Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements

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Abstract

Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements.— Human presence influences survival of large carnivores in several ways and even outdoor activities can be a source of disturbance. As ungulate prey provide the Eurasian lynx (*Lynx lynx*) with food for several nights and the pattern of lynx activity is mainly shaped by searching for and consuming large prey, the need to move decreases strongly while the prey is eaten. However, during the day, human activity may drive lynx to move to safe shelters and habitat features such as dense vegetation may increase tolerance. In the Bohemian Forest (Czech Republic), we found 116 prey killed by five GPS–collared lynxes. We tested whether the kill sites were located farther from roads or tourist trails than a set of randomly generated locations and whether presence of roads or tourist trails and habitat structure influenced the distance 'kill site to daytime resting sites'. At night, with low human activity, lynxes did not avoid roads and even selected the surroundings of tourist trails. The distance 'kill site to daytime resting sites' correlated negatively with presence of habitat concealment and distance to tourist trails, suggesting that outdoor activities may have to be considered in lynx management plans.

Key words: *Lynx lynx,* Kill site, Resting site, Tourist trail, Paved road, Habitat structure.

Resumen

Influencia del turismo y del tráfico sobre la caza del lince boreal y sus desplazamientos diarios.— La presencia humana influye de diversas formas sobre la supervivencia de los grandes carnívoros, e incluso las actividades al aire libre pueden ser una fuente de perturbaciones. Dado que los ungulados son la presa que proporciona al lince boreal (*Lynx lynx*) alimento para varias noches, y que el patrón de la actividad del lince está diseñado principalmente para buscar y consumir presas de gran tamaño, la necesidad de desplazarse disminuye mucho mientras está devorando la presa. No obstante, durante el día, la actividad humana puede obligar al lince a desplazarse a refugios seguros, y las características del hábitat tales como una vegetación densa pueden aumentar su tolerancia. En los bosques de Bohemia (República Checa), hallamos 116 presas cazadas por cinco linces provistos de collares GPS. Estudiamos si los lugares de la matanza estaban situados más lejos de las carreteras o de los senderos turísticos que si los lugares hubieran sido elegidos al azar, y si la presencia de carreteras o senderos turísticos y la estructura del hábitat influían en la distancia “lugar de caza a zonas de descanso diurnas”. Por la noche, con una actividad humana baja, los linces no evitaban las carreteras e incluso elegían los alrededores de los senderos turísticos. La distancia “lugar de caza a zonas de descanso diurnas” estaba correlacionada negativamente con la presencia de hábitat críptico y con la distancia a los senderos turísticos, lo que sugiere que las actividades al aire libre podrían tomarse en consideración en los planes de gestión de los linces.

Palabras clave: *Lynx lynx*, Lugar de caza, Lugar de reposo, Sendero turístico, Carretera pavimentada, Estructura del hábitat.

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Introduction

Since the 1950s, after almost two centuries of dramatic declines and extinctions, the populations of large carnivores are slowly recovering in several European countries (Linnell et al., 2001, 2005). This has been achieved by a change in people´s attitude towards these species and by the consequent adoption of favorable legislation, as a result of both spontaneous expansion and reintroduction programs (Boitani, 2000; Breitenmoser et al., 2000; Swenson et al., 2000).

At least in Central Europe, nonetheless, only few areas can be still considered 'natural' or 'semi–natural' and most of the areas to which bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*) are returning include human–modified habitats, which can be quite different from their original habitats (Basille et al., 2009). Therefore, their ability to coexist with man is probably one of the most important factors influencing their long–term survival (Breitenmoser et al., 2000; Boitani, 2000; Basille et al., 2009).

There are several human activities that can negatively affect the survival of large carnivores. For example, hunting, poaching (Jędrzejewska et al., 1996; Andrén et al., 2006) and road intensive usage causing vehicle collisions (Kaczensky et al., 2003; Andrén et al., 2006) have a direct effect, while forestry activity and road network development leading to habitat fragmentation (Theuerkauf et al., 2001; Huck et al., 2010) and game management influencing prey availability and distribution (*e.g.* Putman & Staines, 2004; Milner et al., 2007; Hothorn & Müller, 2010) can have an indirect influence.

In spite of this, large carnivores in Europe still show a certain degree of tolerance to humans (Linnell et al., 2000; Theuerkauf et al., 2003; Bunnefeld et al., 2006). Studies have shown that they are able to permanently occupy areas with a low degree of urbanization (Basille et al., 2008, 2009) and survive, under certain conditions, even in areas with high human density (Linnell et al., 2001).

On the other hand, in natural and semi–natural areas, generally associated with a low human density, there has been a noticeable increase in outdoor activities, especially in the last decades (Thiel et al., 2008; Balmford et al., 2009). Concerning the influence of such activities, an increasing number of studies (Burger & Gochfeld, 1998; Duchesne et al., 2000; Taylor & Knight, 2003; Dyck & Baydack, 2004; Thiel et al., 2007) seems to prove that nonlethal disturbance stimuli can produce the same effect as predation risk on the species fitness: they might induce an 'antipredator response' that has a cost to other activities (Frid & Dill, 2002). In addition, human hunters have represented a real threat for large carnivores over evolutionary time (Frid & Dill, 2002). Thus, in some cases, such as when people approach on foot, disturbance stimuli and true predatory stimuli may be indistinguishable from these animals' perspective (Frid & Dill, 2002).

Although literature about the effects of human disturbance on animal behavior is quite rich and several authors have studied the effects of human activity in general on large carnivores (Amstrup et al., 1993; Thurber et al., 1994; Kerley et al., 2002; Theuerkauf et al., 2003; Bunnefeld et al., 2006; Kolowski & Holekamp, 2009), to date only a few studies (*e.g.* Goodrich & Berger, 1994, reviewed in Linnell et al., 2000; Creel et al., 2002) have investigated the effect of recreational activities on such species. Creel et al. (2002) found that the levels of glucocorticoids (indicating physiological stress) in wolves were substantially higher at locations and times with more intense touristic activity.

According to a study run by Linnell et al. (2001), the Eurasian lynx is the only species of large carnivore in Europe for which a statistically significant correlation between human population density and historical extinction since the early 1800s has been observed. However, this was probably linked to a greater sensitivity to human influence on their ungulate prey rather than to disproportionate human persecution (Linnell et al., 2001). With regard to present coexistence with people, at a European scale no relationship was found between human density and the status of lynx populations (Linnell et al., 2001).

