Felid bedrooms with a panoramic view: selection of resting sites by Eurasian lynx (*Lynx lynx*) in a karstic landscape

Lan Hočevar¹, Teresa Oliveira¹, Miha Krofel¹

¹*Department of Forestry, Biotechnical Faculty, University of Ljubljana, Večna pot 83, SI-1000 Ljubljana, Slovenia*

*Corresponding Author: Lan Hočevar; Lan.Hocevar@bf.uni-lj.si; lanushocevar@gmail.com

Abstract

Eurasian lynx (*Lynx lynx*) is a crepuscular-nocturnal carnivore and mostly spends daytime resting. Although resting sites represent an important part of the lynx habitat and can be negatively affected by human activities, it is still poorly known how lynx select these sites, especially in regions with rugged topography characteristic for much of the species' range. We analysed micro-scale habitat selection of lynx resting sites at the home-range level in a karstic landscape of the Dinaric Mountains, Slovenia, using a use-availability study design. We also searched for differences in the selection of resting sites in respect to the presence of ungulate kills, which often limit the available resting sites during the prey-consumption period. Using generalized linear mixed models (GLMM) we tested which environmental features and human infrastructure are important for lynx when choosing resting sites. Lynx selected mountain ridges and hilltops, as well as locations with steeper slopes and lower local visibility. Such locations likely provide concealment from potential danger or prey and, at the same time, offer good overview of the surroundings. There was also a tendency to avoid forest cabins and to select rocky terrain and southern exposures, but support in the data for this was lower. When lynx were not limited by the presence of fresh kill, the selection tended to be stronger, but the differences were not significant, except for visibility, which was lower at resting sites near prey remains. Results likely reflect high availability of suitable resting sites in a rugged terrain of karstic landscape.

Keywords: daybed, micro-scale habitat selection, kill site, infrastructure, large carnivores, habitat use

Significance Statement

Animals are often most vulnerable during sleep, thus the resting site should ideally provide them with cover to reduce exposure and at the same time give them good overview of the surroundings to detect any approaching danger. We used snow tracking and GPS telemetry, for the first time in combination with data from activity sensors, to reliably determine resting sites of Eurasian lynx in a rugged karstic landscape. We showed how lynx

face the trade-off of the need to be concealed, yet at the same time attain good view, by selecting structured microhabitats on top of the ridges and on steep slopes. Our results also suggest that in the regions with rugged terrain the influence of human infrastructure might be lower compared to the study areas of previous research.

1. Introduction

Resting and sleeping are essential for any animal, but being asleep is often the most vulnerable state (Kusler et al. 2017). Consequentially, the selection of a safe resting site is crucial for individual survival. This is increasingly more important nowadays, when humans became globally-important super predator for many animals, including apex predators (Darimont et al. 2015). As a result, many species adapted to the nocturnal life to avoid encounters with people and use daytime to rest, often in remote or hidden locations (Ordiz et al. 2012; Gaynor et al. 2018).

Large carnivores need extensive home ranges with good habitat connectivity, which is essential also for dispersal that allows exchange of genetic material among populations (Nowell and Jackson 1996; Crooks et al. 2011). Therefore, a considerable amount of research focuses on movement or habitat selection at a large scale to understand, among other things, the influence of habitat fragmentation and related problems (e.g. Kramer-Schadt et al. 2004; Blanco et al. 2005; Roever et al. 2010; Dellinger et al. 2013; Squires et al. 2013; Gehr et al. 2017). However, also micro-scale selection represents an important part in carnivore ecology, especially when linked with behaviours that are essential for individual survival and persistence of viable populations (Podgórski et al. 2008). This includes feeding sites, mating areas, dens, scent-marking sites, as well as resting sites (also known as daybeds). Human-dominated landscapes can be particularly challenging for large carnivores to persist in the face of human disturbance and several anthropogenic mortality factors (Sazatornil et al. 2016). In Europe and other areas with high human footprint, carnivore home-ranges are generally fragmented and under certain level of human disturbance, thus availability of suitable microhabitats plays a crucial role for conservation of many species and can influence the habitat suitability at larger scales (Wilson and Nielsen 2007; Belotti et al. 2013, 2018). Therefore, identifying species' micro-scale habitat requirements can be instrumental to ensure proper land-use management in these critical habitats (Kolowski and Woolf 2002).

Felids are characterised by elusive behaviour and often select inaccessible and secluded sites to remain hidden during their resting period. In addition, they often choose resting sites at higher elevation, which gives them good overview of the surrounding area, as well as south-facing slopes that provide better climatic conditions. For example, snow leopards (*Panthera uncia*) in Himalayas select resting sites on top of mountain ridges and hilltops

with a good view and, at the same time, locations where they are not visually exposed (Jackson 1996). Iberian lynx (*Lynx pardinus*) in Spain choose well-hidden patches of shrubs and bushes for resting (Fernández et al. 2003). European wildcats (*Felis silvestris*) in the Harz Mountains, Germany, select resting sites with southern exposure in areas with abundant deadwood and lower canopy cover, while avoiding open areas (Jerosch et al. 2010). Similarly, mountain lions (*Puma concolor*) preferentially rested on sunny slopes and on inaccessible locations, which helped them in preserving the energy and offered a quick escape route from wolves or humans (Kusler et al. 2017).

