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Original article

Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills

Iris Podolski, Elisa Belotti, Luděk Bufka, Holger Reulen & Marco Heurich

Activity patterns of predators are influenced by several factors including season and temperature as well as the availability of prey species. We investigated the activity of six free-living Eurasian lynx *Lynx lynx* (four males and two females without kittens) in the Bohemian Forest along the border between Germany and the Czech Republic. The lynx were tagged with GPS-collars with acceleration sensors in 2005, 2010 and 2011. Activity was measured every 5 minutes on 1,360 days (403,467 measurements) to detect circadian activity patterns. All lynx were predominantly crepuscular, with an average activity of 8.9 hours/day and with the lowest activity at midday. The activity patterns of male and female lynx did not differ significantly. With each 10°C increase in the mean air temperature per day, the lynx decreased their daily activity by 30 minutes. In winter, activity was concentrated at dusk. We also investigated whether lynx activity was influenced by the availability of freshly killed roe deer *Capreolus capreolus*, red deer *Cervus elaphus* or European hare *Lepus europaeus*. We compared the activity data of 357 days with a kill (109 recorded kills) and 316 days without a kill and calculated generalised additive mixed models. On days with a kill, the lynx were 3.3 hours/ day less active than on days without a kill. The activity on consecutive days with a killed prey did not differ. The pattern of activity on days with a kill differed little from the pattern of activity on days without a kill.

Key words: acceleration sensor, Eurasian lynx, GPS-telemetry, Lynx lynx, predation, roe deer, temporal behaviour

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Many factors affect the activity of animals, including the sex and reproductive status of the animal (Schmidt 1999, Kolbe & Squires 2007) and environmental factors such as temperature (Beltran & Delibes 1994), light (Nielsen 1983) and season (Manfredi et al. 2011). For many carnivores, including wild felids, other important factors are the availability and activity of prey species (Ferguson et al. 1988, Beier et al. 1995). For example, Iriomote cats *Prionailurus iriomotensis* (Schmidt et al. 2009), jaguars *Panthera onca* and pumas *Puma concolor* (Harmsen et al. 2011) synchronise their activity peaks with those of their prey. The avoidance of humans can also influence the behaviour as it has been shown for snow leopards *Uncia uncia* (Wolf & Ale 2009) and wolves *Canis lupus* (Theuerkauf et al. 2003).

The Eurasian lynx *Lynx lynx* mainly hunts ungulates and generally chooses prey species which are

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slightly larger than itself and most common in a certain area (Jedrzejewski et al. 1993, Sunquist & Sunquist 2002, Breitenmoser & Breitenmoser-Würsten 2008). In the Bohemian Forest, roe deer *Capreolus capreolus* is the main prey of the lynx (Heurich et al. 2012). Other prey include red deer *Cervus elaphus*, especially calves, yearlings and females, as well as birds and small mammals (Fejklová 2002).

How lynx activity changes after having made a kill has not yet been studied in detail. A large kill provides enough food for several days (Okarma et al. 1997). During these days the need to hunt may stop or is at least reduced, and the lynx can spend longer time eating or performing other activities. Bernhart's (1990) and Reinhardt & Halle's (1999) observations on two and one lynx, respectively, support this hypothesis, showing that the lynx were less active on days when a killed prey was available. In a third study, Schmidt (1999) found that the activity of the lynx is lowest on the first day after the kill and increases gradually as the available meat decreases.

Former activity studies on large felids mainly focused on animal movements, recorded by radio-tracking (Bernhart 1990, Odden & Wegge 2005, Schmidt et al. 2009), camera trapping (Kolowski & Alonso 2010, Harmsen et al. 2011), or by only analysing indirect signs such as footprints or faeces (Saunders 1963, Wolf & Ale 2009). Reinhardt & Halle (1999) and Schmidt (1999) used activity sensors, which were not limited to only one type of activity, but were able to detect every possible action of an animal except resting or sleeping. Nonetheless, in the 1990s the sensors in radio-collars could only provide a relatively small amount of data. Nowadays, the new generation of GPS-collars include acceleration sensors, which detect the activity of an animal on a finer scale and allow collection of a large amount of data (Löttker et al. 2009). Gervasi et al. (2006) found good correspondence between sensor-measured and observed activity on brown bears *Ursus arctos*. This method is especially useful to investigate the behaviour of cryptic, mainly night active, forest living species occurring at low densities such as the Eurasian lynx, which can rarely, if at all, be directly observed (Altmann 1974).

