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Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*

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Eurasian lynx *Lynx lynx* L. are recolonizing parts of their former range in Europe. Not only are lynx strictly protected as a species, but also their habitat and in particular their resting sites are protected. As the known characteristics of lynx resting sites are restricted to vegetation structure, it is difficult to take resting sites into account in planning processes. Here, we show the importance of rock formations for potential resting sites selection and analyzed the frequencies at which GPS-collared lynx returned to potential resting sites in the Bohemian Forest Ecosystem at the border between the Czech Republic and Germany. Lynx showed a strong selection for proximity of rocks for resting site selection, and the distance of potential resting sites to rocks was an important predictor for determining whether lynx return to the resting site or not. Furthermore, the frequency of returns to the resting site was positively influenced by the distance to roads and geomorphology. Our findings highlight the importance of rock formations as resting sites for lynx, which can help with the implementation of concrete protection measures.

Keywords: sleeping sites, felids, human disturbance, return to resting sites

Lynx *Lynx lynx* (L.) are strictly protected by national and international legislation, but they are still rare and patchily distributed in most of central and western Europe (Linnell et al. 2008, Kaczensky et al. 2013). Humans pose the greatest threat to populations of this felid in multiple ways (Heurich et al. 2018). First, lynx are frequently illegally killed by some members of stakeholder groups, especially hunters, whose attitudes oppose those of conservationists (Červený et al. 2002, Lüchtrath and Schraml 2015). Second, lynx are threatened by infrastructure development and the subsequent increase in collisions with vehicles. Consequently, some lynx populations in Europe are under high pressure, stagnate or decline despite ongoing conservation efforts (Kaczensky et al. 2013).

Protected areas in central Europe are usually too small for viable predator populations (Chapron et al. 2014). However, lynx can coexist with humans also outside protected areas by adapting their spatio-temporal behavior to avoid human activity (Chapron et al. 2014, Filla et al. 2017, Gehr et al. 2017). For lynx to survive in a human-dominated landscape, the availability of high-quality diurnal resting sites is likely an important prerequisite; suitable resting sites are located where the risk of human encounters is low and therefore where little energy has to be spent in order to avoid humans while resting (Watts et al. 1991, Sunde and Kvam 1998). Accordingly, the European Commission Habitats Directive (1992) prohibits not only the deliberate capture and killing of lynx (Annex II), but also the 'deterioration or destruction of breeding sites or resting places' (Annex IV). Therefore, detailed knowledge about lynx resting sites is necessary for improving conservation measures and law enforcement.

Lynx prefer resting sites with dense vegetation and low visibility, in rugged terrain and far from human infrastructure (Podgórski et al. 2008, Belotti et al. 2012, Bouyer et al. 2015). However, this information alone is insufficient for the protection of resting sites and their consideration in planning processes given the large territories occupied by lynx, with many sites fulfilling these conditions (Schadt et al.

2002, Herfindal et al. 2005). Recent findings indicate that lynx select rock formations during daylight (i.e. the time when lynx rest; Filla et al. 2017). This preference for rock formations has two important implications for conservation. On the one hand, rock formations are distinct features in the landscape and are thus easier to identify and to potentially protect than sites of dense vegetation and rugged terrain. Studies of other felids, e.g. snow leopard *Panthera uncia* (Jackson and Ahlborn 1984) and puma *Puma concolor* (Pia et al. 2013), have indicated that rock formations are important for resting site selection, and provide outlooks to scan the surrounding area. On the other hand, rock formations are also popular for recreational activities, such as climbing and geocaching (Pieber et al. 2012), which could lead to new conflicts among stakeholders. In our study, we investigated the importance of rock formations as resting sites for lynx. We hypothesized that rock formations represent a considerable proportion of the diurnal resting sites used by lynx, that lynx select rock formations as resting sites, and that the distance of resting sites to the next rock formation affects both the probability that the lynx will return to a previously visited potential resting site, and the frequency of returns.

Methods

Study area

The study was conducted in the Bohemian Forest Ecosystem, which comprises the Bavarian Forest National Park (242 km²; Germany) and Šumava National Park (680 km²; Czech Republic), and is one of the largest strictly protected areas in central Europe. The altitude of the study area ranges from about 300 m to 1400 m a.s.l. The vegetation consists mostly of mountainous forests dominated by Norway spruce *Picea abies* (L.) and European beech *Fagus sylvatica* ((L.); Cailleret et al. 2014 for details). The geological bedrock consists mostly of gneiss and granite (Fig. 1 for a rock formation typical of the study area).