Selection of secluded resting sites could be especially important for species living in human-dominated landscapes, such as Eurasian lynx (*Lynx lynx*; hereafter, lynx) in Europe. Human-caused mortality nowadays poses the greatest threat to many European lynx populations with illegal killings, vehicle collisions and infrastructure development leading to habitat loss and fragmentation often reported as the main reasons of lynx decline (Breitenmoser and Breitenmoser-Würsten 2008; Heurich et al. 2018). Although circadian activity can vary with several factors (such as age, sex, reproductive status, temperature, moonlight and prey behaviour), the peaks of activity for lynx are typically in the evening and morning twilight (Heurich et al. 2014), which is also the period when they most often hunt and feed (Krofel et al. 2019). As in most other cat species, lynx spend the majority of the day resting and sleeping (Schmidt 1999). For this period, they need to find a secure place to avoid detection and disturbance by humans or competitors (Podgórski et al. 2008; Belotti et al. 2018; Signer et al. 2019).

Many studies on lynx' habitat requirements did not differentiate habitat use among different behavioural states (but see e.g. Podgórski et al. 2008; Bouyer et al. 2015; Signer et al. 2019), which can have important consequences for conservation and management (Roever et al. 2014). Additionally, the scale of the selection was usually broad and did not consider local characteristics measured in-situ, such as local visibility and microhabitat structure. Obtaining these measures is time consuming, since it requires a visit to each location, thus many previous studies relied only on variables already available, such as land cover and topographic features. Only a small number of studies have focused on lynx micro-scale habitat selection of resting sites, and they are limited to three study areas. In Norway, lynx were noted to avoid areas modified by humans (Bouyer et al. 2015). In the lowland forest in Białowieża, Poland, lynx were selecting resting sites with lower visibility (Podgórski et al. 2008), similar to Bohemian Forest along the German-Czech border, where lynx preferentially used dense vegetation locations and inaccessible terrain to avoid human recreational activities (Filla et al. 2017; Belotti et al. 2018). There, lynx were also observed to select resting sites near or on rock formations, which are relatively rare

in the region (Signer et al. 2019). Currently, we are still lacking studies on the selection of resting sites from regions with rugged terrain and predominantly rocky landscapes, which are characteristic for much of the lynx range in the Alps, Carpathians, Dinaric Mountains and the Balkans. These regions are of particular conservation concern, as they include some of the most endangered lynx populations in Europe (Kaczensky et al. 2012).

In this study, we analysed for the first time how lynx select resting sites in a karstic landscape of Northern Dinaric Mountains, where widespread rugged and heterogeneous relief with numerous rocky areas suggested high availability of suitable habitats for daybeds. First, we compared how lynx resting sites differ at a micro-scale from random locations within the lynx home ranges according to several environmental covariates (e.g. vegetation, topography and visibility) and distance to human infrastructure (e.g. forest cabins and road network) and tested a set of hypotheses on how these factors could influence the resting site selection (Table 2). Next, we tested if lynx select different resting sites on days when they are feeding on a kill compared to days when they are not feeding. Eurasian lynx are characterised by relatively long feeding times when they kill the main prey (i.e. ungulates). For example, in Slovenia the average feeding time is 3.2 days and during this period lynx mostly stay in the close vicinity of the kill site (median distance to the kill site is 67 m) (Krofel et al. 2013). Such attachment to the kill site location limits lynx' choice of potential resting sites and, therefore, we hypothesized that selection of the preferred attributes will be weaker during the feeding period compared to days when lynx are not having a kill and can choose their resting sites at a larger scale.

Previous studies assumed that lynx always rest around midday and only used time of the day to identify resting sites. However, activity data indicate that lynx can be active also in midday (on average in about 15%; Heurich et al. 2014), which could introduce errors since some of the sampled locations might not have been located at the actual resting sites (type I error). To overcome this issue and reduce the bias, we used activity sensors in the GPS collars that register animal movement to filter the data and only sampled midday locations, when lynx was not moving and thus provide more reliable results.

This study provides the first insight into lynx' microhabitat use of resting sites in a karstic landscape, which contributes to our knowledge of lynx behavioural ecology across the species' distribution range and gives us better understanding of possible effects of human development on lynx habitat use. This could be used in future spatial planning of infrastructure in forest habitats to help minimize negative impact on lynx and protect habitats most important for this species.

2. Material and methods

2.1. Study area

The study was conducted in the north-western part of the Dinaric mountain range in Slovenia (45°30–45°47' N, 14°19–14°51' E; Fig. S1). The study area is located in the High Karst region with predominant limestone and dolomite geology, which results in a rugged karstic relief and abundant karstic structures, such as cliffs, dolines, caves, rock shelters, dolines, steep canyons and uvalas, as well as rocky hilltops and ridges (Fig. S2). The altitude ranges from 165 m to 1796 m. The climate is a mix of influences from the Alps, the Mediterranean Sea, and the Pannonia Basin with average annual temperature of 7 °C, ranging from an average monthly maximum of 18 °C to an average monthly minimum of –2 °C, and average annual precipitation of 1700 mm. During the winter, the snow depth can reach 2 m and the snow can last for a couple of months in higher areas.

The region is covered with mixed temperate forests intermixed with agricultural fields and small settlements. Most of the forests belong to the fir-beech association (*Omphalodo – Fagetum dinaricum*) with silver fir (*Abies alba*), common beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and sycamore maple (*Acer pseudoplatanus*) being the predominant tree species (Kordiš 1993; Fig. S2). Average human population density is 28 people/km² with most settlements concentrated in the larger valleys. There are several scattered forest cabins and hunting hides throughout the forest, but they are not regularly used by people, and some of them are completely abandoned. Main roads are mostly located in valleys and lowlands, but there is a dense network of forest road infrastructure spread throughout the study area with an average density of approximately 2 km of gravel forest roads and 10 km of dirt skidding trails per km² of forest (Krofel et al. 2017).