We studied the behaviour of free-living Eurasian lynx in the Bohemian Forest using GPS-collars with acceleration sensors. We investigated the daily activity patterns, their seasonal changes, the influence of ambient temperature and sex of the lynx on activity, and whether the activity changes on days after successful hunting of prey.

Material and methods

Study area

The Bohemian Forest represents a forested mountain range along the border between Bavaria (Germany) and the southwestern part of the Czech Republic. The core area of our study was located in two contiguous protected areas, the Bavarian Forest National Park (240 km^2; 49°3'19''N, 13°12'9''E) and the Šumava National Park (690 km^2; 49°7'0''N, 13°36'0''E). Data were also collected from the adjacent Bavarian Forest Natural Park (3,007 km^2) and the Bohemian Forest Protected Landscape Area (1,000 km^2). Together, the four parks form the largest strictly protected continuous forest expanse in Central Europe, the so-called Bohemian Forest Ecosystem. Compared to elsewhere in Europe, the human population density is very low; < 2 inhabitants/km^2 in the core area and at the margins (outside the national parks) approximately 70 inhabitants/km^2 in Germany and < 30 inhabitants/km^2 in the Czech Republic. The elevation ranges from 600 to 1,453 m a.s.l., with an average annual temperature of 6.5°C at lower elevations and 3.0°C at higher elevations. The mean annual precipitation is between 830 and 2,230 mm. Snow cover persists for 7-8 months at the higher elevations and for 5-6 months in the valleys.

Three major forest types dominate the vegetation. Above 1,200 m a.s.l., a montane spruce forest with Norway spruce *Picea abies* and mountain ash *Sorbus aucuparia* is found. Between 600 and 1,000 m a.s.l., mixed montane forests with Norway spruce, silver fir *Abies alba*, European beech *Fagus sylvatica* and sycamore maple *Acer pseudoplatanus* grow on slopes; and spruce forests with Norway spruce, silver birch *Betula pendula*, downy birch *Betula pubescens* and mountain ash grow in wet depressions with cold air pockets (Heurich & Neufanger 2005). Large parts of the forest, as well as some secondary treeless areas, are left to develop naturally without human intervention (Albrecht 2003).

The primary species of wild ungulates are red deer, roe deer and wild boar *Sus scrofa*. The Eurasian lynx is the only large carnivore species currently living in this area.

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Table 1. Summary characteristics and activity data of the GPS-collared lynx. Data analysis indicate whether data were used for descriptive and/or statistical (GAMM) analysis. Lynx M1 was captured and collared twice.

					Data analysis	
Lynx	Sex	Age class	Period of activity data	Number of 5-minute intervals	Descriptive	GAMM
M1	♂	Adult (~ 5 years)	07.03.2005 - 25.07.2005 10.11.2005 - 19.02.2006	68313	Yes	Yes
M2	♂	Adult (~ 6 years)	16.03.2010 - 17.02.2011	102875	Yes	Yes
M3	♂	Adult (~ 5 years)	29.03.2010 - 18.05.2010	15081	No	Yes
M4	♂	Subadult	15.01.2011 - 03.03.2011	13365	No	Yes
F1	♀	Adult (~ 3 years)	17.03.2010 - 07.02.2011	99451	Yes	Yes
F2	♀	Subadult	17.03.2010 - 02.03.2011	104382	Yes	Yes

Data recording

In 2005, 2010 and 2011, we captured six free-living Eurasian lynx (four males and two females without kittens) in box traps (Table 1). After trapping, they were anaesthetised, tagged with GPS-collars (GPS Plus Mini; Vectronic Aerospace, Berlin, Germany) and later set free at the same place (Heurich 2011). The collars carried dual-axis acceleration sensors (x- and y-axes) that detected the movement of the lynx every eight second and summarised it in 5-minute intervals. Since 96% of the x- and y-activity data correlated, we only analysed the x-activity; as Löttker et al. (2009) did for red deer. We monitored the lynx during periods of different length. In summary, we acquired 403,467 data points of activity at 5-minute intervals on a total of 1,360 monitoring days (see Table 1).

We defined movement of the lynx body as activity, because it included all possible actions (e.g. climbing, feeding or patrolling the territory). The more the lynx body moved the higher were the values detected by the acceleration sensors. The value scale ranged from 0 (no activity) to 255 (very high activity). However, it was not possible to distinguish the different types of behaviour on the basis of the sensors, except the distinction between activeness and inactiveness, which included resting and sleeping. Therefore, we defined all values from 0 to 27 as inactive behaviour. This limit was chosen because the acceleration sensors were very sensitive to movements of the collar and also detected light head shakings of the lynx, which cannot be stated as activity. This threshold was established in a preliminary study with a captive lynx (P. Löttker, M. Traube, A. Rummel, A. Stache & M. Heurich, unpubl. data).