Lynx and location data

Eight lynx were captured within the study area, equipped with GPS collars, and released (for details see Belotti et al. 2015 and Filla et al. 2017). The locations were recorded between 2009 and 2014 within the study area using GPS telemetry. The temporal resolution of the recordings differed among individuals owing to the use of different technical GPS systems and within individuals owing to occasional lack of a satellite signal.

Since lynx show a crepuscular and nocturnal activity pattern, we used only the 12:00 UTC location (within a 30-min time window). The position of the noon location corresponds most of the time (>85%) to resting locations (Podolski et al. 2013, Heurich et al. 2014; to account for this uncertainty, we will use the term potential resting sites onward). To exclude effects of potential kills, we ran the analyses twice – once with all daytime resting sites and once only with resting sites that were used at least five days apart (Okarma et al 1997, Jobin et al. 2000, Belotti et al. 2015).


Figure 1. A typical rock formation of the Bohemian forest with a resting lynx (Photo credit: Rainer Simonis).

We created a grid of 100 × 100 m cells for the entire study area, counted the number of resting sites within each cell, and subtracted 1 to obtain the frequency of returns to the sites. We tested for sensitivity to grid cell size by running the entire analysis on two additional grid widths (50 and 200 m) and concluded that the results were robust (Supplementary material Appendix 1).

Environmental covariates

We used distance to rock formations, distance to roads, distance to buildings, terrain ruggedness and terrain morphology as covariates in the analyses. Locations of rock formations were recorded and provided by the survey administrations of the Czech Republic (ČÚZK – Český úřad zeměměřický a katastrální for Šumava National Park) and Bavaria, Germany (Agency for Digitization, High-Speed Internet and Surveying for Bavarian National Park). A rock formation was defined either as a solitary rock outcrop of at least 15 m height, or several rocks (with heights >3 m) within a 300 m² area (see also Fig. 1 for an example). We downloaded data on roads and buildings from OpenStreetMap at <http://download.geofabrik.de/> and considered all road types available therein. We then calculated the Euclidean distance from the centroid of each grid cell to the closest rock formation, road or building. Terrain ruggedness and terrain morphology were calculated from an ASTER digital elevation model. For terrain morphology, we grouped the initial 10 categories into three groups: flat (flat, pit and valley), slope (foot-slope, hollow, slope, spur), top (shoulder, ridge and peak). Prior to statistical analyses we assessed the correlation between environmental covariates. Since none of the correlation coefficients were above 0.7 in absolute terms, we retained all environmental covariates for the statistical analyses. All geographic data were analyzed using GRASS 7.4 (Neteler et al. 2012).

Statistical analyses

To explore how rock formations were used as potential resting sites, we calculated the proportion of observed day resting sites that were located within a 50-m buffer around rock formations and the same number of randomly located points within a convex hull of all potential resting sites. We used a 50-m buffer to account for GPS measurement error (Stache et al. 2012) and to consider that lynx might rest in the close proximity of rock formations. Next we tested if rock formations are preferred over random sites using a resource selection function. We generated 10 times as many random points from within the same convex hull as we had observed potential resting sites (n = 25 796). We then extracted for each point (random and observed) whether or not the point was within 50 m of a rock formation and fitted a logistic regression.

We proceeded by modeling the frequency of lynx returning to resting sites. We compared four different model specifications to model lynx revisits to resting sites, namely a Poisson model and a negative-binomial regression model, and a Poisson hurdle model and a negative-binomial hurdle model. Hurdle models can be regarded as a mixture of two processes: first, the probability of a return to a resting site is modeled using a Bernoulli distribution (hurdle part), and second, once a return to a resting site in a grid cell is encountered, the frequency of returns to that site is modeled with a Poisson or negative-binomial distribution (count part). We used an information-theoretic approach for model selection of the response family (Poisson and negative binomial) and the model complexity (ordinary model and hurdle model). We applied Akaike's information criterion (AIC; Akaike 1974) to select the best model, which is characterized by the lowest AIC value. We used the software R ver. 3.4 for all statistical analyses (<www.r-project.org>) and in particular the packages pscl (Zeileis et al. 2008) for fitting hurdle models and rhr (Signer and Balkenhol 2015) for preparing movement data.

Results

Selection and filtering of lynx telemetry data revealed 2569 potential resting sites. Of these, 12.3% were located within a 50-m buffer around rock formations (ranging from 3.6% to 19.9% for individual lynx). Only 1.7% of the random points were located within the same distance around rock formations. On average, 10.3% (ranging from 2% to 21%) of rock formations within a lynx home range were used at least once as a resting site. We found a strong selection for rock formations for potential resting sites if compared to random points within the availability domain ($\beta_{\text{Intercept}} = -2.42$, SE = 0.02, $p < 0.001$); $\beta_{\text{rock}} = 2.38$, SE = 0.08, $p < 0.001$).