Eurasian lynx in Slovenia are part of the Dinaric lynx population, one of the most threatened populations in Europe (Krofel and Jerina 2016). Dinaric lynx mainly hunt wild ungulates, which together represent 88 % of the biomass consumed by the lynx. Roe deer (*Capreolus capreolus*) are the main prey species (79 % of consumed biomass), and edible dormouse (*Glis glis*) and red deer (*Cervus elaphus*) are the most important alternative prey, each representing approximately 7 % of consumed biomass, while other species are less important (Krofel et al. 2011, 2014). The average lynx home-range size (females and males) in the region is 215 km² (Krofel 2012). Besides Eurasian lynx, brown bear (*Ursus arctos*) and grey wolf (*Canis lupus*) are present in the area, as well as several species of smaller carnivores.

2.2. Identifying the resting sites

We located lynx resting sites of eight lynx (four females and four males) using GPS telemetry fixes ($n_{\text{lynx}}=6$) in combination with activity data and with the use of snow tracking ($n_{\text{lynx}}=2$; Fig. S3, S4). Telemetry data came from three females and three males, tracked between 2007 and 2019. All lynx were captured using standard protocols (for details, see Krofel et al. 2013) and were equipped with GPS collars with remote GSM download technology and a programmable drop-off system (three collars from TVP Positioning AB, Sweden and three collars from Vectronic Aerospace GmbH, Germany). Five animals with collars were resident individuals, while one individual (male) was translocated from Romania. This male was later released in Slovenia, and we only used his resting locations after he established his permanent territory in the study area. The collars were scheduled to attempt between 3 and 8 fixes per day.

We defined resting sites from telemetry data based on two criteria. The first was the time of the day and we used fixes obtained during the middle of the daylight, when lynx usually rests, that is, from 3 h before to 3 h after noon. The second criterion was the movement activity data obtained by a sensor in the collar that measures acceleration in crosswise and longitudinal direction. Previous studies established that values 0-11% of the maximum activity correspond to resting behaviour (Heurich et al. 2014) and we applied this threshold also in our study. Because we did not have activity data available for one of the male lynx, we only used the first criterion to identify resting sites for this individual.

In addition to GPS telemetry, we used snow-tracking of one male and one female (identified by genetic analyses) to locate additional resting sites with an average snow-tracking transect of 5 km. When we found fresh tracks in the snow, we followed them (front-tracking) until we found signs of resting in the snow (i.e. bed site with lynx hair). After finding a resting site, we continued tracking for at least 500 meters to establish whether there might have been a kill site in the vicinity. We only included resting sites for which we were sure that lynx used for actual resting, and not just for a short break, which were distinguished by the stamped thawed and afterwards frozen snow (Fig. S4). It was not possible to record data blind because our study involved focal animals in the field.

2.3. Predictor covariates

Overall, we considered 12 covariates potentially influencing lynx resting site selection (see Table 1 for descriptions and ranges of each covariate). We categorized covariates into four groups: vegetation, topography, human infrastructure, and visibility. Vegetation covariate included ‘forest’, ‘bush’ and ‘open’ as categories. Topographic covariates included ‘rocky terrain’, ‘southern exposition’, ‘slope’, ‘altitude’, and ‘ridge’. The later

included locations on top of the ridges or hilltops. We considered as human infrastructure covariates ‘road presence’, ‘minimum distance to road’ and ‘cabin presence’. The latter included cabins and hunting hides. ‘Exposition’ and ‘altitude’ were derived from a digital elevation model (5x5m), and minimum distance to roads was calculated from a vector shapefile of forest roads (publicly available from the Surveying and Mapping Authority of the Republic of Slovenia), using Euclidean distances tool with ArcGis Desktop 10.1 (ESRI, Redlands, CA, USA). We measured the average local visibility of each site by placing a backpack (green and orange colour, approximately 0.5 x 0.3 m) on the place of the resting site, and walking in each cardinal direction, counting the steps (0.75 m in length) until we could no longer see the backpack. We then averaged values for all four cardinal directions (N, W, S, E) to obtain an average visibility. The remaining covariates were sampled in the field, as described in the Table 1.

To test the effect of presence of kill sites, we divided resting sites into two groups: during the feeding period (i.e. ‘with prey’) and searching period (i.e. ‘without a prey’). We used GPS cluster analysis to identify kill sites and defined feeding period as the time between the estimated time of killing of large prey and until the lynx left the carcass without returning (Krofel et al. 2013).

We always conducted the sampling of a resting site in the same season when the lynx use it in order to ensure same vegetative conditions. We excluded from analyses locations in which we observed that logging, windstorm or ice storm occurred between the lynx visit and our sampling, as these events often considerably changed the vegetative cover.

2.4. Data analyses

We investigated resting site selection at the home range level, following Johnson (1980). We followed a use-availability study design (Manly et al. 2002), where resting sites were the “use” sample. As “availability” sample, we created a set of random points equal to the number of lynx resting sites, within the lynx home ranges (95% Minimum Convex Polygon of the locations from each of the collared or snow-tracked lynx; to estimate home ranges of the snow-tracked lynx we used combination of snow-tracking and camera-trapping data). We sampled the random points in the same way as the actual resting sites. This includes the same proportion in respect to the vegetative seasons to ensure comparability according to the seasonal changes in the vegetation structure. We used ArcGIS Desktop 10.1 to estimate home ranges and to generate random points.