The mean air temperature per day was calculated from data of one meteorological station in Germany (Waldhäuser) and one in the Czech Republic (Zhuři).

On the basis of 133 clustered GPS positions, we identified 109 kills (82%) in the field during the whole monitoring period: 87 kills were roe deer, 17 were red deer and five were European hares *Lepus europaeus*. We identified a cluster visually using the program ArcGIS 9.2 (Esri 2009) and it was defined as GPS positions within a circle of about 200 m in diameter (Ersson 2011). We defined days 'with kill' (N = 357) as the days on which we knew a killed prey was available because the lynx visited the same place during at least two consecutive nights, and we could find the carcass in the field. These days were subdivided into four categories: day 1 (N = 109), i.e. the day with the first GPS position of the lynx at the kill site (assumed to be the day when the prey was killed); day 2 (N = 105), the day following the kill if the lynx still visited the kill; day 3 (N = 85), the day following day 2 if the lynx still visited the kill; and day > 3 (N = 58), representing the group of days following day 3 if the lynx still visited the kill. The period of time a lynx fed on a kill was determined relying on GPS positions. On average, the lynx consumed a killed roe deer within three days (SD = 1), a red deer within four days (SD = 1) and a hare within two days (SD = 1). The days when we assumed that the lynx had no kill, because the GPS positions did not show any cluster, were summarised into a fifth category 'no kill' (N = 316). The last category 'unknown' (N = 687) included all days when GPS positions were lacking (although activity data were recorded) or when we in the field could not confirm whether the lynx had a kill or not.

Data analysis

We analysed the daily activity patterns of four lynx: M1, M2, F1 and F2. The other two lynx (M3 and M4) were not included in this first descriptive part of the analysis as their collars only recorded activity

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data for a few months (see Table 1). We calculated the average activity of the single values (5-minute intervals) per hour for each lynx to obtain a general circadian activity pattern as well as seasonal variation in this general pattern. We defined seasons as spring (March-May), summer (June-August), autumn (September-November) and winter (December-February).

To speed up the following calculation, we used a more parsimonious 15-minute time interval grid instead of the original activity observations on a 5-minute time interval grid. We calculated the respective average values by pooling adjacent original continuous activity observations corresponding to one 15-minute interval, getting 67,048 data points of activity at 15-minute intervals. This data reduction was not accompanied by any substantial loss of information.

To determine the effects on activity as dependent variable, we pursued two different settings, based on generalised additive mixed models (GAMM; Bolker 2008). In a first model, we analysed the duration of activity as response variable, defined as hours per day when the lynx was active (Table 2). In a second model, we analysed the strength of activity as response variable, which is represented by the single continuous values (average values on 15-minute intervals) of the activity. Date, daytime (defined below), sex of the lynx, mean air temperature per day and prey usage were considered as covariates. Temporal dependence of activity measurements was considered by the smooth estimation of the daytime effect. The variable prey usage included the categories 'with kill' and 'no kill' and is therefore based on 673 days. We included the name of the lynx as random effect to consider the consecutiveness of data collection for each of the lynx (Fahrmeir et al. 2007).

We based analysis on all six lynx, relying on data of all four 'with kill' categories ('day 1' - 'day > 3') and the category 'no kill', in the first model and to the 15-minute intervals in the second model. As a further descriptive analysis, we calculated the variation of the circadian activity pattern among these five categories ('with kill' and 'no kill'). Tests for differences in the activity patterns should be based on simultaneous bands for penalised spline estimators. However, these are difficult to achieve and subject to current research in generalised models and correlated data (Krivobokova et al. 2010).

Since we were interested in mean effect of daytime across the year in the second model, the daytime variable was included in the model, which was transformed to become independent of the seasonality of day length. We used daily geo-information of sunrise and sunset and fixed these to 6 am and 6 pm at the transformed daytime, thus twilight was always at the same time across the whole year. The different numbers of 15-minute intervals in between these two time points at each day were stretched adequately. For all analysis, the Central European Time (CET = UTC+1) was used.

All calculations were carried out with the statistical

Table 2. Variables considered in the first (1st) and/or second (2nd) generalised additive mixed model (GAMM).

