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Research Article

First insight into the spatial and foraging ecology of the critically endangered Balkan lynx (*Lynx lynx balcanicus*, Buresh 1941)

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Abstract

Spatial and foraging ecology of the Eurasian lynx (*Lynx lynx*) has been well recognized, however due to the distinct taxonomic position and geographic isolation of its Balkan population, it is important to learn and compare its ecology to other populations of this felid. Therefore, the paper offers the first ever investigation into the spatial and foraging ecology of this predator. To that aim, we used modern GPS/GSM telemetry methods, allowing proper research of animal spatial requirements and diet preferences. Individuals were captured using walk-through, double-door box-traps and foot-snares placed on fresh lynx kills. Average home range size of males is 373 km^2 (95% MCP) and 400 km^2 (0.7 Kernel), while the female's home range is 119 km^2 (95% MCP) and 108 km^2 (0.7 Kernel). GPS clusters showed prey remains of 153 kills from five different species: roe deer, chamois, brown hare, red fox and marten. Data collected for the Balkan lynx suggest lower kill rates, probably associated with lower ungulate densities in the study area compared to most of Central Europe, also indicated by the relatively long search time. Although Eurasian lynx can adapt to lower ungulate prey densities by increasing hunting effort, changing spatial organization or switching to smaller prey, this, in turn, can have adverse demographic effects on the critically endangered Balkan population. Using GPS telemetry, we provided first insight into the space use of this small population, and show that the spatial and foraging ecology of the Balkan lynx appear similar to other European populations of this species, especially those from Central Europe with similar home range size and principal prey preference.

Introduction

Despite the copious spatial and foraging ecology studies of various Eurasian lynx (*Lynx lynx*) populations (Haller and Breitenmoser, 1986; Krofel et al., 2013; Schmidt et al., 1997; Sunde et al., 2000a), the Balkan lynx (*Lynx lynx balcanicus* Bureš, 1941), due to the distinct taxonomic position and geographic isolation, has never been a subject of any systematic study of this kind. Several authors have guesstimated its home range sizes and diet preferences based on anecdotal observations. Kappus (1933) stated that on average, Balkan lynx territories range from 26 to 40 km^2. Mirić (1981) assumed the home range of the Balkan lynx to be 15 km^2–30 km^2, depending on the prey availability. Based on this, he gave an approximation of the population size of 280 individuals. Conversely, the robust telemetry studies of other Eurasian lynx populations living in Europe show great discrepancies in home range sizes compared to these early estimates for Balkan lynx (for instance Moa et al., 2001; Schmidt et al., 1997; Breitenmoser et al., 1993). This in particular can affect the estimation of various ecological traits (like population size) and inevitably lead to incorrect conservation status evaluation. Regarding the diet and foraging behaviour of the Balkan lynx there is considerable disagreement among previous authors. Mirić (1981) reported anecdotal cases of predation on wild and domestic ungulates, like roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*) and domestic goats (*Capra aegagrus hircus*). Bekavac (2012) suggested that Balkan lynx rely on small prey, such as lagomorphs, rodents and birds, as in regions where small ungulates are rare or absent, like parts of Finland and Turkey, and Eurasian lynx rely mainly on small prey (Mengüllüoğlu et al., 2018; Pulliainen, 1981).

Understanding predation ecology and the land tenure system of large carnivores is essential for achieving proper decision-making for their conservation and management. This is especially relevant for small and isolated populations threatened with extinction. The Balkan lynx is a critically endangered subspecies of the Eurasian lynx with an estimated population of less than 50 mature individuals (Melovski et al., 2015). Poaching of lynx and overharvesting of its prey (roe deer and chamois) are obvious threats to the survival of the Balkan lynx, while habitat degradation (e.g. deforestation) and inbreeding are also likely to affect its population (Melovski et al., 2015). Implementing conservation efforts is challenging due to poor understanding of the subspecies' basic ecology. While the current range of the subspecies is confined to the south-western Balkans, its historic range covered more or less the entire peninsula (Melovski, 2012; Mirić, 1981; Von Arx et al., 2004), including areas which are now subject to reintroduction and augmentation (Sindičić et al., 2013). Therefore, understanding the basic ecology

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of the Balkan lynx is crucial to properly select source animals that will provide ecological functions similar to those once performed by the locally extinct (sub)population (IUCN guidelines for reintroductions).