We developed generalized linear mixed-effect models (GLMMs) with a binary response variable representing “use” and “available” points (1 and 0, respectively), and fitted the model with a logit link function. We included

lynx ID as random effect to account for inter-individual variation and uneven sample size (Gillies et al. 2006). We followed an Information Criteria Approach (Burnham and Anderson 2002) and specified *a priori* set of 10 models based on our knowledge of the species' biology and the study area (Table 2). We started by building a model with all covariates included (M1), and then selected specific groups of variables and combined them to test a set of hypotheses which we believed could influence the selection of resting sites by lynx (Table 2). We also included a null model (i.e., a model with no covariates included) to test the strength of our hypotheses and importance of the covariates chosen. We ranked the models according to the Akaike's Information Criteria (AIC) and considered models with ΔAIC values <2 from the lowest AIC value as the best models (Burnham and Anderson 2002). The coefficients of each variable included in these models were assessed following a model averaging approach (Burnham and Anderson 2002). Prior to modelling, we checked for correlation between each pair of covariates using the variance inflation factor (VIF) (Fox and Monette 1992; Zuur et al. 2010). We used a cut-off value of 3 and excluded sequentially the variable with higher VIF, repeating the analyses afterwards. If VIF values were similar, we excluded the covariate we considered to be less meaningful for the lynx according to our knowledge of its biology (Zuur et al. 2010). All continuous covariates were standardized to z-scores before modelling, and we excluded models that failed to converge.

We used k-fold cross validation to assess model fit. We followed the approach developed by Boyce et al. (2002), and used 80% of the data for modelling procedures, which were then used to predict the probability of use for the remaining 20%. This procedure was repeated five times until all data was used. Then, we used Spearman rank correlations to evaluate the relationships between the frequency of cross-validated used locations and 10 probability bins of similar size, representing the range of predicted values. A model with good predictive performance should show a strong correlation ($\rho > 0.80$; Boyce et al. 2002).

For testing differences between the lynx resting sites with and without prey, we used a subset of the main dataset, which includes only data from the resting sites used by lynx, and we used a response variable representing resting sites with prey and without prey (1 and 0, respectively). We followed the same statistical approach as used for the selection of resting sites in respect to availability and applied the same set of models (Table 2). However, in order to obtain a more balanced dataset, we did not include 'cabins' and level 'open' of the vegetation covariate in these models (Table 3), because we observed only one case of cabin presence among the lynx resting sites with a kill nearby and only one resting site in the open. Therefore, the vegetation covariate has only two levels in this analysis ('forest' and 'bush').

In order to check for potential bias in our results due to the inclusion data obtained through snow-tracked, we conducted the analyses twice, with and without the two animals sampled with snow-tracking. As the results did not change significantly, we choose to include the analyses obtained with all samples. Nevertheless, we also present the results without the two snow-tracked lynx in the supplementary material (Online Resource Material 3).

All statistical analyses were conducted using software R version 1.2.5033 (R Core Team 2018). All GLMMs and respective k-fold cross-validation were developed using lme4 v1.1-21 R-package (Bates et al. 2015). We used MuMIn v1.43.10 (Barton 2018) to perform model averaging. Results are presented as mean $\pm$ standard error, except when stated otherwise.

3. Results

Overall, we sampled 302 locations in the field, including 151 lynx resting sites and 151 random points within the lynx home ranges. Among the resting sites, 58 were used during the feeding period (i.e. with prey) and 93 were used without prey. We sampled 18% of resting sites and 19 % of random points during the non-vegetative season (November-March) and 82% and 81%, respectively, during the vegetative season (April-October). A total of 142 lynx resting sites were identified through telemetry data and 9 through snow tracking.

The model that best explained lynx resting site selection compared to availability included covariates related to topography and visibility (M10; Table 2). The next two best models, M1 and M2, had Δ AIC values <2 (Table 2), and included vegetation and human infrastructure covariates as well. The cross-validation procedure revealed moderate model fit for M1, M2 and M10 ($\rho = 0.69\text{--}0.71$; Table 3). The averaged coefficients of this set of models suggested that lynx selected locations with lower local visibility, steeper slopes, and sites located on top of ridges or hilltops (Fig. 1). Lynx also tended to select rocky terrain and southern exposures and to avoid cabins, but the selection/avoidance had lower support for these covariates, as it was significant only in some of the models, but not in the averaged model (Online Resource 2, Fig. S5). Presence and distance to forest roads, altitude and vegetation type did not influence resting site selection (Fig. 1).

The model that best explained resting site selection when considering the presence or absence of a kill included all covariates (M1), although all models had similar AIC values (Table 3), and model fit was low to moderate ($\rho_{\min} = 0.23$, $\rho_{\max} = 0.60$; Table 3). During the feeding period, lynx selected resting sites with lower visibility and avoided bushes (Fig. 2). We did not detect any significant selection in respect to the topographic or human infrastructure covariates. However, according to the proportions of locations on ridges and in rocky terrain and

the mean values of altitude and slope, we observed a trend towards stronger selection of these topographic features in resting sites without prey than in resting sites with prey (Table 1). When snow-tracking data was excluded, selection for lower altitude during the feeding period became marginally significant (Online Resource 2, Fig. S8).

4. Discussion

We observed that lynx were not using resting sites randomly, but selected locations in respect to their local visibility, topographical covariates, and, to a lesser extent, possibly also according to the human objects in the forest. On the other hand, vegetation types and forest roads did not seem to affect their decision where to rest during the day.