			GAMM		
Name	Scale	Value range	1st	2nd	Description
Activity:					
Strength (5-minutes)	Continuous	(0; 255)	No	No	Value of lynx activity on original time grid of the GPS-collar
Strength (15-minutes)	Continuous	(0; 255)	Yes	Yes	Average value of lynx activity calculated on an artificial 15-minute time grid
Behaviour	Categorical	Inactive; active	No	No	Inactive: resting or sleeping; active: e.g. feeding or moving
Behaviour	Continuous	(0; 27); (28; 255)	Yes	Yes	Inactive: (0; 27); active: (28; 255)
Duration	Continuous	(0; 24)	Yes	No	Hours per day when the lynx was active
Date	Continuous	See Table 1	Yes	Yes	Date
Daytime	Continuous	(0; 24)	No	Yes	Time of the day
Lynx	Categorical	M(1; 4); F(1; 2)	Yes	Yes	Name of the lynx individual
Prey usage	Categorical	With kill; no kill	Yes	Yes	Availability of a freshly killed prey
Sex	Categorical	Male; female	No	Yes	Sex of the lynx
Temperature	Continuous	(-20; 30)	Yes	No	Mean air temperature per day (°C)

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software R 2.11.1 and version 1.6-2 of R package mgcv (Hornik 2011, Wood 2011).

Results

Activity patterns

All four lynx showed similar patterns of activity (Fig. 1). The highest level of activity was reached at twilight, at around 4 am and 7 pm, and the lowest level at midday. Thus, all four lynx were nocturnal and predominantly crepuscular. The activity peak at dusk tended to be higher than the one at dawn. The effects of the covariate daytime on the activity was confirmed statistically using the GAMM ($P < 0.001$, $N = 67{,}048$). These patterns did not differ between male and female lynx (GAMM; $P = 0.952$, $N = 67{,}048$). On average, the mean activity was 8.9 hours/day ($SD = 1.0$).

The daily activity patterns varied among seasons. In spring and summer, all lynx showed the general pattern described above. However, for some animals, we could detect changes that began in autumn and culminated in winter: M1 and M2 reduced their activity at dawn and F1 was much more active at dusk. The only exception was the subadult lynx F2, which showed the same activity patterns throughout the year. Nonetheless, the activity of all adult lynx in winter was concentrated at dusk (see Fig. 1).

Also the ambient temperature influenced the activity. With each 10°C increase in the mean air temperature per day, the lynx decreased their daily activity by 30 minutes (GAMM; $P = 0.001$, $N = 673$).

Activity with killed prey

The availability of a fresh kill had a highly significant influence on the duration of activity (Fig. 2). On days with a kill (all four 'with kill' categories combined), the lynx were 3.3 hours/day less active than on days without a kill (GAMM; $P < 0.001$, $N = 673$).

Furthermore, the 15-minute intervals were 14-17 units lower on days with a kill in comparison to the days without a kill (GAMM; $P < 0.001$, $N = 67{,}048$); i.e. when the lynx were active on days with a kill, the single values of the activity were not as high as on days without a kill. Therefore, the strength of activity also changed. Concerning the consecutive days after a kill (categories 'day 1' - 'day < 3'), neither the duration nor the strength of activity differed among these days.

However, the availability of a fresh kill barely

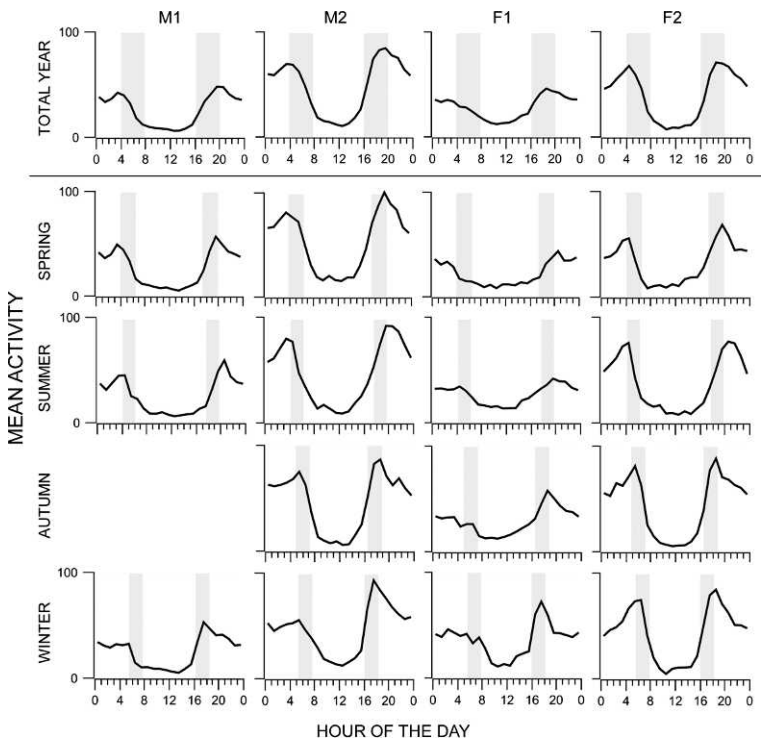


Figure 1. Average (original value range: 0-255) daily activity patterns of GPS-collared lynx (M1, M2, F1 and F2) per season. Grey bars indicate periods of dawn and dusk. For lynx M1, activity data in autumn were lacking.