When we modeled the probability of a lynx returning to a site and the frequency of a lynx returning to a site, the negative binomial hurdle model outperformed all other models (Table 1). The model selection and coefficients were similar for all three cell sizes (50 × 50 m, 100 × 100 m and 200 × 200 m) of the grid that we used to calculate the frequency of returning to the site (Supplementary material Appendix 1). Likewise, the time interval chosen to separate different returns to the sites did not affect the model selection and the biological meaning of coefficients (Supplementary material Appendix 1).

In the model that best predicted the probability of lynx returning to a resting site (negative binomial hurdle model; Table 1), we found effects for only three covariates: a positive effect of the distance to roads for the count process of the model (frequency of returning to the site), effects of the distance to rock formations (negative) and distance to roads (positive) for the hurdle process of the model (probability of returning to the site; Table 2, Fig. 2), and a negative effect of selecting flat terrain compared to hill tops. (for the hurdle and the count model).

Table 1. Comparison of different model classes using AIC. For each model, we used all covariates (distance to roads, distance to buildings, distance to rock formations, geomorphology and terrain ruggedness), also for the count and hurdle processes of the hurdle models.

Model	AIC	ΔAIC
Negative binomial (hurdle)	2794	0
Negative binomial	2804	10
Poisson (hurdle)	3018	224
Poisson	3484	690

Discussion

Our analyses indicated that rock formations are important for characterizing potential lynx resting sites and that they positively affect the probability of a lynx returning to potential resting sites. Moreover, we found that the probability of a lynx returning to a site and the frequency of the returns increases with the distance to roads, and that lynx prefer hilltops over flat areas for potential resting sites. These findings improve our understanding of lynx resting behavior and can contribute to the improvement of conservation measures of this protected species.

Although other studies have identified rocky sites as important for lynx, e.g. for den site selection (Boutros et al. 2007), increased hunting success (Krofel et al. 2007) and scent marking (Vogt et al. 2014), our study is to the best of our knowledge the first to empirically stress the significance of rock formations as resting habitats for lynx. In general,

Table 2. Coefficients of the count process and hurdle process of the negative binomial hurdle model. Coefficients of the hurdle process indicate the effect of covariates on the probability of a lynx returning to a resting site. The coefficients of the count process indicate how covariates affect the frequency of returning to a resting site, if a lynx returns to the site (i.e. conditioning on the hurdle model). Coefficients at a 0.05 significance level are in bold.

Predictor	Estimate	SE	p-value
Count process			
Intercept	−11.57	73.82	0.885
Distance rocks [m]	−0.000074	0.00016	0.659
Terrain = slope	−0.09	0.29	0.742
Terrain = flat	−1.39	0.55	**0.011**
Distance roads [m]	0.0012	0.000059	**0.038**
Distance buildings [m]	0.00052	0.00028	0.0641
Terrain ruggedness	0.03	0.03	0.173
log(theta)	−11.91	82.75	0.886
Hurdle process			
Intercept	−1.31	0.22	**<0.001**
Distance rocks [m]	−0.00015	0.000058	**0.008**
Terrain = slope	−0.16	0.16	0.321
Terrain = flat	−0.63	0.25	**0.011**
Distance roads [m]	0.0011	0.00032	**<0.001**
Distance buildings [m]	−0.00012	0.00012	0.301
Terrain ruggedness	0.03	0.02	0.078