Since the Balkan lynx is critically endangered, it requires conservation efforts based on solid scientific data. The present study therefore aims to: 1) gain insight into the Balkan lynx spatial needs by estimating the individual home-range size and overlap; 2) provide first reliable information on lynx predation by estimating ungulate kill rates and monitoring lynx feeding behaviour through prey species analysis. By merging datasets on space use and foraging behaviour we also aim to 3) study the distribution of kills within individual home-ranges and analyse the habitat use of the lynx against their prey distribution and human presence. Finally, we 4) compare our findings with the corresponding information from other lynx studies to assess the ecological particularity of the Balkan lynx. This will help to establish the relative position of the Balkan lynx in respect to other populations of this continent. Finally, we identify remaining ecological knowledge gaps and provide directions for future research on this critically endangered taxon.

Materials and methods

Study area

It is presumed that, historically, the Balkan lynx occupied most of the Balkan Peninsula (Mirić, 1981). However, the range reduction has been apparent in the last three decades (Breitenmoser-Würsten and Breitenmoser, 2001; Melovski, 2012). The current range comprises the mountain massifs of western Macedonia and eastern Albania with sporadic occurrences in western Kosovo (Melovski et al., 2018). According to Melovski et al. (2018), the stronghold of the population is Macedonia's Mavrovo National Park bordering Albania, where the present study was centred (Fig. 1). This protected area was founded in 1949 and covers 730 km^2. Together with surrounding landscapes in the south and east, the total study area covered stretches over around 1800 km^2 (Fig. 1). The study area has a mountainous character with high peaks, river canyons, steep slopes and an altitudinal range from 570 m to 2763 m. The habitat is mostly forest, represented by European beech (*Fagus sylvatica*), King Boris fir (*Abies borisii-regis*), several oak species (*Quercus* spp.) and mixed beech-fir forest communities. Wild ungulates present are roe deer, chamois and wild boar (*Sus scrofa*). Other large carnivores present in the area are grey wolf (*Canis lupus*) and brown bear (*Ursus arctos*) (Melovski et al., 2009). The area is moderately populated by humans with approximately 65 people per km^2 (State Statistical office of the Republic of Macedonia, 2016).

Captures and home-range estimation

We used walk-through, double-door box-traps (3x0.9x0.9 m and 2.5x1x1 m) placed on narrow passages frequently used by lynx (Melovski et al., 2009). Box-traps were active for 2287 trapping nights (Tab. S1), while foot-snares trapping effort was 10 trapping attempts at fresh lynx kill sites. In total, we captured six males and one female Balkan lynx and recaptured four of them using a combination of box-traps and foot-snares on lynx kills (Tab. S1). The capture rate using box-traps only was one lynx in 326 days. Due to box-trap malfunctions (trap door or trigger malfunction, alarm system failure), nine additional opportunities for lynx captures were missed. Using foot-snares, in seven out of ten times we failed to capture/recapture a lynx since they either did not return after one night (n=3), or triggered the snare but did not get caught (n=4). By-catches in box-traps included: brown bear (1), roe deer (1), wildcat (*Felis silvestris*) (2), badger (*Meles meles*) (2), birds (6), and stray dogs (19). Trapping period was generally in winter and early spring, because Eurasian lynx increase their movement during the mating season (Jędrzejewski et al., 2002) but also to avoid possible capture of pregnant females. The capture took place inside Mavrovo NP and in its close vicinity (Fig. 1). From 2015 onwards, video camera-traps (Cuddeback Digital C123®) were placed at both ends of the trap in order to document the trapping behaviour of the animals, and lynx were lured with urinated hay from lynx kept in a zoo.