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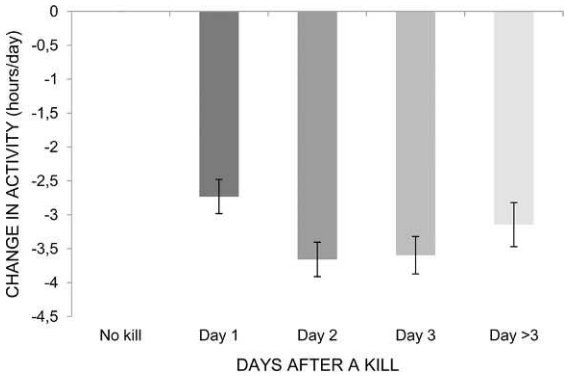


Figure 2. The influence of the availability of a kill on the duration of lynx activity. Days with no kill differed from all other days after the kill (GAMM; $P < 0.001$, $N = 673$).

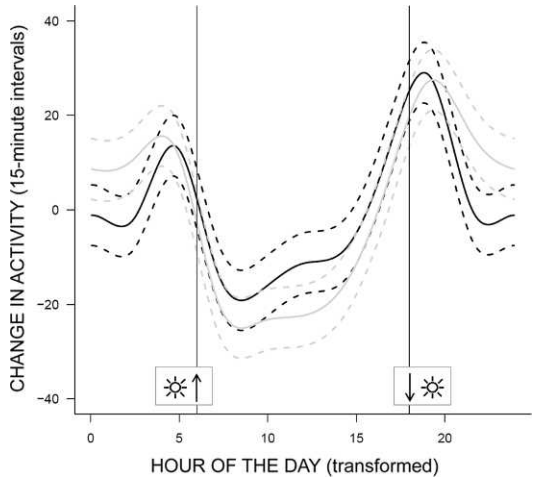


Figure 3. Estimated effects of the transformed daytime on activity of lynx on days with (black lines) and without (grey lines) a kill in the second model. Dashed lines indicate point wise 95% confidence intervals.

changed the daily activity pattern (Fig. 3). During daylight hours, the activity on days with a kill tended to be higher than on days without a kill. At twilight it changed, so that during the night, the activity on days without a kill seemed to be higher. Actually, the only period when 95% confidence intervals did not overlap, and the activity levels therefore differed, was from 9 pm to 11 pm. At that time, the lynx were more active on days without a kill than on days with a kill.

Discussion

Although the activity of an animal would be best analysed by direct observations (Naguib 2006), other methods have to be applied in the case of wild, cryptic species with a low population density (Altmann 1974, Karanth et al. 2010). Camera trapping has been used to analyse activity patterns of ocelots *Leopardus pardalis* (Kolowski & Alonso 2010), jaguars and pumas (Harmsen et al. 2011), but in these studies, the activity is represented only as the percentage of all collected photos and the individuals cannot always be identified. Both radio-telemetry and GPS-telemetry focus on the movement of an animal and provide more detailed data on activity (Odden & Wegge 2005, Mattisson et al. 2010). However, both methods are invasive (requiring the physical capture of the animals), they can be financially and technically demanding and they imply dealing with ethical matters about animal welfare. Therefore, in general only a limited number of specimens can be monitored by telemetry techniques. Nevertheless, since this is currently the best way to monitor lynx, we used GPS-telemetry, but we acquired fine-scale information on the animals' activity by using GPS-collars with acceleration sensors (Löttker et al. 2009).

