated with the hours at the prey, but contrary to our expectations this correlation was negative. Finally, the expected effect of the level of protection was only partially confirmed: both during daytime and during nights with no prey, the probability of lynx occurrence was higher in protected than in unprotected areas, however no difference in the time spent at killed prey was found between areas.

Effects of season

In accordance with previous findings (e.g. Belotti et al., 2015), we found an effect of season on all considered aspects of lynx ecology. Specifically, the smaller portion of the study area used by lynx during nights with no prey (when lynx was likely hunting or patrolling its territory) in winter is most likely a consequence of more clumped deer distributions in winter compared to summer (e.g. Cagnacci et al., 2011), and the widespread presence of deer winter feeding sites outside of National Parks (e.g. Heurich et al., 2015; Ossi et al., 2017). Furthermore, harsher climatic conditions at higher altitudes in the BFE may also influence lynx independent of deer densities (see Belotti et al., 2015). This can also explain the observed decrease in the proportion of grid cells used by lynx during nights with no prey in the protected part of the BFE from summer to winter and the corresponding increase in the unprotected part of the BFE, which includes the lowest altitudes (Belotti

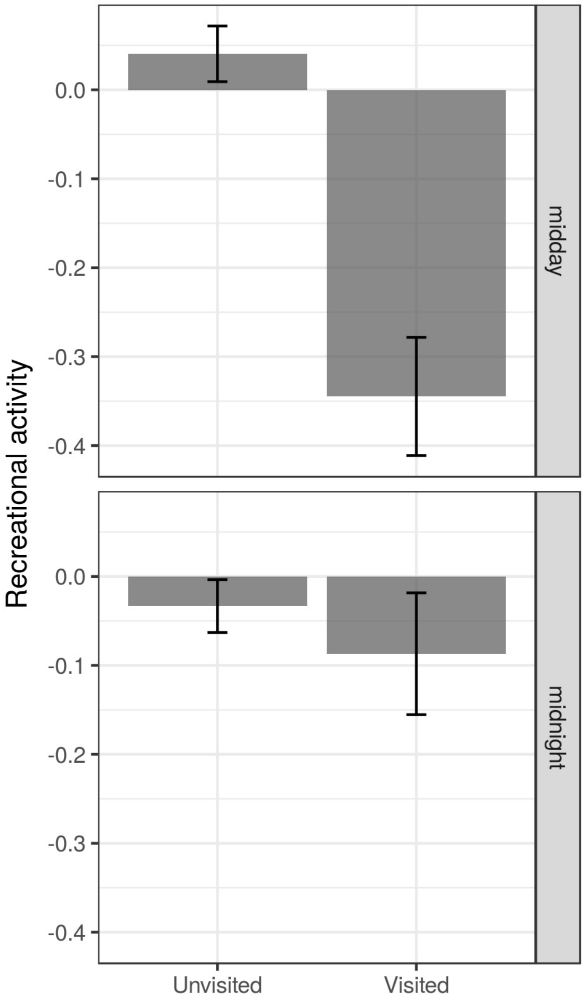

Figure 4 – Recreational activity index in the 50-hectare grid cells included in the study area that were visited by lynx (A) at midday and (B) at midnight (in nights with no prey) vs. those where lynx presence during the same periods of the day was not recorded. Bar height correspond to mean recreational activity and error bars to 95% confidence intervals.

et al., 2015), where deer concentrate in winter (e.g. Cagnacci et al., 2011; Ossi et al., 2017). Accordingly, our previous studies showed that the spatial distribution of lynx kills is less homogeneous in winter compared to summer (Belotti et al., 2015) and lynx are less active in spring and winter compared to autumn and summer (Heurich et al., 2014). The smaller portion of the study area used by lynx for daytime resting in winter compared to summer was most likely related to this general pattern, and to the possible unsuitability of a large proportion of the unprotected part of the BFE for resting lynx. In fact, in the unprotected area during winter, the increase in the proportion of grid cells used by lynx at midday (about +1.5% compared to summer) did not compensate for the corresponding decrease in the proportion of grid cells used at midday in the protected area (about -5%). In addition, consistent with Podgorski et al. (2008) and Schmidt (2008), we assume that the more widespread summer distribution of lynx daytime resting sites could be linked to a higher availability of areas suitable for resting throughout the BFE during summer, when deciduous trees and shrubs with leaves likely provide "protective ground cover" at more locations than in winter. This is supported by Filla et al. (2017) results for the BFE, that in summer, lynx had a slight preference for deciduous forest over coniferous forest during the daytime.