At a population scale, lynx proved to chose habitats with a medium level of human presence (Basille et al., 2009), probably as a consequence of the habitat choice of their main prey, the roe deer (*Capreolus capreolus*), which benefit to a large extent from current human land use practices (Mysterud, 1999). On the other hand, the only study conducted at a finer scale (Sunde et al., 1998) indicated that resting lynxes avoided humans, showing different responses to disturbance depending on the type of habitat. Therefore, the mechanisms of avoidance for this species may work at a finer scale, both spatially and temporally, as was found for wolves (Theuerkauf et al., 2003). Furthermore, different human activities may have different effects (Bunnefeld et al., 2006) and the sensitivity to disturbance may vary while animals are performing different activities.

Bunnefeld et al. (2006) analyzed the places chosen by lynx when hunting or resting in an area characterized by a low human density. There, lynx did not avoid the surroundings of agricultural fields and roads, where the main activity was in the form of wheeled vehicles, but they avoided the surrounding of permanently occupied houses, that were the most consistent source of human activity in the area (Bunnefeld et al., 2006), *i.e.* likely the places with the highest probability of encountering humans *per se*.

No study to date has focused on the potential effect of intense touristic activity on lynx behavior; nonetheless, at least during the main touristic season, proximity to tourist trails may also be linked to a high probability of encountering humans.

The present study aimed to investigate the potential effect of tourism and traffic on two aspects of the Eurasian lynx's behavior: the hunting of an ungulate prey and the choice to move and find a suitable daytime resting site on the days when a large prey was consumed. Firstly, we hypothesized that at night, when human activity is low, lynx hunting behavior may not be influenced by the presence of roads or trails and therefore lynx may kill ungulate prey independently of the proximity to such structures. Secondly, we focused on the mean distance moved by the lynx from a kill site to the corresponding daytime resting sites (hereafter: distance 'kill site to daytime resting sites'). As large prey provide the lynx with food for several nights (Jobin et al., 2000) and the pattern of lynx activity was found to be shaped mainly by searching for and consuming large prey (Schmidt, 1999; Jędrzejewski et al., 2002), the need to move strongly decreases while the prey is eaten (Schmidt, 1999). However, during the day lynx may be led to move to safe shelters due to human activity in the surroundings of the kill site. Therefore we hypothesized that the distance 'kill site to daytime resting site' may increase when the kill site is located near a tourist trail or a road. Also, we assessed whether this distance was influenced by habitat features at the kill site (whether they give the lynx the possibility to hide or not; Sunde et al., 1998) and whether there were differences between male and female lynxes. Finally, as individual variations have been observed in the rhythms or levels of activity among lynxes of the same sex, age and status (Schmidt, 1999), we also checked for individual differences.

Material and methods

Study area

This study was conducted in the Bohemian Forest, a forested mountain range in South–West Czech Republic, along the border with Germany (48° 55' – 49° 17' N, 13° 13' – 13° 47' E). This region encompasses the Šumava National Park (680 km²) and a surrounding wide belt of Protected Landscape Area (PLA, 990 km²), where the main human activity is tourism and, to a less extent, forest management outside the non–intervention zones of the National Park. The foothills around the PLA are characterized by a denser net of paved roads, several small human settlements and a stronger influence of forestry and agricultural activities. Touristic activity is marginal in the surroundings closest to the PLA (10 km belt), except for a few renowned localities close to the main towns. Also due to this region's recent history, the mean human population density of the whole area is low: about 20 ind./km^2 and only 1.9 ind./ km^2 in the central parts (Wölfl et al., 2001; Mašková et al., 2003). The Eurasian lynx is the only large carnivore species currently living in the area (Koubek & Červený, 1996) and it is present with a reintroduced population for which the estimated count, in 2001 was fewer than 70 individuals (jointly estimating the Czech, German and Austrian sides Wölfl et al., 2001). More recent data, obtained from a camera trapping project in the two National Parks Šumava and Bavarian Forest, led to an estimated density of 1.19 lynxes/100 km² (Weingarth et al., 2011). Throughout the whole region, the most common carnivore is the red fox (*Vulpes vulpes*), which is present in relatively high numbers. The primary species of wild ungulates are red deer (*Cervus elaphus*), roe deer —which is the main prey of the lynx (Okarma et al., 1997)— and wild boar (*Sus scrofa*). Among the mentioned species, the red fox is probably the most common mammal scavenger on lynx kills (Jędrzejewska & Jędrzejewski, 1998; Selva et al., 2005; Helldin & Danielsson, 2007) although wild boar often feed on carcasses as well (Selva et al., 2005).

Lynx data

During winters 2009/2010 and 2010/2011, lynxes were live–trapped using box–traps set on traditional lynx paths or at a fresh kill. The individuals were immobilized with 'Narketan' (10% ketamin), measured, fitted with GPS/GSM–collars (from Vectronics Aerospace, Berlin) and set free at the same place where they were captured. In this way we GPS–collared five lynxes: two females without kittens (F1 and F2), two adult males (M1 and M2) and one young male (M3). Collars were programmed to take one GPS position at midday, when the lynx is supposed resting (Schmidt, 1999), and one GPS position at midnight, when the lynx is supposedly active, hunting or moving through the territory (Schmidt, 1999). In addition to this schedule, for one month each season of the year, the collars took two additional GPS positions per day, at dawn and twilight, in order to obtain the complete series of ungulate prey killed by each collared lynx. Finally, every second week each animal had a 16–hour 'intensive monitoring period', when collars took one GPS positions per hour (from 4.00 p.m. to 8.00 a.m. at the following day). We obtained GPS positions from collars via SMS and downloaded them to a portable GPS (Trimble Juno SB), which was used to search for potential prey in the field. The actual prey site was then saved in the portable GPS.

On the basis of the GPS fixes, from April 2010 to August 2011 we found 140 killed ungulate prey. In 116 cases collars also successfully measured the corresponding distance to 'daytime resting sites' of the lynx, represented by the midday GPS positions between two consecutive nights spent at the kill. For each of these 116 killed ungulate prey (fig. 1), we calculated the mean distance between the kill site and its corresponding distance 'kill site to daytime resting sites'.

Explanatory variables

We took into consideration nine potential explanatory variables (table 1), accounting for information about habitat structure and human activity in the surroundings of the kill sites and about potential changes in human activity and lynx behavior throughout the year.