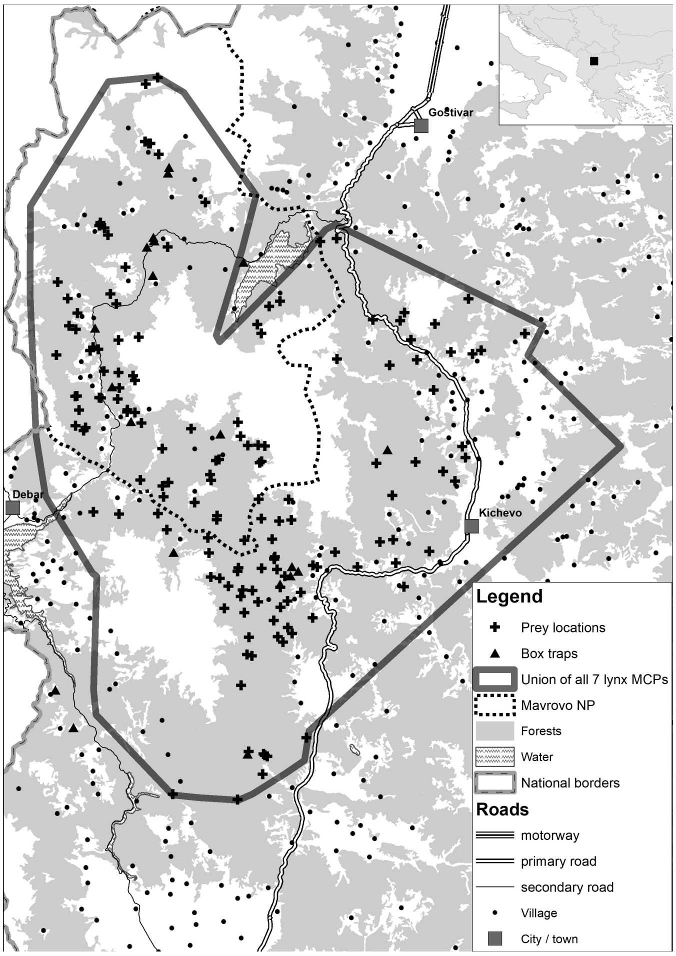

Figure 1 – Study area in western Macedonia showing Mavrovo National Park and merged 100% minimum convex polygons of the seven radio-tracked Balkan lynx. Prey documented in the study, alongside the populated places, box-trap locations and main roads are presented.

The immobilisation of the captured animals was done using 2.8 mL of medetomidine (Domitor®) and 0.8 mL of ketamine (Ketasol®) for anaesthesia and 2.8 mL of atipamezole (Antisedan®) for reversal. We fitted the animals with GPS/GSM (Global Positioning System/Global System for Mobile) collars (Vectronic Aerospace GmbH, Germany and LoTek Wireless Inc., Canada). In order to change the battery-exhausted collars, we tracked the lynx and searched for prey remains using the last GPS positions (clusters), as well as 'homing-in' using the VHF frequencies of the collar. We attempted to recapture the animals by setting spring-loaded foot-snares on fresh lynx kills. Trapping of the Balkan lynx was approved by the Macedonian Ministry of Environment and Physical Planning (permits number: 11-2186/2; 11-546/2; 11-1006/10).

The collars placed on the males were programmed to obtain four to seven fixes per day: one at noon, two during dusk and one in the night in order to increase the chance of finding kills. When more than four fixes were scheduled, the collar took additional one fix at dawn and two at dusk, assuming that lynx mostly feed at dusk (Jobin et al., 2000). The collar placed on the female F01, and males M05 & M06 worked with the following schedule: four fixes per day, each in intervals of six hours (0, 6, 12, 18 hours).

For calculating home-ranges we chose minimum convex polygons (MCP) and kernel density estimator (KDE) as the most widely-used home-range estimators (Kie et al., 2010; Laver and Kelly, 2008). The home-ranges were estimated using 95% and 100% MCPs and 50% and 95% KDE (Fig. 2). Choosing a smoothing factor (bandwidth) is crucial in order to properly estimate the home-range and utilisation distribution for KDE (Wand and Jones, 1995; Silverman, 1986). To use a biologically meaningful bandwidth (h) for estimating KDE home-ranges, we chose the one that reflects the relationship between the animal's move-

Table 1 – Home-range calculations of the Balkan lynx using minimum convex polygons (MCPs) and Kernel density estimation (0.7 reference bandwidth value and biologically meaningful bandwidth). The relative difference in area is calculated. We favoured $h_{ref} \times 0.7$ in order to avoid oversmoothing of the utilization distribution due to irregular daily intervals of the fixes.