Finally, the smaller number of nights and the greater number of hours per night that lynx spent at killed prey in winter when compared to summer, may be explained by different mechanisms, including lower attractiveness of frozen carcasses (Pulliainen et al., 1995), greater efficiency of lynx to kill new large prey in winter (Belotti et al., 2015), increased energy requirements in winter (Karasov, 1992; Rizzuto et al., 2017), or a more intense activity of scavengers in winter compared to summer (Selva et al., 2005; Krofel, 2011). Data about the amount of meat consumed by lynx (and scavengers) would be needed to determine which mechanism contributed the most to our results.

Recreational activity and time at the killed prey

Given the seasonal effects described above, seasonal differences in the effect of recreation on the nights at the prey could also be expectable. However, the fact that recreational activity was negatively correlated with the nights at the prey in winter only is surprising, because in the BFE recreation is generally much more intense during summer than during winter (Čihař, 2008; Seibold and Shao, 2014). Furthermore, in summer, without snow and with berries and mushrooms growing inside and outside protected areas, recreationists are more likely to leave marked trails and disperse throughout the entire area. According to Carter et al. (2012) and Taylor and Knight (2003), more dispersed human activity likely has a stronger influence on wildlife compared to activity concentrated on trails, and several studies have indicated that animals react more strongly to spatially and temporally unpredictable activities (e.g. Miller et al., 2001; Braunisch et al., 2011). Altogether, this would rather have supported a stronger effect of recreational activity in summer compared to winter. However, our counterintuitive findings may be related to a more prominent influence of safety factors on lynx choices in winter, possibly because in winter lynx spend more time hunting outside protected areas and may thus experience a higher number of risky encounters with hunters (Filla et al., 2017). In addition, in the BFE (as in the entire Northern hemisphere) during winter, the duration of daytime (in terms of light hours) is shorter than in summer, and lynx tends to increase their activity level earlier in the afternoon (Heurich et al., 2014), concentrating their activity at evening twilight (Podolski et al., 2013). According to Seibold and Shao (2014), in the study area from October to March, recreationists are often active on trails until or slightly after evening twilight, which may increase the probability that they would accidentally disturb lynx at kills during winter. Nonetheless, the negative effect of recreational activity on the hours that lynx spent at the prey (in a single night) was significant year-round, which suggests that this is not the only mechanism accounting for our results.

The effect of recreational activity on the hours at the prey can be explained combining findings from previous studies, mainly that year-round the distance from a given kill site to the nearest tourist trail was negatively correlated with the mean distance lynx walked from the kill site to its corresponding daytime resting sites (Belotti et al., 2012). In the BFE, this mean distance ranged between a few meters and 4.8 km (Belotti et al., 2012), on average 1.1 km, i.e., about 10-15% of lynx mean daily movement distance (DMD - Jedrzejewski et al., 2002; Belotti et al., 2012). According to Jedrzejewski et al. (2002), lynx move at an average speed of 1 to 1.5 km/hour. Furthermore, lynx in the study area were active for about 9 hours per day, and activity was reduced to about 6 hours during days with available kills and concentrated during twilight and night hours (Podolski et al., 2013). Thus, in areas characterized by a higher recreational activity index (i.e. likely including frequented tourist trails), the number of hours at the prey per night could decrease year-round because lynx spent a larger proportion of night hours moving between kill site and the corresponding daytime resting sites, which reduced the number of night hours to spend at carcasses (either feeding or resting and digesting).

Recreational activity and choice of resting sites

In this study, we assumed lynx GPS midday positions to be representative of lynx daytime resting sites, without taking into account activity data, which were not available for the entire monitoring period of each collared animal. Although we acknowledge that lynx midday positions may not always exactly correspond to daytime resting sites, we are confident that this did not introduce any relevant bias, because the analysis of available activity data in our previous study (Podolski et al., 2013) revealed that year-round the activity of all monitored individual was lowest at midday and remained very low in the 2-3 hours preceding and following midday. Furthermore, in this study the effects of all variables on the presence of resting sites were evaluated at the 50- ha grid cell level, and lynx mostly moved very short distances during the period around midday, which implies that actual resting sites were not located far from lynx GPS midday positions and thus were most likely included in the same grid cell (e.g., excluding the neonatal period for family groups, in 150 cases collars recorded one position at midday and one at 3 PM, when the level of lynx activity starts increasing: in about 60% of cases the distance between these positions was shorter than 100 m and in 90% of cases it was shorter than 707 m, i.e. the length of our grid cells).