The free-living Eurasian lynx in our study area were nocturnal and predominantly crepuscular. In contrast, Reinhardt & Halle (1999) described different daily activity patterns of lynx in Slovenia, which had a higher level of activity during daytime than at night. However, they studied one female lynx with kittens, and other studies have also described different activity patterns for leading females (Schmidt 1999, Kolbe & Squires 2007). The female lynx in our study had no kittens, which could have accounted for the similarities in the activity patterns between the sexes. Bernhart (1990) and Schmidt (1999) found activity patterns of lynx similar to us, with the highest activity at twilight and a higher activity at night than during daytime. Roe deer, the main prey species of Eurasian lynx, and red deer are most active at twilight (Clutton-Brock et al. 1982, Chapman et al. 1993, Danilkin 1996), which may have an influence on the lynx activity patterns, as predators often adapt their behaviour to the activity of their main prey (Ferguson et al. 1988, Beier et al. 1995). Furthermore, in general, lynx and cats hunt predominantly by using their highly developed senses of sight, smell and hearing (Sunquist & Sunquist 2002). Therefore, they are optimally adapted to the conditions at twilight when they are not easily detected by the prey and still can see enough for hunting. Another potential explanation for this activity pattern could be that the lynx avoided humans, whose activity is

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concentrated during the day. The human population density in our study area is low, but touristic activity must be mentioned and also poaching is a problem (Wölfl et al. 2001). This avoidance behaviour has been shown for snow leopards (Wolf & Ale 2009) and wolves (Theuerkauf et al. 2003), but has not been confirmed yet in the case of the lynx (Sunde et al. 1998, Basille et al. 2009).

The daily activity patterns of the lynx varied among seasons, with activity in winter being concentrated at dusk. This is consistent with the observations of the Canadian lynx *Lynx canadensis* by Kolbe & Squires (2007). This may be at least indirectly related to the higher ambient temperature at dusk than at dawn. The roe deer, which is the main prey of the lynx, shifts its activity peak from dawn to later in the morning in winter when it is frosty (Clutton-Brock et al. 1982). Daylight may not ensure the best conditions for hunting activity by the lynx. In fact, in our study, we observed no increase in the activity of the lynx during daylight hours in winter. Nonetheless, although we are aware that lynx is not active only when hunting, the change in roe deer activity (related to changes in temperature) may have played a role in the observed decrease in lynx activity at dawn, making it less profitable for the lynx to hunt at dawn than at dusk. The one exception was lynx F2, which was as active at dawn as at dusk. It is unclear whether the subadult status and lower hunting experience of lynx F2 influenced this pattern.

As observed in our study, Beltran & Delibes (1994) and Schmidt (1999) also found that lynx avoid high ambient temperatures, especially in summer.

In general, it takes longer than one night for lynx to consume large ungulate prey (Breitenmoser & Breitenmoser-Würsten 2008). This allowed us to detect the presence of potential kills based on cluster analysis of the positions provided by the GPS-collars. Using this method, we could find and verify most of the killed ungulate prey in the field, while smaller prey animals were difficult to recognise, only five hares were identified as consumed prey. However, we performed a scat analysis and only found hair from hares in 5% of the scats. In about 15% of the scats, we found other small mammals, like mice that do not change the activity or movement behaviour. This indicates that we did not miss much.

In accordance with previous studies (Bernhart 1990, Reinhardt & Halle 1999, Schmidt 1999), we found that both the duration and the strength of lynx activity were significantly lower on days when a kill was available than on days with no kill. This could be explained by the lack of need to hunt for several days (Okarma et al. 1997), and by the lynx staying near the kill to prevent losses to scavengers. This would also explain why the level of activity on consecutive days with a kill remained constant. In contrast, Schmidt (1999) found a lower activity on the first day 'with kill' than on the next days spent consuming the kill. However, his analysis was limited to the movement of the lynx, which is just one aspect of all activities. Jedrzejewski et al. (2002) found that activity is highest on days without a kill and lowest on the first day after a kill.

In our study, the activity pattern of the days with a kill differed from the pattern of days without a kill only during a 2-hour period, from 9 pm to 11 pm. On days without a kill, lynx may use this time interval to patrol their territories and visit various hunting grounds (Jedrzejewski et al. 2002, Breitenmoser & Breitenmoser-Würsten 2008), whereas on days with a kill, they probably consume their prey during this time interval. The lynx activity pattern during the rest of the day was independent of the availability of a kill. Other environmental factors, such as the temperature, clearly had a greater effect on the activity pattern.

In conclusion, our study indicated that there are detectable differences in duration, strength and patterns of activity between the days with and without consumption of a prey. On this basis, it may be possible to develop a method to detect the presence of a kill by analysing the activity data (in combination with the information from the GPS positions). This would greatly reduce the time effort required for searching for kills in the field, and it would especially help when studying the lynx, whose weight and lifestyle impose limitations to battery size and therefore to the obtainable number of GPS positions. Increasing the availability of data on the hunting rates of this species, would improve our knowledge about an important aspect of this species' ecology.