		MCP (km^2)			Kernel95			Kernel50		
Lynx ID		100%	95%	50%	$h_{ref} \times 0.7$	"biol" method	difference %	$h_{ref} \times 0.7$	"biol" method	difference %
M01		350.70	276.80	111.00	289.60	413.10	29.90	76.90	113.40	32.20
M02		434.10	369.20	155.00	422.90	534.40	20.90	128.30	157.70	18.60
M03		454.30	422.50	183.00	464.00	598.00	22.40	121.10	164.90	26.60
M04		888.10	640.20	281.00	712.00	942.10	24.40	164.90	243.10	32.20
M05		326.70	247.30	76.20	222.00	329.10	32.50	50.60	83.70	39.50
M06		368.20	283.80	114.80	293.60	431.70	32.00	87.40	124.10	29.60
	Average (males)	466.30	373.30	153.50	400.70	541.40	27.00	104.90	147.80	29.80
F01		164.90	119.20	40.80	108.50	172.20	37.00	34.00	48.20	29.50

ment behaviour and the sampling interval. Specifically, we first created a 'virtual' time series for each individual lynx that started with the date of the first available telemetry location, ended on the day of the last location and included time steps of 12 hours. For each virtual date, we selected the real data point with the shortest interval between the real and the virtual point (difference in time). Based on the selected points only, we measured spatial distances (in meters) between each location and the previous one. Finally, we calculated the mean of the spatial distances but excluded cases when telemetry locations were less than six hours or more than 18 hours apart and used it as a smoothing factor. Thereby, we expected to obtain representative minimum estimates of spatial distances covered by each individual. In order to reduce oversmoothing, we calculated the KDE taking a fixed proportion of 0.7 as suggested by Kie et al. (2010). The data were analysed using the `adehabitatHR` (Calenge, 2006), `rhr` (Signer and Balkenhol, 2015), rgdal (Keitt et al., 2018) and `lubridate` (Grolemund and Wickham, 2011) packages in the R statistical environment (R Development Core Team, 2015).

To properly calculate the home-ranges, we tested if the individuals exhibit resident status by calculating cumulative home-ranges for each day passed after the first location (Laver and Kelly, 2008). The established home-range for resident animals was identified when the asymptote had reached a horizontal level and did not increase for more than 10 km^2 in one-month period. Lynx home-ranges were estimated as 95% MCP. To check if autocorrelation of locations has any effect on home-range estimation, we analysed the data using a) all available locations and b) only one randomly selected location per day. These analyses were done using the `sp` (Bivand et al., 2013; Pebesma and Bivand, 2005), as well as `adehabitatHR` (Calenge, 2006) packages in R. To account for the spatial overlap of the lynx M05 and M06 which were tracked simultaneously, we calculated their overlap of 100% MCP and 95% href*0.7 KDE in ArcGIS. We did the same for the home-ranges of M04, M03 and M02, tracked in different years (Tab. S3) in order to infer for the possible replacement of territories due to death or dispersal. We calculated the straight-line distance (SLD) between consecutive locations taking one location per day. Then, we grouped the mean SLDs into three months periods starting from January, in order to account for seasonal differences in daily displacement.

Predation

We used a geographic information system (GIS — ArcGis Desktop, ESRI, Redlands, CA, USA, 2013) to analyse GPS locations as they were received via GSM network and visually identified all aggregations — GPS location clusters (GLCs; Merrill et al., 2010). Previous research using GPS telemetry on Eurasian lynx showed that in most cases after killing an ungulate, lynx will return to kill sites or stay within 300 m radius for more than one night (Krofel et al., 2013). Therefore we defined a GLC as a potential ungulate kill site when at least two locations were detected less than 300 m apart within the time frame of more than 24 hours and less than three days (i.e. interval between locations of a GLC could be more than three days, but at least two of them should be recorded within three-day time span). Nevertheless, we also visited several shorter GLCs to detect kill sites that lynx may abandon early in the consumption process (e.g. due to kleptoparasitism by dominant scavengers, such as bears; Krofel et al., 2012) or constituted smaller prey items (Vogt et al., 2018). When a potential kill site was suggested by the GLC, we field-checked the site looking for prey remains. We used a handheld GPS to first search the area around the centre of the GLC, and continued in the area within a 150 m radius of each cluster location. If the area was particularly rugged or densely vegetated, the search was extended. As scavenging is very rare among Eurasian lynx (Krofel et al., 2011), we regarded all carcasses detected at GLCs as lynx kills.