To evaluate the possibility for the lynx to hide near the kill site we adapted the 'cover pole method' (Pierce et al., 2004) to our aims: for each killed ungulate we verified in the field we placed a 2m–high pole, divided into 10 colored segments, at the location where the kill was found and we recorded how many segments were hidden for more than 50% when observed at a distance of 20 m in each cardinal direction, at a height of 1 m (fig. 2). By calculating the mean value for the four cardinal directions, we obtained an 'index of the presence of hiding places' ('habitat concealment', table 1). As lynx are known to prefer areas with steep

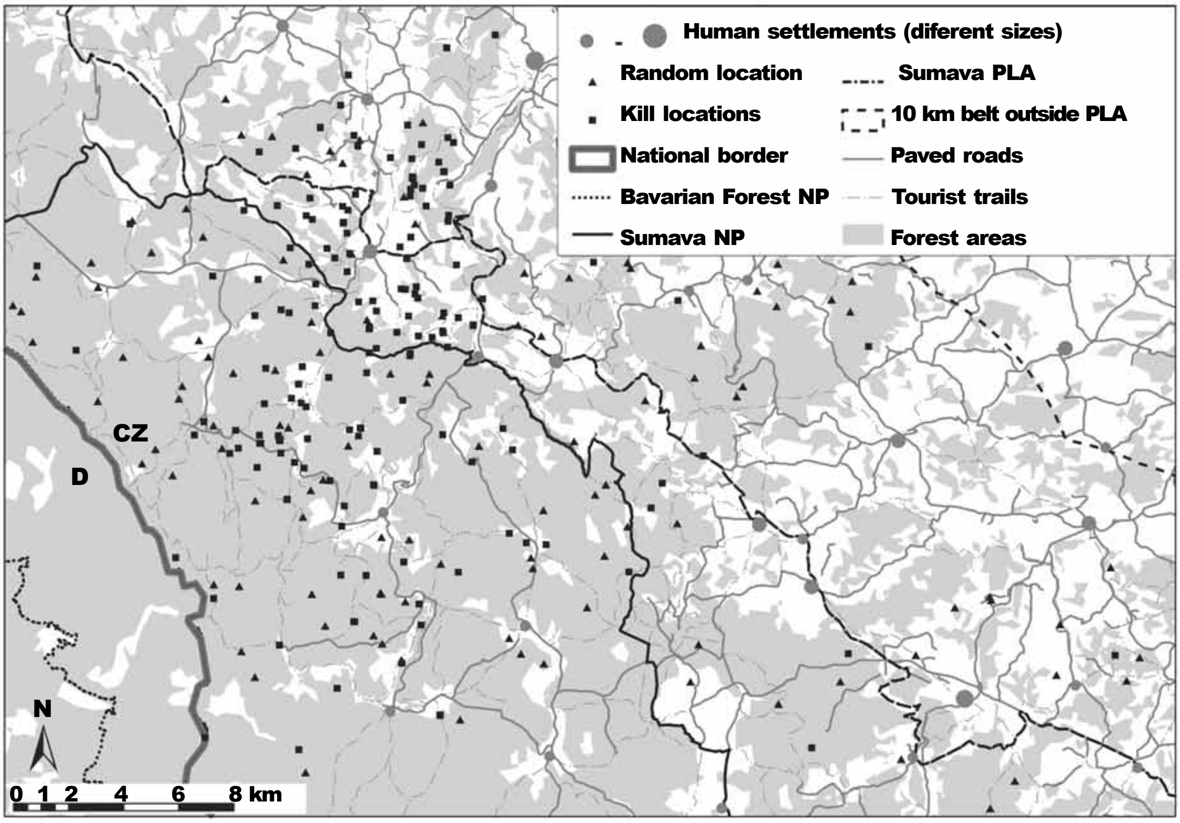

Fig.1. Distribution of the kill locations (n=116) and random locations (n = 116) throughout the Sumava National Park (NP), Protected Landscape Area (PLA) and a 10 km belt around the PLA.

Fig. 1. Distribución de las presas cazadas por los linces (kill locations, n = 116) y de las localizaciones elegidas al azar (random locations, n = 116) en el Parque Nacional de Sumava (NP), en el Área de Paisaje Protegido (PLA) y en un cinturón de 10 km alrededor del PLA.

slopes (Basille et al., 2008) we also calculated the slope ('slope', table 1) for each kill site using a GIS layer with a 15 x 15 m–resolution (source: Český Úřad Zeměměřický a Katastrální–ČUZK, Praha).

To take into consideration the potential effect of traffic and tourism, using specific GIS layers (sources: Český Úřad Zeměměřický a Katastrální–ČUZK, Praha and Sprava NP a CHKO Šumava) we calculated the distance of each kill site to the closest paved road (used mainly by motorized vehicles– 'Roads', table 1) and the closest tourist trail (used mainly by hikers and bikers). The most important factor influencing an animal's behavior is likely to be the level of human activity on a road and not the presence of the road itself (Theuerkauf et al., 2003). Unfortunately, as we had no information about the actual number of tourists and vehicles using a trail or a road throughout the day and throughout the year, we used three alternative ways to include this information: (1) we divided the year into three periods (main summer tourist season from July to September, main winter tourist season from January to February and the two periods in between, pooled together), according to the data collected by NP rangers about attendance at the main touristic localities ('period', table 1); (2) on the basis of our personal knowledge of the area and of existing GIS layers, we distinguished the 'main tourist trails' (mostly located inside the NP and PLA and around the main surrounding towns) from the 'irregularly used tourist trails' and we calculated the distance to tourist trails including first only the main tourist trails ('TurtraMAIN', table 1), then all the tourist trails without any distinction ('TurtraALL', table 1); and (3) because of the differences in the main human activities among the NP, PLA and the surroundings of PLA, we recorded in which of the three sub–areas the kill site was located ('area', table 1).

Finally, about potential changes in lynx behavior, by distinguishing the kills that were found in the period from mid–January to the end of March from the others, we took into consideration the potential variation in the lynx behavior during the mating season ('mating_season'; table 1) as a period of higher mobility (Jędrzejewski et al., 2002).

Table 1. Explanatory variables used in the analysis (see further details in the text): [a] Square–root transformed; [b] Log transformed.

Tabla 1. Variables explicativas utilizadas para los análisis (para mayor detalle, véase el texto): [a] Transformada por raíz cuadrada; [b] Transformada logarítmicamente.