As lynx spend most daylight hours resting and sleeping (Podolski et al., 2013; Heurich et al., 2014), it is intuitive that they will search for safe and quiet areas during daytime. Because humans are potential predators for lynx, the (mostly diurnal) presence of recreationists often moving off-trails could likely increase the perceived predation risk by this large carnivore and cause avoidance of risky areas (Frid and Dill, 2002). To our knowledge, no study to date has focused on the influence of recreational activity on the choice of resting sites by lynx or other felids; however, our findings are in accordance with the results of studies dealing with the effects of other human activities on resting lynx. Specifically, in Norway, Bouyer et al. (2015a,b) found that lynx avoided areas that were most modified by humans when resting and that the threshold of human permanent residential density which induced lynx to avoid a given area was 20 inhabitants/ km^2. In the protected part of the BFE, human permanent residential density is mostly below this threshold, and it is likely that tolerance thresholds will be much higher for lynx living in the more densely populated Central Europe than for lynx living in Scandinavia. Despite this, we found that the areas with the most intense and regular recreational activity were avoided by resting lynx in the entire study area, suggesting that lynx may react to intense and regular recreational activity similarly as they react to human permanent residential density. Accordingly, Ordiz et al. (2011) demonstrated that intense and interspersed human activity negatively influenced the choice of resting sites by another large carnivore, the brown bear.

Habitat characteristics, level of protection and perceived risk

The need to spend daytime in safe, quiet areas may also explain the strong positive effects of habitat parameters related to inaccessibility (i.e. slope - Jobe and White, 2009) and protective cover (i.e. forest cover - Bouyer et al., 2015a) on the probability that lynx would use a given area for daytime resting. Accordingly, a preference for daytime resting sites located in steeper areas has been found previously in studies on lynx (Sunde et al., 1998; Falk, 2009; Bouyer et al., 2015a) and other felid species (e.g. the bobcat *Lynx rufus* - Anderson, 1990; the cougar - Kusler, 2017). Also, the importance of habitat concealment at lynx resting sites was reported by Sunde et al. (1998) and Podgorski et al. (2008). Similar results were described for other felids (e.g. the bobcat - Kolowski and Woolf, 2002; the cougar - Kusler, 2017) and large carnivores (e.g. the brown bear - Ordiz et al., 2011). A direct negative correlation between these habitat characteristics and the probability that people will reach the resting site can be assumed according to a recent study by Coppes and Braunisch (2013), who found that steeper slope and higher canopy cover resulted in a lower probability that visitors in natural areas would leave marked trails. Accordingly and consistently with Falk (2009) results, slope tended to positively influence the number of hours spent at a given prey during a single night and forest cover tended to positively correlate with the number of nights spent by lynx at killed prey, while they had no influence on lynx space use during nights with no killed prey. Furthermore, in accordance with Bouyer et al. (2015a), in our models, the effect of protective habitat features received support after statistical control for the effect of recreational activity, suggesting that high protective cover and low accessibility increase lynx's perception of safety independently of the actual level of human disturbance.

Finally, the expected and observed higher proportion of grid cells used by lynx at midday inside protected areas compared to unprotected areas is also likely linked to the need to spend daytime in quiet areas that are perceived as "safe". In fact, a relatively large portion of the unprotected part of the study area is occupied by agricultural landscapes, which are generally avoided by resting lynx (Sunde et al., 1998, but see Bouyer et al., 2015a), or by commercial forests (Heurich et al., 2015), where forestry activity can be (locally) intense year-round. Therefore, although lynx permanently inhabit these areas with more human-modified habitats, they may only be able to rest in a smaller portion of the available habitat there compared to protected areas.

Observed effects and potential impacts

Overall, although prey distribution and environmental conditions are likely preponderant in shaping lynx space use and behavior, our results suggest that non-consumptive recreation also has the potential to influence important aspects of lynx ecology. Unfortunately we could not quantify the actual impacts (*sensu* Beale, 2007) on lynx fitness, and similar information from other lynx populations are lacking; in addition, the long-term consequences of the observed effects for individual fitness have rarely been evaluated in other species as well (Blanc et al., 2006).