We only calculated kill rates for ungulates, because smaller prey (e.g. hares, rodents, small carnivores) are often difficult to detect in the field and because it is predation of ungulates that is usually considered most important from the management and conservation perspective (Molinari-Jobin et al., 2002; Jobin et al., 2000). To estimate kill rate, feeding time, and search time we generally followed methods described in Krofel et al. (2013). Thus, we estimated feeding time at each kill site as the time period between the estimated time of killing and until the lynx left the carcass without returning (time of departure). Time of killing was set in the middle between the last GPS location before a GLC and the first location at the GLC. Time of departure was set in the middle between the last GPS location at the GLC and first location >300 m from the GLC after which the lynx stopped returning to the GLC. If there was a time gap of >24 h with no successful GPS fixes between the last GPS location before a GLC and the first location at the GLC, the data were excluded from further analysis. The same approach was used for time of departure. We also excluded the data for certain kills when it seemed that the lynx left the carcass as a result of research-related disturbance (e.g. during recapture attempts to change the collar). Similar to the feeding time, we estimated the search time as the time between time of departure of a given kill and time of killing the next one. We calculated kill rate (the number of ungulates killed per unit time) from the average time interval between the two consecutive kills (i.e. feeding time + search time).

Data on lynx kills were analysed in two ways. First, we used only the data for the consecutive field-confirmed ungulate prey remains between which there was no other potential ungulate kill site ("field-checked estimate"). If there was a GLC indicating a potential kill site, but no prey was found or the GLC was not inspected in the field, we terminated the kill series and started from the beginning after the next confirmed kill. Because this approach can give biased results due to failure in finding the kills and to scavenger activity (Krofel et al., 2013), we also calculated kill rate and feeding/search times based only on GLC analyses, regardless of whether the prey remains were found in the field or not ("GLC-based estimate"). Because we observed that lynx in our study area sometimes spent >24 hours also at non-ungulate kill sites (e.g. after killing hares or martens), we corrected the GLC-based estimates to account for the non-ungulate prey within the sample. The longest feeding time at a kill site where non-ungulate prey was found (without having an ungulate kill at the same time) was 43 h, thus we regarded feeding times in the interval 24 h–43 h as including both ungulate and non-ungulate prey. Based on the prey remains found in the field, the proportion of ungulate prey at GLCs lasting 24 h–43 h was 23.5% (n=17). We used this proportion and applied it to those GLCs lasting 24 h–43 h that where not checked in the field or no prey remains were found. Among them we randomly selected 23.5% of the GLCs and included them in the analyses in order to be able to estimate the total ungulate kill rate, while the remaining 76.5% were discarded. Because sometimes lynx abandoned ungulate kills in less than 24 h (mating season or scavengers), we also corrected for this bias by increasing the estimated kill rate for the proportion of found ungulate kills with GLCs lasting <24 h (4.2%, n=71). In order to enable comparison with some of the previous studies on Eurasian lynx diet, we report in the results the field-checked estimates, the uncorrected GLC-based estimates and the corrected GLC-based estimates, but regard the latter as the most realistic estimate. Finally, we used the surface of the 95% MCP home-range of each lynx and combined it with the estimated number of ungulates killed annually by given lynx in order to calculate the average kill rate per 1 km^2 (Krofel et al., 2014). The average distance between consecutive ungulate kills was calculated for each lynx taking the corrected GLC-based estimates.

With the intention to account for the ecological factors, all kills that were documented in the field were analysed taking three different aspects: a) habitat preferences – the relation of certain habitat type to its overall availability in the respective home-range of the individuals, b) distance of the kills to the nearest inhabited areas (rural and urban), and c) topography of the terrain represented by: altitude, aspect (side of the world) and ruggedness. We used CORINE Land cover vector data (v. 2018, available at http://www.eea.europa.eu/publications/COR0-landcover) for the habitats that were available within the 100% MCPs of the lynx (third order of selection, Johnson, 1980). Similarly to Filla et al. (2017), we first merged all the 100% MCP boundaries of the lynx (Fig. 1) and within them we counted and calculated the availability of the habitats. Out of the 17 habitat types found, we ended up with four classes of grouped habitats based on their ecosystem affiliation (Tab. S5). We placed the remaining habitat types into a fifth class (others) in order to form a threshold value of each class containing at least 5% area inside the MCPs (Avukatov, 2013). To compensate for the relatively small sample size of prey remains found, but also attribute the prevalence of the kills in the available habitats, we calculated the Resource Selection Index (RSI) by dividing the percentage of prey found in a certain habitat by the expected percent of prey in the same habitat (area representation of this habitat in the total area of interest). Thus, we wanted to avoid situations where an incidental kill in a habitat (including the buffer) would impact the values of hunting preferences or if no kills would be located in habitats that are rare in the MCPs of the monitored lynx.