Variable name	Description
Fixed effects	
Habitat concealment [a]	Index of the presence of hiding places at the kill site, calculated adapting the 'pole method' (Pierce et al., 2004) Values: 0 (totally open habitat), 10 (totally closed habitat)
Slope [b]	Slope (with 15 x 15 m resolution)
TurtraMAIN [b]	Distance from the kill site to the closest main tourist trail (in m)
TurtraALL [b]	Distance from the kill site to the closest tourist trail, without distinction (in m)
Roads [b]	Distance from the kill site to the closest paved road
Area	NP (the kill site was inside the National Park) PLA (the kill site was inside the Protected Landscape Area) OUT (the kill site was in the surroundings of the PLA)
Period	Y1 (main summer tourist season) Y2 (main winter tourist season) N (both periods between the two main seasons)
Sex	F (female), M (male)
Mating_season	Y (the prey was killed during the mating season) N (the prey was killed during the rest of the year)
Random effect	
Individuals	M1 (adult male 1), M2 (adult male 2), M3 (young, non territorial male), F1 (adult territorial female), F2 (young territorial female)

Statistical analysis

Using 'Hawth's Tools' (Beyer, 2004) extension for ArcGIS 9.2 (ESRI, 2009) we created a set of random locations (n = 116) inside the whole study area (delimited by the National Border, by the border of the 10 km belt around the PLA and by the super home range of the five GPS–collared lynxes, estimated using the Kernel estimator at 100%). For each random location we calculated the distance to the closest paved road and the closest tourist trail (without any distinction), as we did for the kill sites (see above).We used Generalized Least Square regression (GLS) to test if the killed prey were located significantly closer or farther to roads and tourist trails than the random locations. Gaussian spatial correlation structure was specified to take spatial autocorrelation of individual observations into account.

By means of Linear Mixed Effect Models (hereafter LME, fitted using the nlme package (Pinheiro et al., 2012) we tested if the mean distance 'kill site to daytime resting sites' was influenced by the distance to nearest paved roads or tourist trails, by the habitat structure, by the sex of the lynx and whether it varied between the different periods of the year (mating season; main touristic season) or between the different sub–areas (National Park, Protected Landscape Area, closest surroundings outside the PLA). The identity of a given individual was included as random intercept into LME to take statistical non–independence of our data into account. LMEs did not exhibit any sign of spatial autocorrelation (assessed based on semivariogram). We therefore did not explicitly specify information on geographic locations of individual observations in LMEs. To achieve normality of residuals and homogeneity of variance the response variable (distance 'kill site to daytime resting sites') was Box Cox transformed ($\lambda = 0.3$). Square–root transformation was further used in the case of habitat concealment and log transformation in the case of distance to nearest paved roads and tourist trails and in the case of the slope. Although these transformations improved fits of evaluated models, their effect on the significance of individual exploratory variables were negligible. Collinearity is unlikely to affect our interpretations as correlation between explanatory variables was low; Spearman's r ranged from –0.0150 to 0.1599 with the exception of the correlation between the distance

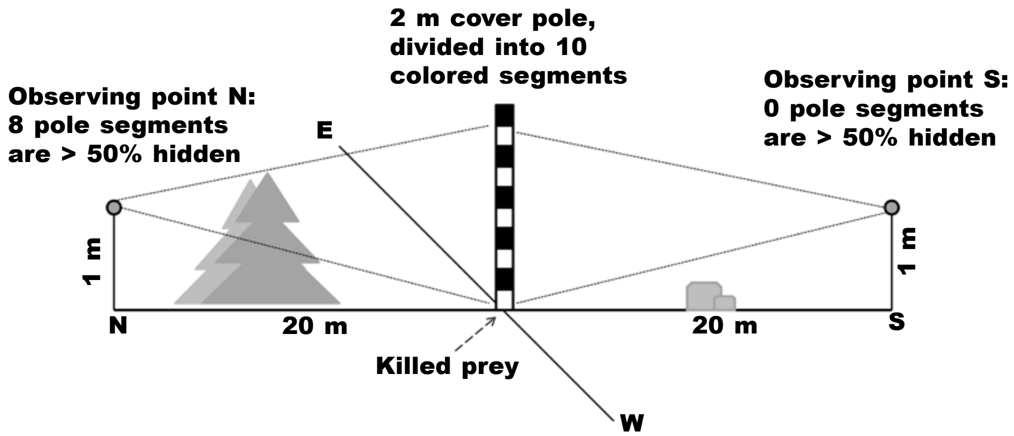

Fig. 2. Adapted version of the 'cover pole method' (Pierce et al., 2004): we obtained a measure of habitat concealment for each of the four cardinal directions and we then calculated the mean value.

Fig. 2. Versión adaptada del "método del poste" (Pierce et al., 2004): obtuvimos una medida de la ocultación del hábitat para cada uno de los cuatro puntos cardinales, y luego calculamos su valor medio.

to the nearest tourist trails and the distance to the nearest main tourist trails (r = 0.7329). These two variables were, however, never included in the same model simultaneously (see below).

We used a backward stepwise procedure to select the best minimal adequate model (hereafter MAM), *i.e.* the most parsimonious with all the effects being significant (Crawley, 2007). The significance of a particular explanatory variable was based on the change in deviance between the model containing this term and the reduced model, assuming a χ^2 distribution of the deviance change (Crawley, 2007). All calculations were carried out with the statistical software R 2.14.1. (R Development Core Team, 2011).

Results

Kill sites tended to be closer to tourist trails than random points (mean distance to all tourist trails for kill locations = 343 m, for random locations = 470 m – GLS: Δ df = 1, Likelihood ratio = 3.159, p = 0.0755), while we found no difference in the distance to paved roads (mean distance to paved roads for kill locations = 893 m, for random locations = 865 m – GLS: Δ df = 1, Likelihood ratio = 0.020, p = 0.8849).

For each of the five collared lynxes we calculated the minimum, maximum and mean distance kill site to daytime resting sites', which are summarized in table 2. The mean distance values ranged from 752 m for female F1 to 1746 m for male M2 (table 2) and differed significantly between individuals (Anova: $F_{(4,110)}$ = 2.471, p = 0.0488).

Finally, we tested the effect of each of the explanatory variables on the distance 'kill site to daytime resting sites' and we found that such distance was negatively related to the 'index of the presence of hiding places' (habitat concealment, fig. 3A) and to the distance to all tourist trails (fig. 3B). The effect of other explanatory variables (area, mating season, roads, period, sex and slope) was not significant (table 3). Approximate $\mathbf{r}^2$ for the MAM was 0.201. The distance to main tourist trails tended to correlate more strongly with the distance 'kill site to daytime resting sites' when included into the model instead of the distance to all tourist trails (slope = –2.9578 ± 1.1570, Δdf = 1, χ^2 = 6.496, p = 0.0108), yet significance of other explanatory variables remained unchanged when including the former instead of the latter variable into the model.