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References

Albrecht, J. 2003: The Českobudějovicko region. - In: Mackovčin, P. & Sedláček, M. (Eds.); Protected areas of the Czech Republic. 8th edition. Agency of Nature and Landscape Protection of the Czech Republic and Eko-Centrum Brno, Prague, Czech Republic, 808 pp. (In Czech).

Altmann, J. 1974: Observational study of behavior: sampling methods. - In: Baerends, G.P., Fabricius, E., Hediger, H., Kruijt, J.P., Manning, A., Thorpe, W.H., Carpenter, C.R., Grasse, P.P., Vaniersel, J.J.A., Leyhausen, P. & Marler, P. (Eds.); Behaviour 49: 227-267.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Hogda, K.A. & Gaillard, J-M. 2009: What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? - Ecography 32: 683-691.

Beier, P., Choate, D. & Barrett, R.H. 1995: Movement patterns of mountain lions during different behaviors. - Journal of Mammalogy 76: 1056-1070.

Beltran, J.F. & Delibes, M. 1994: Environmental determinants of circadian activity of free-ranging Iberian lynxes. - Journal of Mammalogy 75: 382-393.

Bernhart, F. 1990: Untersuchungen des Aktivitätsmusters des Luchses *Lynx lynx* in der Schweiz: Experimente und Felduntersuchungen. - M.Sc. thesis, University of Bern, Bern, Switzerland, 78 pp. (In German).

Bolker, B.M. 2008: Ecological models and data in R. - Princeton University Press, Princeton, New Jersey, USA, 408 pp.

Breitenmoser, U. & Breitenmoser-Würsten, C. 2008: Der Luchs. Ein Grossraubtier in der Kulturlandschaft. - Salm Verlag, Wohlen and Bern, Switzerland, 600 pp. (In German).

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G. & Harris, S. 1993: Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus Capreolus*): a comparative analysis of their ranging behavior, social organization and activity. - Journal of Zoology (London) 229: 623-640.

Clutton-Brock, T.H., Guinnes, F.E. & Albon, S.D. 1982: Red deer: behavior and ecology of two sexes. - The University of Chicago Press, Chicago, Illinois, USA, 400 pp.

Danilkin, A. 1996: Behavioural ecology of Siberian and European roe deer. - Chapman and Hall, London, UK, 300 pp.

Ersson, L. 2011: Estimating lynx kill rate on reindeer using GPS-locations and lynx movement pattern. - M.Sc. thesis, Swedish University of Agricultural Sciences, Grimsö, Sweden, 19 pp.

Esri 2009: ArcGIS 9.2. - Environmental Systems Research Institute, Inc., Redlands, California, USA.

Fahrmeir, L., Kneib, T. & Lang, S. 2007: Regression - Modelle, Methoden und Anwendungen. - Springer-Verlag, Berlin and Heidelberg, Germany, 502 pp. (In German).

Fejklová, P. 2002: The food composition of the Eurasian lynx (*Lynx lynx*) and the red fox (*Vulpes vulpes*) in the Bohemian Forest. - M.Sc. thesis, Charles University Prague, Prague, Czech Republic, 96 pp. (In Czech).

Ferguson, J.W.H., Galpin, J.S. & De Wet, M.J. 1988: Factors affecting the activity patterns of black-backed jackals *Canis mesomelas*. - Journal of Zoology (London) 214: 55-69.

Gervasi, V., Brunberg, S. & Swenson, J.E. 2006: An individual-based method to measure animal activity levels: a test on brown bears. - Wildlife Society Bulletin 34: 1314-1319.

Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T. & Doncaster, C.P. 2011: Jaguar and puma activity patterns in relation to their main prey. - Mammalian Biology 76: 320-324.

Heurich, M. 2011: Berücksichtigung von Tierschutzaspekten beim Fang und der Markierung von Wildtieren. - 12. Internationale Fachtagung zu Fragen von Verhaltenskunde, Tierhaltung und Tierschutz, Deutsche Veterinärmedizinische Gesellschaft, Gießen, Germany, pp. 142-158. (In German).

Heurich, M., Möst, L., Schauberger, G., Reulen, H., Sustr, P. & Hothorn, T. 2012: Survival and causes of death of European roe deer before and after Eurasian Lynx reintroduction in the Bavarian Forest National Park. - European Journal of Wildlife Research 58: 567-578.

Heurich, M. & Neufanger, M. 2005: Die Wälder des Nationalparks Bayerischer Wald. Ergebnisse der Waldinventur 2002/2003 im geschichtlichen und waldökologischen Kontext. - Wissenschaftliche Reihe, Grafenau, Germany, 176 pp. (In German).