Local visibility (i.e. the distance from which lynx could be seen) was the covariate with the strongest effect. Local visibility can be influenced by several factors in the environment, such as vegetation density, terrain ruggedness and presence of various objects in the forest that can conceal an animal (e.g. fallen trees, tree stumps, and rock boulders). Lynx in the Dinaric Mountains selected microhabitats that provided better concealment, which likely helped them to avoid being detected by humans or larger competitors (e.g. grey wolves and brown bears). At the same time, we noticed that lynx prefer to rest on top of the mountain ridges or hilltops, as well as on steep slopes, which often provide a good view of the surrounding area to detect any potential incoming danger. These results likely indicate a trade-off faced by many felids between being concealed and, at the same time, still be able to survey the surroundings. Selection of well-structured microhabitats on locations with good outlook, which we observed to be lynx' the most selected places, could represent the optimal choice to meet both requirements. This trade-off between concealment and surveillance appears to be evident also from the previous research on resting site selection of felids across the world. Selection for low local visibility at the resting sites was for example observed for Eurasian lynx in Poland (Podgórski et al. 2008), Iberian lynx in Spain (Fernández et al. 2003), bobcats (*Lynx rufus*) in Midwest U.S.A (Kolowski and Woolf 2002), European wildcats in Germany (Jerosch et al. 2010) and pumas in the Rocky Mountains in U.S.A. (Kusler et al. 2017), while the use of conspicuous locations that provide good outlook of the surrounding was reported also for Eurasian lynx in Germany (Signer et al. 2019) and for snow leopards in the Himalayas (Jackson 1996).

Furthermore, the use of well-concealed locations on ridges or hilltops can help predator to detect and ambush potential prey. Lynx is a stalking and ambush hunter, therefore spotting prey from afar before being detected is essential for a successful hunt (Breitenmoser and Breitenmoser-Würsten 2008). Similar behaviour was reported

for snow leopards, which often use ridges for hunting (Jackson 1996). Besides, since winds often blow upwards during the daytime, resting on a ridge or hilltop can help the predator to detect approaching prey sooner and, at the same time, prevent the prey from detecting the predator's scent. Also, some of the prey species in the study area, like red deer (*Cervus elaphus*), regularly use ridges and hilltops during the day rest (Jerina 2006), which could be another reason for lynx to use such locations, as it likely increases the chances of encountering potential prey.

Steeper slopes and rugged terrain are also less accessible to people, which could reduce the human disturbance from recreation and logging activities (Sunde et al. 1998; Bouyer et al. 2015; Belloti et al. 2018) and provide some shelter from unfavourable weather conditions (Falk 2009). Selection of steep slopes for resting sites appears to be a common feature of several felid species, as also snow leopards (Jackson 1996) and pumas were reported to select steep slopes, supposedly to reduce encounters with other predators, especially with wolves (Kusler et al. 2017). Avoidance of competition with wolves could also be a reason for lynx' selection of steep slopes in our study area, although currently there is limited support that lynx would be avoiding wolves (Krofel 2012). Probably more important is the avoidance of rugged terrain by some of the important scavengers, like the wild boar (*Sus scrofa*) (Dul'a and Krofel et al. 2020). Avoidance of scavengers was also suggested to be the reason for use of steep slopes by lynx in Norway (Falk 2009).

In the Bohemian Forest along the German-Czech border, where rocky outcrops are generally rare (less than 2% of random points were within 50 m of rock formations), lynx were selectively resting on or near rock formations to shelter them from heat or cold, reduce encounters with people (which tend to avoid inaccessible terrain) and increase the success of scent-marking by using conspicuous locations (Signer et al. 2019). Although some of the models suggested that lynx selectively used rocky terrain and a large proportion (52%, Table 1) of the resting sites were located at such places, the selection was not as strong as observed in the Bohemian Forest. We suggest that this could be linked with functional responses in habitat use due to higher availability of the rocky terrain (15% of random points were located in rocky terrain). This characteristic provides abundant options for choosing a good resting site and probably makes these predominantly karstic regions, such as Dinaric Mountains, very suitable for lynx. We observed also some support for the selection of southern expositions, which might provide better thermal conditions, especially in cold weather. Similar selection was reported for the European wildcats in Germany (Jerosch et al. 2010) and pumas in the Rocky Mountains, U.S.A., suggested to maximize sun exposure in the cold months and thus promote thermoregulation (Kusler et al. 2017).

Avoidance of human infrastructure was less conclusive. Although we found fewer resting sites in the vicinity of roads, none of the best models suggested that lynx avoided forest roads. Forest roads are frequently used by lynx when they are active for movement and scent-marking (Krofel et al. 2017), which mainly occur at night, when roads are rarely used by people. During the day, the forest roads probably represent areas with highest human activity, but overall the use by people is low and apparently this does not have important effect on lynx selection of resting sites. On the other hand, some of the models suggested that lynx are avoiding forest cabins and we observed only one case when lynx rested near the forest cabin in winter, while several ($n = 14$; Table 1) random locations were located near this infrastructure. This suggests that construction of new cabins might reduce suitability of some locations for lynx resting sites. Abandoned or less-used cabins are, however, often used as marking objects by the lynx in the Dinaric Mountains (Allen et al. 2017), so they might even attract lynx during the active period (i.e. night, when human disturbance is generally low).

When lynx are staying near kill sites, their options for finding resting sites are likely limited, as they usually stay in the vicinity of prey remains. Although the data showed some trends towards stronger selection of several topographic characteristics for resting sites without prey (Table 1), as we hypothesized, the differences were mostly small and not statistically significant. This likely reflects high availability of suitable resting sites throughout the region, so lynx are able to find appropriate locations also in the limited radius around kill sites. The most important difference between the resting sites with and without prey was visibility, which was lower during the feeding periods. This is similar to observations in Polish lowlands by Podgórski et al. (2008), who attributed this to lynx feeling more threatened when near a kill site, which attracts various scavengers. In our study area, where the scavenger guild also includes brown bear, the largest carnivore in Europe and frequent kleptoparasite of lynx kills (Krofel and Jerina 2016), lynx likely have an additional reason to conceal themselves. The model also indicated that during the feeding period lynx avoid resting in bushes, which might be connected with the type of habitats where lynx kill their prey. Local data support this, as lynx kill sites were often found in the rugged terrain, but rarely in dense vegetation (Krofel et al. 2007).