Discussion

Regarding our first hypothesis, we found that the distribution of the kill sites was actually independent of the proximity to paved roads, and kill sites were even closer to tourist trails than random locations (almost significantly, see above). In several studies it has been observed that at night both carnivores and ungulate used at least the smallest and less frequented gravel roads, probably to move quickly and save energy (Stener, unpubl. data cited in: Sunde et al., 1998; Creel et al., 2002; Dickson et al., 2005). Sunde et al. (1998) also concluded that the avoidance of human facilities by the lynx is likely linked to the presence of people rather than to the alteration of the habitat (*i.e.* the mere presence of roads, trails and houses). Therefore, considering that people use human facilities mainly during the day and lynx mainly hunt during night time (Schmidt, 1999; Bunnefeld et al., 2006), our results are in accordance with these previous findings.

During the day, we found that the longest mean and maximum distance 'kill site to daytime resting

Table 2. Distances 'kill site to daytime resting sites' walked by each individual (in m): mean (± standard error), minimum and maximum distance. Na. Number of kills found for which the corresponding GPS daily positions were available; MD. Mean distance (mean ± SE); MinD. Minimum distance; MaxD. Maximum distance.

Tabla 2. Distancias "lugar de caza a zonas de descanso diurnas" andada por cada individuo (en m): distancia media (± error estándar), mínima y máxima: Na. Número de presas halladas para las que estaban disponibles las posiciones diarias por GPS correspondientes; MD. Distancia media (media ± EE); MinD. Distancia mínima; MaxD. Distancia máxima.

	Monitoring period	Na	MD kill–rest	MinD	MaxD
F1	March 2010–May 2011	29	752 ± 153	15	3,716
F2	March 2010–August 2011	42	1115 ± 131	33	4,249
M1	March 2010–July 2010	9	936 ± 264	107	2,172
M2	February 2010–March 2011	21	1746 ± 337	101	4,835
M3	January 2011–August 2011	15	820 ± 146	7	1,709

sites' were walked by adult male M2 (table 2), which is consistent with the general result that territorial males generally travel longer daily distances than females (Schmidt, 1999; Jędrzejewski et al., 2002), probably due to their much larger territories (Schmidt et al., 1997). Data from a previous lynx radiotelemetry study in the Bohemian Forest (Bufka et al., in prep.) confirm this general result: the mean yearly home range size proved to be 438 km^2 for adult males and 278 km^2 for adult females, while the mean daily movement distance (DMD, *sensu* Jedrzejewski et al., 2002) was 11.5 Km for males and 6.5 for females. In the case of the second adult male, M1, we found the longest minimum distance 'kill site to daytime resting sites', while the mean distance value calculated for this male might be underestimated, as the data about M1 were collected only outside the mating season (table 2), when territorial males showed a longer locomotory activity than during the rest of the year (Schmidt, 1999; Jędrzejewski et al., 2002). In the case of the young male M3, the distances 'kill site to daytime resting sites' (mean, minimum and maximum) were shorter than the ones walked by both adult males, which is partially in contrast with what found by Schmidt (1999) when comparing adult and subadult males. This may be due to the low amount of data available for M3 (table 2) or simply to individual differences between lynxes (Schmidt, 1999). Nonetheless, a possible explanation may also be that M3 seemed to be still a floater: his home range included a large part of the territory held by male M2 minimally for the last three years and he used the whole home range in a very irregular way, spending several consecutive weeks in a restricted area and then moving far elsewhere (Bufka & Belotti, unpubl. data).Therefore, the movements of M3 may not have been influenced by the need to patrol a territory, which proved to be among the strongest motivations for movement in the case of males (Jędrzejewski et al., 2002). Both females, F1 and F2, walked very short minimum distances 'kill site to daytime resting sites' and female F1 walked also the shortest mean distance. This is consistent with findings by Jędrzejewski et al. (2002), that females in general walked shorter daily distances than territorial males, and findings by Schmidt (1999), that individual differences among lynxes of the same sex and status may play a role. Although previous studies (Schmidt, 1999; Jędrzejewski et al., 2002) found different daily activity and movement patterns for lynxes of different sex, age and status, with the data available for our study (five collared lynxes) we could only test for differences between male and female lynxes. We found no significant differences, although this could be due to the limited number of GPS–collared individuals.

In general, lynxes seemed to react to the presence of tourist trails, where people mainly move on foot, by bike, or by cross country skiing: they walked farther during the day when the prey was located closer to a tourist trail and this negative correlation tended to be stronger when we considered only the main trails. Although the possible reaction of lynx to touristic activity has not been taken into consideration previously, this may be considered consistent with findings by Bunnefeld et al. (2006) that showed that lynxes in less urbanized areas avoided the surroundings of occupied houses much more than the surroundings of roads, probably because houses were associated with a higher probability of encountering people on foot. Schmidt (1999) also found that human disturbance may have an effect on the behavior of females with kittens: they observed that, during daylight hours, the level of activity was lower in females living in an area where human activity was high than in females occupying low density urbanized areas. Although there is also evidence that reactions to disturbance may vary for lynxes of different sex, age and status (Bunnefeld et al., 2006), as mentioned above we could not test for such differences because we had data on