Hornik, K. 2011: R: A Language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/ (Last accessed on 7 March 2012).

Jedrzejewski, W., Schmidt, K., Milkowski, L., Jedrzejewska, B. & Okarma, H. 1993: Foraging by lynx and its role in ungulate mortality: the local (Bialowieza Forest) and the palaearctic viewpoints. - Acta Theriologica 38: 385-403.

Jedrzejewski, W., Schmidt, K., Okarma, H. & Kowalczyk, R. 2002: Movement pattern and home range use by the Eurasian lynx in Bialowieza Primeval Forest (Poland). - Annales Zoologici Fennici 39: 29-41.

Karanth, K.U., Funston, P. & Sanderson, E. 2010: Many ways of skinning a cat: tools and techniques for studying wild felids. - In: Macdonald, D.W. & Loveridge, A.J. (Eds.); Biology and conservation of wild felids. - Oxford University Press Inc., New York, New York, USA, pp. 197-216.

Kolbe, J.A. & Squires, J.R. 2007: Circadian activity patterns

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of Canada lynx in Western Montana. - Journal of Wildlife Management 71: 1607-1611.

Kolowski, J.M. & Alonso, A. 2010: Density and activity patterns of ocelots (*Leopardus pardalis*) in northern Peru and the impact of oil exploration activities. - Biological Conservation 143: 917-925.

Krivobokova, T., Kneib, T. & Claeskens, G. 2010: Simultaneous confidence bands for penalized spline estimators. - Journal of the American Statistical Association 105: 852-863.

Löttker, P., Rummel, A., Traube, M., Stache, A., Šustr, P., Müller, J. & Heurich, M. 2009: New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: an attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*. - Wildlife Biology 15(4): 425-434.

Manfredi, C., Lucherini, M., Soler, L., Baglioni, J., Vidal, E.L. & Casanave, E.B. 2011: Activity and movement patterns of geoffroy's cat in the grasslands of Argentina. - Mammalian Biology 76: 313-319.

Mattisson, J., Andren, H., Persson, J. & Segerström, P. 2010: Effects of species behaviour on Global Positioning System collar fix rates. - Journal of Wildlife Management 74: 557-563.

Naguib, M. 2006: Methoden der Verhaltensbiologie. - Springer-Verlag, Berlin and Heidelberg, Germany, 235 pp. (In German).

Nielsen, E.T. 1983: Relation of behavioural activity rhythms to the changes of day and night. A revision of views. - Behaviour 89: 147-173.

Odden, M. & Wegge, P. 2005: Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. - Wildlife Biology 11(2): 145-152.

Okarma, H., Jedrzejewski, W., Schmidt, K., Kowalczyk, R. & Jedrzejewska, B. 1997: Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. - Acta Theriologica 42: 203-224.

Reinhardt, I. & Halle, S. 1999: Time of activity of a female free-ranging lynx (*Lynx lynx*) with young kittens in Slovenia. - Zeitschrift für Säugetierkunde 64: 65-75.

Saunders, J.K. 1963: Movement and activities of the lynx in Newfoundland. - Journal of Wildlife Management 27: 390-400.

Schmidt, K. 1999: Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in Bialowieza Primeval Forest, Poland. - Journal of Zoology (London) 249: 417-425.

Schmidt, K., Nakanishi, N., Izawa, M., Okamura, M., Watanabe, S., Tanaka, S. & Doi, T. 2009: The reproductive tactics and activity patterns of solitary carnivores: the Iriomote cat. - Journal of Ethology 27: 165-174.

Sunde, P., Stener, S.O. & Kvam, T. 1998: Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. - Wildlife Biology 4(3): 177-183.

Sunquist, M. & Sunquist, F. 2002: Wild cats of the world. - The University of Chicago Press, Chicago, Illinois, USA, 462 pp.

Theuerkauf, J., Jedrzejewski, W., Schmidt, K. & Gula, R. 2003: Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). - Journal of Wildlife Management 67: 706-716.

Wölfl, M., Bufka, L., Cerveny, J., Koubek, P., Heurich, M., Habel, H., Huber, T. & Poost, W. 2001: Distribution and status of lynx in the border region between Czech Republic, Germany and Austria. - Acta Theriologica 46: 181-194.

Wolf, M. & Ale, S. 2009: Signs at the top: habitat features influencing snow leopard *Uncia uncia* activity in Sagarmatha National Park. - Journal of Mammalogy 90: 604-611.

Wood, S.N. 2011: Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. - Journal of the Royal Statistical Society, Series B 73: 3-36.

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