Given that roe deer are abundant in most of the BFE (Heurich et al., 2015; Belotti et al., 2015), we expect that a reduction in the time spent at killed prey (associated with a reduction in food intake or not) will likely have no serious impact on lynx survival; however, the observed effect may have more serious consequences in areas characterized by low prey availability. In addition, an indirect impact on lynx survival may arise. In fact, in the BFE, we found that during the period of the year when the number of nights at the prey was lower, kill rates were higher (Belotti et al., 2015). Therefore, also in accordance with findings by (Smith et al., 2015) on pumas, it is expected that intense, recurrent recreation reducing the number of nights at the prey will similarly increase kill rates. In addition, prey killed by lynx in frequented areas are more likely to be noticed by people. Altogether, this may cause an exacerbation of conflicts between lynx and hunters, especially in the PLA Šumava, where the local level of recreation is high and where commercial hunting is performed on both state and private hunting grounds. Besides, as suggested by Smith et al. (2015), an increase in ungulate carcasses abandoned by predators in disturbed areas may impact the entire biotic community, providing additional subsidies to scavengers. Finally, a reduced feeding time may also negatively influence reproductive success, as observed in leopards (*Panthera pardus*) even in areas with high prey densities (Balme et al., 2017).

Access to safe resting is likely another fundamental factor for felids (e.g. Kolowski and Woolf, 2002) and recreational activity seems to have the potential to reduce the size of resting habitat for lynx. Although habitat availability does not seem to be the limiting factor for lynx distribution in the BFE (Magg et al., 2015), this may have greater impacts in those regions where small, isolated lynx populations have limited amounts of suitable habitat at their disposal (Sunde et al., 1998). Finally, according to Lima et al. (2005), the quality of sleep can be altered by predation risk. Therefore, we speculate that this may also affect lynx in those areas where recreation is not sufficiently intense to displace lynx, but is sufficiently intense to reduce the suitability of otherwise optimal resting areas and possibly weaken the restorative function of sleep (Siegel, 2003).

Conclusions and practical implications

In summary, we suggest that the potential impacts on lynx should be better investigated and taken into consideration when managing recreation in protected areas. In particular, it is important to ensure that a sufficient amount of areas, especially those naturally suitable for daytime resting, are kept free from human disturbance. This can be achieved by maintaining a reasonable trail density, keeping in mind the spatial distribution of known resting sites when considering new trail development and construction, and effectively preventing visitors from leaving marked trails (Coppes and Braunisch, 2013; Park et al., 2008) in adequately large portions of protected areas. In addition, efforts should be made to keep disturbance around (potentially) active lynx kill sites as limited as possible. While reducing the accessibility for people to the areas preferred by hunting lynx is not always feasible, as these areas are often much more open compared to those selected by lynx for resting (e.g. Podgorski et al., 2008; Filla et al., 2017), this goal could be achieved by educating recreationists and local people not to remove accidentally found prey remains (e.g. see Krofel et al., 2008) and leave them undisturbed.

Finally, we suggest that preserving patches of habitat characterized by high levels of protective cover (e.g. spots of dense shrubs) may work as a mitigating measure, especially in those localities where recreationists are concentrated (Thiel et al., 2017; Ordiz et al., 2011) and/or slope is not very steep. Wherever possible, this should also be done in unprotected commercial forests surrounding protected areas, as ecological processes taking place in adjacent areas often influence one another (Hansen and DeFries, 2007), and conservation of species with large spatial requirements generally cannot rely on protected areas alone (Linnell et al., 2015).

More general, our results suggest that non-consumptive recreation can influence even a species which is considered quite tolerant to human presence (Linnell et al., 2015; Bouyer et al., 2015a,b), indicating that the impact of recreational activities on different species are not fully understood. Given the increasing trends in ecotourism and non-consumptive recreation over the last decades in large parts of the world (Balmford et al., 2009), more long-term research on this topic is needed.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Example of spatial distribution and distances between consecutive kills made by a male and a single female lynx between the end of March and the end of April.

Supplemental material S2 Choice of environmental variables.

Figure S3 Spatial variation in the recreational activity index in the study area.

Table S4 Likelihood ratio-based significance of individual predictors.