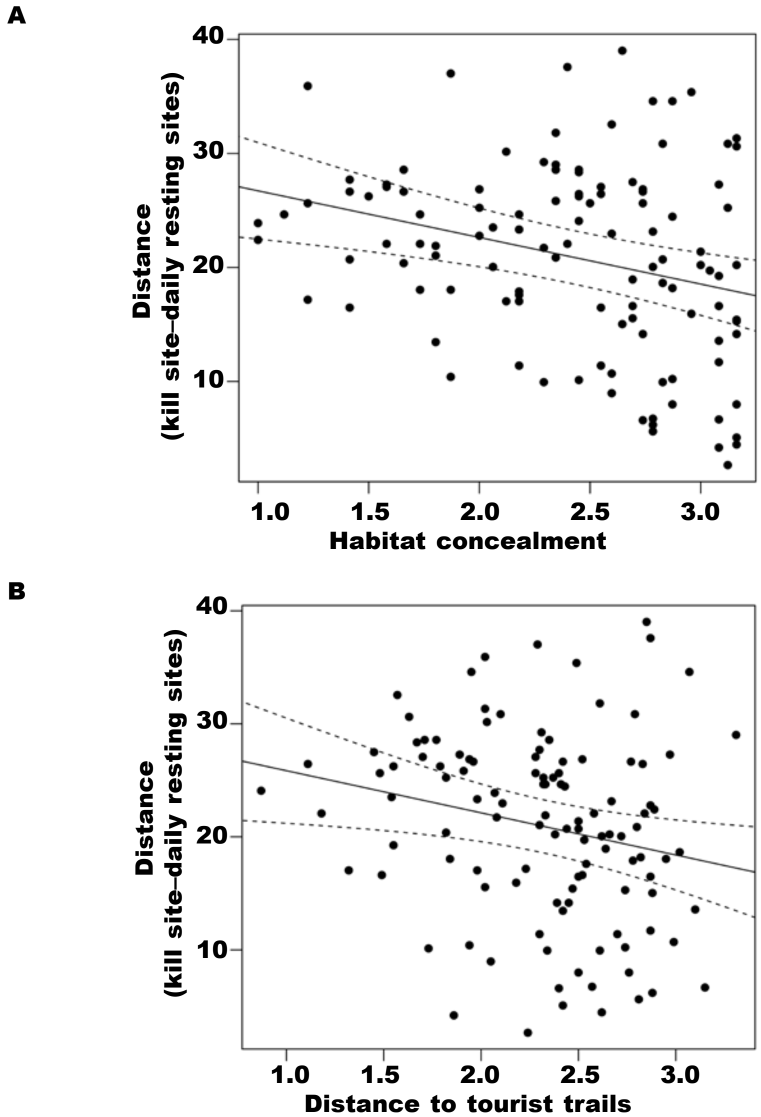

Fig. 3. Relationship between the distance 'kill site–daily resting site' (Box–Cox transformed, λ = 0.3) and: habitat concealment (square–root transformed, A); distance to the closest tourist trail (log transformed, B). Regression slope and 95% confidence intervals correspond to LME based predictions.

Fig. 3. Relación entre la distancia "lugar de caza a zonas de descanso diurnas" (transformada Box–Cox, λ = 0,3) y: cripticismo del hábitat (transformada por raíz cuadrada, A); distancia del lugar del sacrificio al sendero turístico más cercano (transformada logarítmicamente, B). La pendiente de la regresión y los intervalos de confianza del 95% corresponden a las predicciones basadas en LME.

too few GPS–collared lynxes. Also, because we could not count on accurate data about the real amount of people using a trail, we could not precisely determine whether the intensity of human activity plays a role. The fact that we found a stronger negative correlation when the distance 'kill site to closest tourist trail' was calculated only considering the regularly used tourist trails may indicate that tolerance to humans varies according to the intensity of human activity. Nonetheless, we also obtained a negative correlation when we considered all tourist trails, and we found no difference between the mean distances 'kill site to daytime resting sites' walked by lynx during the two main tourist seasons and during the rest of the year. This may mean that the level of activity outside the main tourist seasons and even on the less used tourist trails is enough to have an effect on lynx behavior. Nonetheless, to clarify this aspect, more precise estimations of the spatial and temporal changes in the intensity of human activity are required.

Table 3. Effect of the explanatory variables on the distance 'kill site to daytime resting sites' (Box–Cox transformed, λ = 0.3) based on the linear mixed effect model with normal distribution of errors. Backward elimination of non–significant terms was used to select the best minimal adequate model (MAM) with all its significant effects (see Methods for details). Models were compared using the likelihood ratio test. Significant factors included in the MAM are in boldface. Values of parameter estimates and their significances are statistically controlled for all effects included in MAM.

Tabla 3. Efecto de las variables explicativas sobre la distancia "lugar de caza a zonas de descanso diurnas" (transformada Box–Cox, λ = 0,3) basado en un modelo de efectos mixtos lineal con una distribución normal de los errores. Se utilizó la eliminación posterior de los términos no significativos para seleccionar el mejor modelo adecuado mínimo (MAM), siendo todos sus efectos significativos (véase Métodos para más detalles). Se compararon los modelos utilizando el test de razón de verosimilitud. Los factores significativos incluidos en el MAM están en negrita. Los valores de las estimas de los parámetros y de sus significancias están controlados estadísticamente para todos los efectos incluidos en el MAM.

	Estimate	± S.E.	Δdf	Likelihood ratio	*p*
(Intercept)	**37.375**	**4.441**	**1**	**25.081**	**< 0.0001**
TurtraALL_log	**–3.163**	**1.481**	**1**	**4.547**	**0.033**
Habitat concealment_rad2	**–3.756**	**1.238**	**1**	**9.010**	**0.003**
Roads_log	–1.045	1.645	1	0.415	0.520
Sex (females *vs.* males)	2.512	2.234	1	1.158	0.282
Mating_season (N *vs.*Y)	2.423	1.723	1	2.017	0.156
Period (N *vs.* Y1)	0.383	1.866	2	2.179	0.336
Period (N *vs.* Y2)	2.749	1.904			
Area (CHKO *vs.* NP)	–0.554	1.805	2	0.826	0.662
Area (CHKO *vs.* OUT)	–1.890	2.091			
Slope_LOG	–1.572	0.887	1	3.179	0.075

We found no effect of the proximity to paved roads mainly used by motorized vehicles. This may be explained by the fact that most human activity associated with paved roads is in the form of vehicles, which may not be perceived by animals as being as risky as humans *per se* (Andersen et al., 1996). Main paved roads (and highways, which were absent in our study area) are known to have a negative effect on dispersal and on connectivity among a species' populations (Schadt et al., 2002), and this can be a serious problem for long–term conservation of large carnivores such as the Eurasian lynx (Breitenmoser et al., 2000). Nonetheless, paved roads are probably not perceived as a source of disturbance by animals performing activities such as feeding or resting (Bunnefeld et al., 2006).

Concerning the habitat structure, we found that the presence of habitat features that are linked to a higher level of horizontal cover correlated negatively with the mean distance 'kill site to daytime resting sites' walked by the lynx. This is consistent with findings by Sunde et al. (1998) who reported that lynxes are able to tolerate the presence of people even at short distances if the habitat structure offers them sufficient cover.

We found a marginally insignificant negative correlation between the slope and the distance 'kill site to daytime resting sites'. Consistently with this result, Sunde et al. (1998) found that habitat inclination had no influence on the tolerance distance of lynx, and they concluded that the general preference for steep resting sites may be a result of preference for uncultivated forest stands, which are likely most abundant in steeper and less accessible portion of a forest. Indeed, lynx showed a stronger preference for steep slope in densely urbanized regions, where such features may be linked to a low level of human activity (Basille et al., 2008), than in areas with a low level of urbanization (Basille et al., 2009).