This is the first study using more refined approach of incorporating activity data to remove daytime locations when lynx are moving. Since about 15% of lynx daytime locations are not connected with resting behaviour (Heurich et al. 2014), our approach can provide more reliable results and we recommend using activity data for such studies in the future. Nevertheless, our conclusions are comparable with results of previous studies on lynx resting site selection, indicating that also such studies can produce valuable results, when activity data are not available.

In conclusion, our study of lynx resting site selection in a karstic landscape suggests that lynx select resting sites that provide enough structures for concealment, but are at the same time located on elevated or steep locations with good view of the surroundings to easily detect incoming danger or prey. Karstic landscape with rugged and rocky terrain provides high availability of suitable resting sites and provides lynx with several options even when restricted to the vicinity of a kill site. We suggest that in such landscapes human factors may play smaller role as in regions with less heterogeneous terrain, where previous studies were conducted (e.g. Podgórski et al. 2008; Filla et al. 2017; Belotti et al. 2018). Nevertheless, we suggest caution when new infrastructure is planned for construction, especially on the hilltops, mountain ridges or steep slopes, which appear to be important locations for lynx to spend their inactivity periods during the day.

Compliance with Ethical Standards

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and the work conforms to the legal requirements of the country in which it was carried out. Research was approved by the committee at the Slovenian Environmental Agency (no. 35601-45/2006-6 and 35601-76-2020-6).

Conflict of Interest: The authors declare that they have no conflict of interest. All sources of funding are acknowledged and we do not expect any direct financial benefits that could result from this publication.

Data availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

Acknowledgments

We would like to thank Primož Bizjan, Urša Fležar, Igor Hočevar, Maj Hočevar, Franc Kljun, Ivan Kos, Peter Novak, Hubert Potočnik, Nina Ražen, Tomaž Skrbinšek, Petra Štajdohar, Janez Tarman, Jasna Tarman, Uroš Videmšek, Nejc Zorko, Anamarija Žagar, members of the Slovenian Hunting Association and Slovenia Forest Service personnel for help with the fieldwork and to Aleksandra Majić Skrbinšek and Rok Černe for project coordination. We also thank two anonymous reviewers for their valuable and constructive comments that improved this paper. This study was partly financed by the European Union (INTERREG IIIA Neighbourhood

Program Slovenia/Hungary/Croatia 2004-2006, project “DinaRis”) and the European Commission (LIFE16 NAT/SL/000634 project “LIFE Lynx”). TO was supported by a Ph.D. grant from the Fundação para a Ciência e a Tecnologia (FCT; grant reference: SFRH/BD/144110/2019) and MK was supported by the Slovenian Research Agency (grants no. P4-0059 and N1-0163).

References

- Allen ML, Hočevár L, de Groot M, Krofel M (2017) Where to leave a message? The selection and adaptive significance of scent-marking sites for Eurasian lynx. *Behav Ecol Sociobiol* 71:136
- Barton F (2018) MuMIn: Multi-Model Inference. R package version 1.43.10, <https://cran.r-project.org/web/packages/MuMIn/>
- Belotti E, Červený J, Šustr P, Kreisinger J, Gaibani G, Bufka L (2013) Foraging sites of Eurasian lynx (*Lynx lynx*): relative importance of microhabitat and prey occurrence. *Wildlife Biol* 19:188-201
- Belotti E, Mayer K, Kreisinger J, Heurich M, Bufka L (2018) Recreational activities affect resting site selection and foraging time of Eurasian lynx (*Lynx lynx*). *Hystrix* 29:181–189
- Blanco JC, Cortés Y, Virgós E (2005) Wolf response to two kinds of barriers in an agricultural habitat in Spain *Can J Zool* 83:312-323
- Bouyer Y, San Martín G, Poncin P, Beudels-Jamar RC, Odden J, Linnell JD (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biol Conserv* 191:291–299
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecol Model* 157:281–300
- Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs: Ein Grossraubtier in der Kulturlandschaft. Salm Verlag, Wohlen, Bern
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer New York, New York, pp 49-143

Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) The unique ecology of human predators. *Science* 349:858-860

Dellinger JA, Proctor C, Steury TD, Kelly MJ, Vaughan MR (2013) Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biol Conserv* 157:324-330

Duľa M, Krofel M (2020) A cat in paradise: hunting and feeding behaviour of Eurasian lynx among abundant naive prey. *Mamm Biol* (published online, doi:10.1007/s42991-020-00070-6)

Environmental Systems Research Institute (ESRI) (2012) ArcGIS Desktop Help 10.1 Geostatistical Analyst, <http://resources.arcgis.com/en/help/main/10.1/>

Falk H (2009) Lynx behaviour around reindeer carcasses: MSc thesis, Swedish University of Agricultural Sciences, Grimsö, Sweden

Fernández N, Delibes M, Palomares F, Mladenoff D (2003) Identifying breeding habitat for the Iberian lynx: Inferences from a finescale spatial analysis. *Ecol Appl* 13:1310 – 1324

Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M (2017) Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. *Ecol Evol* 7:6367 – 6381

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS (2018) The influence of human disturbance on wildlife nocturnality. *Science* 360:1232-1235