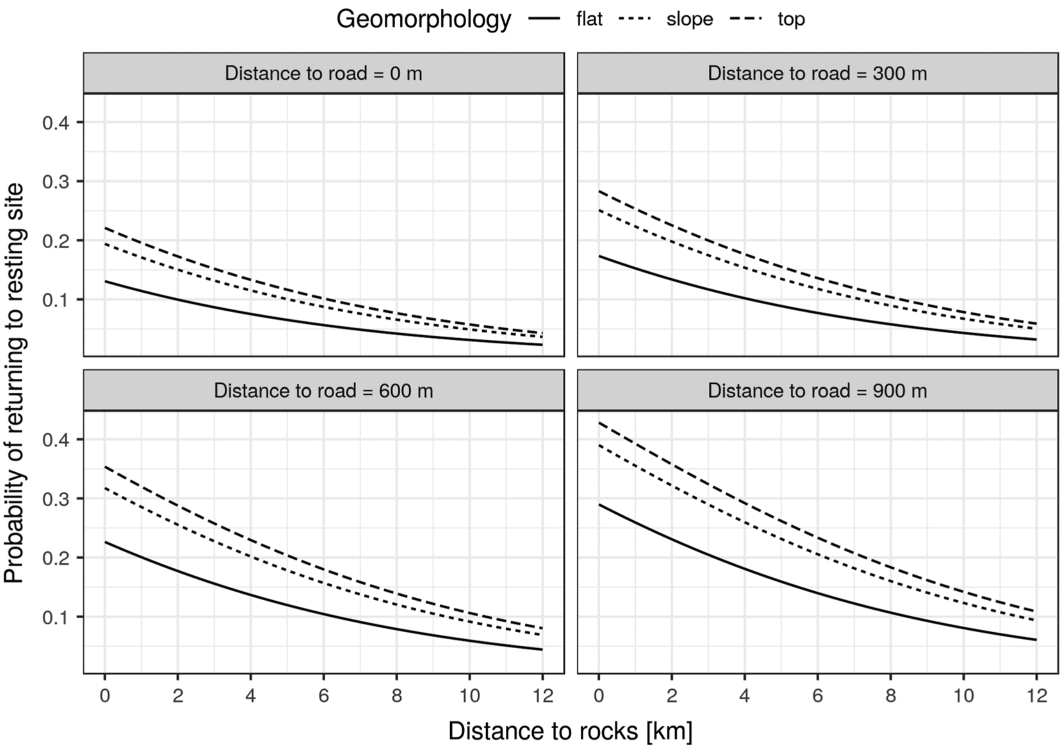

Figure 2. Effects of distance to rocks, geomorphology (line type) and four distances to roads (panels) on the probability of a lynx returning to a resting site. The range of observed distances to roads ranged from 0 to 880 m.

rock formations offer suitable resting conditions by providing cover, shelter from heat or cold, inaccessibility to people, a good overview of the surrounding landscape, and means for territorial marking (Allen et al. 2017).

According to our models, the probability of a lynx returning to a resting site and the frequency of such returns were also influenced by the distance to roads and the geomorphology. Roads facilitate human access and increase human activity, especially during daytime, when lynx are particularly vulnerable (i.e. while resting or sleeping; Basille et al. 2013, Heurich et al. 2014). Since human persecution and, to a lesser extent, collisions with vehicles pose the greatest threats to many European lynx populations, including the population in the Bohemian Forest Ecosystem, human disturbance and perceived mortality risk are likely to increase in areas close to roads (Wölfl et al. 2001, Schmidt-Posthaus et al. 2002, Basille et al. 2013, Kramer-Schadt et al. 2004). Hence, it can be expected that the suitability and quality of resting sites are higher in areas far from roads. This might explain why the probability of lynx returning to a resting site and the frequency of the returns increases with the distance to roads. In general, this finding is in line with the results of Sunde et al. (1998), who found that lynx avoid areas close to roads (<200 m) when resting. Human leisure activities, such as hiking and mushroom collecting, are likely to influence the frequency of lynx returning to resting sites during the day, but studies are lacking (but see Belotti et al. 2018). In terms of the geomorphology, the probability of returning to a potential resting site was higher when the potential resting site was located on hill tops than in flat terrain.

Overall, our findings complement current knowledge on the selection of resting sites by lynx. We demonstrated that lynx show a strong preference for potential resting sites in close proximity to rock formations (within a 50 m radius). Moreover, the probability that a lynx will return to a potential resting site increases with proximity to rocks. The frequency of returns to a potential resting site, however, depend on the distance to roads and terrain characteristics. This implies that particularly rock formations in remote areas are important habitat features that may increase the suitability of a given area for resting lynx. Our results suggest that when new infrastructure is planned or existing infrastructure is evaluated (e.g. roads, hiking trails, geocaching, climbing routes, wind power plants), rock formations should be avoided whenever possible, in order to adhere to Annex IV of the EC Habitats Directive, namely avoiding the deterioration and/or destruction of breeding sites or resting sites. Whether our results hold for other areas or lynx populations remains to be tested. Overall, our results provide further evidence of the importance to protect rock formations for biodiversity conservation. Beside their importance as potential resting sites for lynx and other felids (Jackson and Ahlborn 1984, Pia et al. 2013), rock formation also provide nesting sites for birds, and habitat for plants and fungi (Brambilla et al. 2004, Müller et al. 2004).

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Supplementary material (available online as Appendix wlb-00489 at <www.wildlifebiology.org/appendix/wlb-00489>). Appendix 1.