In summary, our study indicates that even human activities that do not directly aim to damage wildlife (*i.e.* tourism) can influence lynx behavior.

For the lynx, the choice to move longer distances to find a suitable resting site also on days when a large prey is available may have a cost in terms of 'energy expenditure through movements' and, in general, the choice to remain near the prey during the day may have the side effect of keeping scavengers away. In fact, few observations from camera trapping in our study area indicated that fox used lynx kills mainly after adult lynxes had left the site (Bufka et al., unpub. data). This is in accordance with a certain degree of temporal or spatial avoidance of lynx by foxes found in a few studies (discussed in Helldin et al., 2006).

As the density of scavengers (red fox, wild boar) in the study area is rather high, choosing to remain near the prey may be an advantage, especially in the case of red deer prey and especially in winter as meat remains fresh for longer due to the lower temperatures.

However, to determine whether recreational activity can actually have a negative effect on the fitness of the lynx, we believe that the next essential step is to test whether such activity can negatively influence the time lynx spend at the prey (how many times they come back to feed at the same prey and how long they stay at the prey during one night), as this is likely the key factor directly influencing animals' fitness (Hik, 1995; reviewed in Frid & Dill, 2002). Using the lynx GPS positions from the 16–hour 'intensive monitoring periods' it is possible to investigate this aspect; nonetheless, the amount of confirmed ungulate prey that was found during such periods have been insufficient to allow this further step.

Within our ongoing project, we aim to collect more data to answer this question. We also aim to compare the situation on both sides of the border between the Czech Republic and Germany, as lynx and ungulate populations often occupy trans–boundary territories and the two areas are part of the same mountain range, but show several differences (*e.g.* different human population density, primary landscape, landscape use, intensity of tourism).

Over the last two decades, the tourist attractiveness of the Bohemian Forest has increased greatly and the flow of people on the road network and throughout the National border has intensified. This trend is likely to continue in coming years and there is currently pressure to restore several almost unused roads and trails. Therefore, we believe that the effects of human activity should be better studied in different species as they likely show different levels of tolerance to such activities (Frid & Dill, 2002; Taylor & Knight, 2003). Although more precise information about the amount of people using the different tourist trails would be required to determine such levels of tolerance, this study shows that this aspect of lynx coexistence with humans may also deserve more attention. In order to understand lynx responses to recreation further research is surely needed. Such information may help managers setting up recreation plans aiming to minimize the impact of human presence, a fundamental issue to achieve the best compromise between economic development and species conservation.

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References

Amstrup, S. C., 1993. Human disturbances of denning polar bears in Alaska. *Arctic,* 46(3): 246–250.

Andersen, R., Linnell, J. D. C. & Langvatn, R., 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biological Conservation,* 77: 169–176.

Andrén, H., Linnell, J. D. C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P. F., Ahlquist, P., Kvam, T., Franzén, R. & Segerström, P., 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi–use landscapes. *Biological Conservation*, 131: 23–32.

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M. & Manica, A., 2009. A Global Perspective on Trends in Nature–Based Tourism. *PLoS Biol*ogy, 7(6): e1000144. doi:10.1371/journal.pbio.1000144

Basille, M., Calenge, C., Marboutin, E., Andersen E. & Gaillard, J–M., 2008. Assessing habitat selection using multivariate statistics: some refinements of the ecological–niche factor analysis. *Ecological Modelling,* 211: 233–240.

Basille, M., Herfindal, I., Santin–Janin, H., Linnell, J. D. C., Odden, J., Andersen, R., Høgda, A. & Gaillard, J–M., 2009. What shapes Eurasian lynx distribution in human–dominated landscapes: selecting prey or avoiding people? *Ecography,* 32(4): 683–691. DOI:10.1111/j.1600–0587.2009.05712.x

Beyer, H. L., 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Boitani, L., 2000. Action plan for the conservation of wolves (*Canis lupus*) in Europe. *Nature and Environmental Series* 113. Council of Europe, Strasbourg, France.

Breitenmoser, U., Breitenmoser–Würsten, Ch., Okarma, H., Kaphegyi, T. A. M., Müller, U. M. & Kaphygyi–Wallmann, U., 2000. Action Plan for the Conservation of the Eurasian Lynx in Europe (*Lynx lynx*). *Nature and environment,* 112: 1–70. Strasbourg Cedex, Council of Europe.

Bunnefeld, N., Linnell, J. D. C., Odden, J., Van Duijn, M. A. J. & Andersen, R., 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human–dominated landscape: effects of sex and reproductive status. *Journal of Zoology,* 270: 31–39.

Burger, J. & Gochfeld, M., 1998. Effects of ecotourists on bird behavior at Loxahatchee National Wildlife Refuge, Florida. *Environmental Conservation,* 25: 13–21.

Crawley, M. J., 2007. R Book. John Wiley & Sons, Chichester.

Creel, S., Fox, J. E., Hardy, A., Sands, J., Garrott, B. & Peterson, R. O., 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Conservation Biology,* 16(3): 809–814.

Dickson, B. J., Jenness, J. S. & Beier, P., 2005. Influence of vegetation, topography and roads on cougar movement in Southern California. *Journal of Wildlife Management,* 69(1): 264–276

Duchesne, M., Côté, S. & Barrette, C., 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation,* 96: 311–317.