Gehr B, Hofer EJ, Muff S, Ryser A, Vimercati E, Vogt K, Keller LF (2017) A landscape of coexistence for a large predator in a human dominated landscape. *Oikos* 126:1389-1399

Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Joanne Saher D, Stevens CR, Jerde CL (2006) Application of random effects to the study of resource selection by animals. *J Anim Ecol* 75:887– 898

Heurich M, Hilger A, Küchenhoff H et al (2014) Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS ONE* 9:e114143

Heurich M, Schultze-Naumburg J, Piacenza N, Magg N, Červený J, Engleder T, Herdtfelder M, Sládová M, Kramar-Schadt S (2018) Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. *Biol Conserv* 224:355-365

Jackson MR (1996) Home range, Movements and Habitat Use of Snow Leopard (*Uncia uncia*) In Nepal. PhD thesis, University of London

Jerina K (2006) Prostorska razporeditev, območja aktivnosti in telesna masa jelenjadi (*Cervus elaphus* L.) glede na okoljske dejavnike. PhD thesis, University of Ljubljana

Jerosch S, Götz M, Klar N, Roth M (2010) Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): Implications for its conservation. J Nat Conserv 18:45-54

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71

Kaczensky P, Chapron G, von Arx M, Huber D, Andrén H, Linnell JDC (2013) Status, management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe. Istituto di Ecologia Applicata & IUCN/SSC Large Carnivore Initiative for Europe, https://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/task_1_part2_species_country_reports.pdf

Kolowski JM, Woolf A (2002) Microhabitat use by bobcats in Southern Illinois. J Wildlife Manage 66:822-832

Kordiš F (1993) Dinarski jelovo bukovi gozdovi v Sloveniji. Strokovna znanstvena dela 112. University of Ljubljana, Ljubljana, Slovenia

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711-723

Krofel M (2012) Predation-related interspecific interactions in Eurasian lynx (*Lynx lynx*) in northern Dinaric Mountains. PhD thesis. University of Ljubljana

Krofel M, Hočevár L, Allen ML (2017) Does human infrastructure shape scent marking in a solitary felid? Mammal Biol 87:36–39

Krofel M, Huber D, Kos I (2011) Diet of Eurasian lynx *Lynx lynx* in the northern Dinaric Mountains (Slovenia and Croatia): Importance of edible dormouse *Glis glis* as alternative prey. Acta Theriol 56:315-322

Krofel M, Jerina K (2016) Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biol Conserv 197:40-46

- Krofel M, Jerina K, Kljun F, Kos I, Potočnik H, Ražen N, Zor P, Žagar A (2014) Comparing patterns of human harvest and predation by Eurasian lynx *Lynx lynx* on European roe deer *Capreolus capreolus* in a temperate forest. Eur J Wildl Res 60:11-21
- Krofel M, Potočnik H, Kos I (2007) Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. Nat Slov 9:25-36
- Krofel M, Skrbinšek T, Kos I (2013) Use of GPS location clusters analysis to study predation, feeding, and maternal behavior of the Eurasian lynx. Ecol Res 28:103-116
- Krofel M, Skrbinšek T, Mohorović M (2019) Using video surveillance to monitor feeding behaviour and kleptoparasitism at Eurasian lynx kill sites. Folia Zool 68:55-65
- Kusler A, Elbroch LM, Quigley H, Grigione M (2017) Bed site selection by a subordinate predator: an example with the cougar (*Puma concolor*) in the Greater Yellowstone Ecosystem. PeerJ 5:e4010
- Manly BFJ, McDonald L, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Boston, MA
- Nowell K, Jackson P (1996) North Africa and Southwest Asia, Cheetah. In: Nowell K, Jackson P (eds) Wild cats: Status survey and conservation action plan. IUCN/SSC Cat Specialist Group, Gland, Switzerland, pp 41–44
- Ordiz A, Støen O-G, Sæbø S, Kindberg J, Delibes M, Swenson JE (2012) Do bears know they are being hunted? Biol Conserv 152:21-28
- Podgórski T, Schmidt K, Kowalczyk R, Gulczyńska A (2008) Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica, 53:97- 110
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org/>
- Roever CL, Boyce MS, Stenhouse GB (2010) Grizzly bear movements relative to roads: application of step selection functions. Ecography 33:1113-1122
- Roever CL, Beyer HL, Chase MJ, van Aarde RJ (2014) The pitfalls of ignoring behaviour when quantifying habitat selection. Divers Distrib 20:322-333

Sazatornil V, Rodríguez A, Klaczek M et al (2016) The role of human-related risk in breeding site selection by wolves. *Biol Conserv* 201:103-110

Schmidt K (1999) Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in Białowieża Primeval Forest, Poland. *J Zool* 249:417 - 425

Signer J, Filla M, Schoneberg S, Kneib T, Bufka L, Belotti E, Heurich M (2019) Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. *Wildlife Biol* 2019:wlb.00489

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biol Conserv* 157:187-195

Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in hunted population. *Wildlife Biol* 4:177-183

Wilson SE, Nielsen CK (2007) Habitat characteristics of raccoon daytime resting sites in Southern Illinois. *Am Midl Nat* 157:175-186

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems *Methods Ecol Evol* 1:3-14

Figure captions

Fig. 1 Confidence intervals (95%) and respective model-averaged coefficients for each covariate of the best models (M1, M2 and M10; see Tables 2, 3) representing resting site selection in respect to availability within the lynx home ranges in Dinaric Mountains, Slovenia. Confidence intervals containing zero were interpreted as non-significant. Dashed lines separate the different types of covariates (binary, categorical and continuous)

Fig. 2 Confidence intervals (95%) and respective coefficients for each covariate of the best model (M1; Tables 2, 3) reflecting the selection of lynx resting sites with or without prey nearby. Confidence intervals containing zero were interpreted as non-significant. Dashed line separates binary and continuous covariates (above and below the line, respectively).