Dyck, M. G. & Baydack, R. K., 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife–viewing activities at Churchill, Manitoba, Canada. *Biological Conservation,* 116: 343–350.
ESRI, 2009. ArcGIS 9.2. Environmental Systems Research Institute, Inc. Redlands.
Frid, A. & Dill, L., 2002. Human–caused disturbance stimuli as a form of predation risk. *Conservation Ecology,* 6(1):11.
URL: http://www.consecol.org/vol6/iss1/art11
Goodrich, J. M. & Berger, J., 1994. Winter recreation and hibernating black bears. *Biological Conservation,* 67: 105–110.
Helldin, J–O. & Danielsson, A. V., 2007. Changes in red fox *Vulpes vulpes* diet due to colonisation by lynx *Lynx lynx*. *Wildlife Biology,* 13: 475–480.
Helldin, J–O., Liberg, O. & Glöersen, G., 2006. Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden –frequency and population effects. *Journal of Zoology,* 270: 657–663.
Hik, D. S., 1995. Does risk of predation influence population dynamics? *Wildlife Research,* 22: 115–129.
Hothorn, T. & Müller, J., 2010. Large–scale reduction of ungulate browsing by managed sport hunting. *Forest Ecology and Management,* 260(9): 1416–1423.
Huck, M., Jędrzejewski, W., Borowik, T., Milosz–Cielma, M., Schmidt, K., Jędrzejewska, B., Nowak, S. & Myslajek, R. W., 2010. Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. *Acta Theriologica,* 55(2): 177–192.
Jędrzejewska, B. & Jędrzejewski, W., 1998. *Predation in vertebrate communities – The Białowieża Primeval Forest as a case study.* Springer Verlag, Berlin–Heidelberg–New York.
Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L. & Okarma, H., 1996. Population dynamics of wolves *Canis lupus* in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. *Mammal Review,* 26: 103–126.
Jędrzejewski, W., Schmidt, K., Okarma, H. & Kowalczyk, R., 2002. Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland). *Annales Zoologici Fennici,* 39: 29–41.
Jobin, A., Molinari, P. & Breitenmoser, U., 2000. Prey spectrum, prey preference and consumption rates of Eurasian lynx (*Lynx lynx*) in the Swiss Jura mountains. *Acta theriologica,* 45(2): 243–252.
Kaczensky, P., Knauer, F., Krze, B., Jonozovic, M., Adamic, M. & Gossow, H., 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biological Conservation,* 111: 191–204.
Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B. & Hornocker, M. G., 2002. Effects of roads and human disturbance on Amur Tigers. *Conservation Biology,* 16: 97–108.
Kolowski, J. M. & Holekamp, K. E., 2009. Ecological and anthropogenic influences on space use in the spotted hyena. *Journal of Zoology,* 277: 23–36.
Koubek, P. & Červený, J., 1996. Lynx in the Czech and Slovak Republics, *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae BRNO, XXX Nova Series*, 1996: 1–78.
Linnell, J. D. C., Swenson, J. E., Andersen, R. & Barnes, B., 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin,* 28(2): 400–413.
– 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation,* 4: 345–349.
Linnell, J. D. C., Promberger, Ch., Boitani, L., Swenson, J. E., Breitenmoser, U. & Andersen, R., 2005. The linkage between conservation strategies for large carnivores and biodiversity: the view from the 'half–full' forests of Europe. In: *Large carnivores and the conservation of biodiversity*: 381–398 (J. C. Ray et al., Eds.). Island Press.
Mašková, Z., Bufka, L. & Smejkal, Z., 2003. Národní Park a chráněná krajinná oblast Šumava. In: *Chráněná území ČR–Českobudějovicko, svazek VIII*: 578–736 (J. Albrecht a kol, Eds.) Agentura ochrany přírody a krajiny ČR a EkoCentrum Brno, Praha. [in Czech.]
Milner, J. M., Nilsen, E. B. & Andreassen, H. P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology,* 21(1): 36–47.
Mysterud, A., 1999. Seasonal migration pattern and home range of roe deer (Capreolus capreolus) in an altitudinal gradient in southern Norway. *Journal of Zoology (London),* 247: 479–486.
Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R. & Jędrzejewska, B., 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. *Acta Theriologica*, 42(2): 203–224.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & the R Development Core Team, 2012. Linear and Nonlinear Mixed Effects Models. R package version 3.1–103.
R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0. URL http://www.R-project.org/.
Pierce, B. M., Bowyer, R. T. & Bleich, V. C., 2004. Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management,* 68(3): 533–41.
Putman, R. J. & Staines B. W., 2004. Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. *Mammal Review,* 34(4): 285–306.
Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Červený, J., Koubek, P., Huber, T., Staniša, C. & Trepl, L., 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology,* 39: 189–203.
Schmidt, K., 1999. Variation in daily activity of the free–living Eurasian lynx (*Lynx lynx*) in Białowieża Primeval Forest, Poland. *Journal of Zoology, London,* 249: 417–425.
Schmidt, K., Jędrzejewki, W. & Okarma, H., 1997. Spatial organization and social relations in the Eurasian lynx population in Białowieża Primeval

Forest, Poland. *Acta Theriologica,* 42: 289–312.
Selva, N., Jędrzejewska, B., Jędrzejewski, W. & Wajrak, A., 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology,* 83: 1590–1601.
Sunde, P., Sutener, S. Ř. & Kvam, T., 1998. Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildlife biology,* 4: 177–183.
Swenson, J., Gerstl, N., Dhale, B. & Zedrosser, A., 2000. Action Plan for the conservation of the Brown Bear in Europe (*Ursus arctos*). *Nature and Environment,* 114. Council of Europe, Strasbourg.
Taylor, A. R. & Knight, R. L., 2003. Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications,* 13: 951–963. http://dx.doi.org/10.1890/1051–0761(2003)13[951:WRTRAA]2.0.CO;2
Theuerkauf, J., Jędrzejewski, W., Schmidt, K. & Gula, R., 2001. Impact of human activity on daily movement patterns of wolves (*Canis lupus*) in the Białowieża Forest, Poland. In: *Wildlife, land and people: priorities for the 21st Century. Proceedings of the Second International Wildlife Management Congress*: 206–208 (R. Field, R. J. Warren, H. Okarma & P. R. Sievert, Eds.). The Wildlife Society, Bethesda, Maryland, USA.
Theuerkauf, J., Jędrzejewski, W., Schmidt, K. & Gula, R., 2003. Spatiotemporal segregation of wolves from humans in the Białowieża Forest (Poland). *Journal of Wildlife Management,* 67(4): 706–716.
Thiel, D., Ménoni, E., Brenot, J.–F. & Jenni, L., 2007. Effects of recreation and hunting on flushing distance of capercaillie. *Journal of Wildlife Management,* 71: 1784–1792.
Thiel, D., Jenni–Eiermann, S., Braunisch, V., Palme, R. & Jenni, L., 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. *Journal of Applied Ecology,* 45: 845–853 doi: 10.1111/j.1365–2664.2008.01465.x
Thurber, J. M., Peterson R. O., Drummer T. D. & Thomasma S. A., 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin,* 22: 61–68.
Weingarth, K., Bufka, L., Daniszová, K., Knauer, F., Šustr, P. & Heurich, M., 2011. Grenzüberschreitendes Fotofallenmonitoring–wie zählt man Luchse? Berichte aus dem Nationalpark. Nationalparkverwaltung Bayerischer Wald, Grafenau. [in German.]
Wölfl, M., Bufka, L., Červený, J., Koubek, P., Heurich, M., Habel, H., Huber, T. & Poost, W., 2001. Distribution and status of the lynx in the border region between Czech Republic, Germany and Austria. *Acta Theriologica*, 46(2): 181–194.