1 **Figures**

2

3 **Fig.1**

4

5 **Fig.2**

Table 1 Covariates included in the Eurasian lynx resting site selection models. Values for the available and used resting sites are given as mean $\pm$ SE for the continuous covariates and as the proportion of locations with given characteristic or feature present for the binary and categorical covariates. Dashed lines separate the four groups of variables: human infrastructure, visibility, vegetation and topography, respectively

Covariate	Type	Range or categories	Availability (n = 151)	Lynx resting sites			Description
				All (n = 151)	With prey (n = 93)	Without prey (n = 58)	
Road presence	Binary	0-1	24.5 %	14.6 %	8.6 %	18.3 %	Presence of forest road (if seen from the site or not)
Road distance	Continuous	2-1272 m	182 $\pm$ 14.62	230 $\pm$ 21.19	227.2 $\pm$ 31.93	232.3 $\pm$ 28.18	Distance from a resting site to the closest forest road
Cabin presence	Binary	0-1	9.3 %	0.7 %	0 %	1.1%	Presence of cabin or high stand hide for hunting (if seen from the site or not)
Visibility	Continuous	2.25-100 steps	21 $\pm$ 1.04	12.8 $\pm$ 0.66	11.0 $\pm$ 0.82	13.9 $\pm$ 0.93	Average visibility from the four main cardinal directions: North, South, East, West
Vegetation	Categorical	Forest	92.1 %	87.4 %	94.8 %	82.8 %	>10 % of the surface in 50 m radius covered with trees (i.e. tree diameter greater than 10 cm)
		Bush	3.3 %	11.9 %	5.2 %	16.1 %	>10 % of the surface in 50 m radius covered with bush or young forest (i.e. tree diameter smaller than 10 cm)
		Open	4.6 %	0.7 %	0 %	1.1 %	Meadow or forest glade covering >90% of the surface in 50 m radius
Altitude	Continuous	454-1501 m	925 $\pm$ 18.14	1002 $\pm$ 16.31	951.3 $\pm$ 24.87	1033.6 $\pm$ 20.89	Elevation above the sea level
Ridge	Binary	0-1	4.6 %	23.8 %	17.2 %	28 %	Location on the top of a ridge or hilltop
Southern exposure	Binary	0-1	35.1 %	42.4 %	43.1 %	41.9 %	Southern exposure (slope facing South, Southeast or Southwest)
Slope	Continuous	0-75°	14.2 $\pm$ 0.76	22.7 $\pm$ 0.94	21.7 $\pm$ 1.43	23.2 $\pm$ 1.25	Inclination of the terrain
Rocky terrain	Binary	0-1	14.6 %	51.7 %	50 %	52.7 %	Presence of rocks, boulders, rock shelters or cliffs on >50 % of surface in 20 m radius

Table 2 Candidate models of binary logistic regression explaining overall lynx resting site selection (i.e. use vs. available), as well as selection in respect to the presence of kill site (i.e. lynx resting sites with vs. without a prey)

Model	Expression	Hypothesis
M1	1+2+3+4+5+6+7+8+9+10	All covariates affect lynx resting site selection
M2	1+2+3+4+5+6+7+8+9	Topography, human infrastructure and visibility affect resting sites selection
M3	1+2+3+4+5+6+7+10	Topography, vegetation and roads affect resting sites selection
M4	1+2+3+4+5	Only topography affects lynx resting site selection
M5	1+2+3+4+5+10	Topography and vegetation affect lynx resting site selection
M6	6+7+8	Only human infrastructure affects lynx resting site selection
M7	6+7+8+9	Human infrastructure and visibility affect lynx resting site selection
M8	9	Only visibility affects lynx resting site selection
M9	10	Only vegetation affects lynx resting site selection
M10	1+2+3+4+5+9	Topography and visibility are most important for lynx resting site selection
M11	Null	None of the covariates affect lynx resting site selection

1-Altitude, 2-Slope, 3-Ridge, 4-Rocky terrain, 5-Southern exposure, 6-Road distance, 7-Road presence, 8-Cabin presence, 9-Visibility, 10-Vegetation

Table 3 Generalized linear mixed models for resting site selection in respect to the availability within the lynx home ranges (left) and between resting sites with/without prey nearby (right). *k* - Number of model covariates, AIC - Aikake Information Criterion, ρ - Spearman rank correlation

Use vs. availability					With prey vs. without prey				
Model	<i>k</i>	AIC	Δ AIC	ρ	Model	<i>k</i>	AIC	Δ AIC	ρ
M10	7	328.1	0.00	0.71	M1	11	194.2	0.0	0.42
M2	11	329.5	1.40	0.69	M8	3	199.4	5.3	0.25
M1	13	329.51	1.41	0.71	M9	3	199.9	5.8	0.52
M5	7	343.5	15.40	0.95	M7	5	201.0	6.9	0.32
M3	11	346.8	18.70	0.70	M11	2	202.5	8.3	0.52
M4	9	356.4	28.30	0.82	M5	8	203.2	9.0	0.64
M7	6	367.6	39.50	0.92	M6	4	203.6	9.4	0.24
M8	3	372.4	44.30	0.79	M10	8	205.6	11.5	0.40
M6	5	410.3	82.20	0.23	M2	10	206.4	12.2	0.27
M9	4	413.6	85.50	0.52	M3	9	206.9	12.7	0.23
M11	2	422.7	94.60	0.52	M4	7	206.9	12.7	0.53