The disturbance to lynx hunting caused by people was analysed by taking the closest distance to the populated urban and rural settlements using the tool “Near” in ArcGIS. The results are presented as an average distance from urban and rural area for each lynx. Due to the nonexistence of motorways in the study area, we decided to not analyse the roads as a possible disturbance factor. This was supported by the regular crossings of the primary roads by the collared males (Fig. 1).

We calculated the average altitude of the kills made for each lynx in ArcGIS. The terrain aspect dataset used was generated with the ArcGIS toolbox using the Digital Elevation Model from SRTM (1 arcsecond resolution). The angles 0 and 360 (degrees) represent the north, increasing clockwise (90 being the east, 180 is south and 270 is west). The "north-south" index was calculated as the cosine function of the aspect angle.

The Terrain Ruggedness Index is defined as the mean difference in elevation between a central pixel and its surrounding cells. The ruggedness of the kill sites was then compared to the average ruggedness of the grouped MCPs (Fig. 1) in order to detect possible differences in selection of the kill sites. In total, five categories were obtained based on the Jenks natural borders optimisation: mild, small, medium, high and extreme (Jenks, 1967). "Aspect" and "Ruggedness index" variables were generated with "Spatial analyst tools/Surface/Aspect" tool in ArcGIS and "Raster/Analysis/Roughness" in QGIS, using the SRTM DEM dataset (1 arcsecond resolution), which was also used directly as the "Altitude" variable.

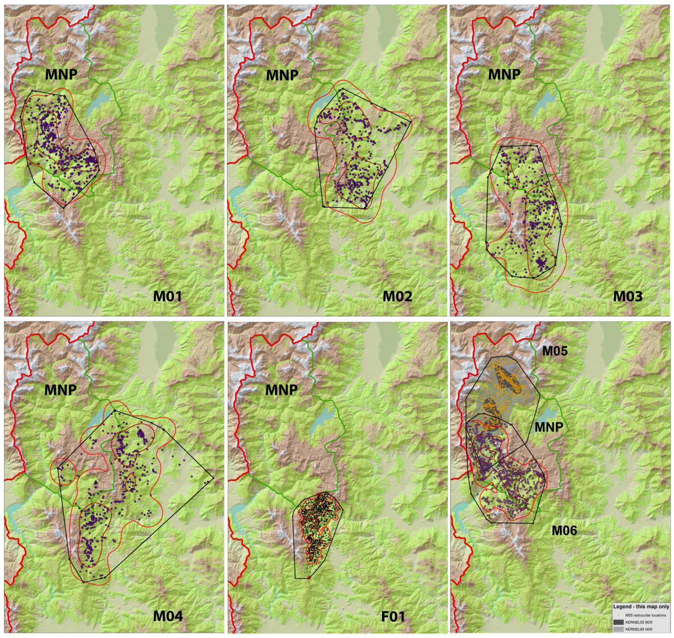

Figure 2 – Kernel 95% (red line) and 50% (brown line) and MCP 100 (black line) polygons for each lynx. Mavrovo National Park: green line; state border: thick line. Due to the fact that were followed simultaneously, the map in the lower right corner contains information on both M05 and M06 in order to show their overlap.

Results

Captures and home-range estimation

The biometric measurements and age estimation of the captured animals was done according to Marti and Ryser-Degiorgis (2018) (Tab. S2). F01 reproduced during both years of monitoring. In 2017 we found a den with one kitten, which did not survive according to the subsequent video recordings from her kills. In 2018 she was again accompanied by single kitten, which was still alive at the age of 4 months, when the last video of F01 was recorded.

The overall success rate of the collars (84.6%) and the number of successful relocations obtained (minimum 593 for M03), allow reliable calculations of home-ranges (Tab. S3, Fig. 3). On average, home-ranges were established after 147 days (SD=78.7 days) (Fig. 3). Males’ average home-ranges reach 373.30 km^2 95% MCP and 400 km^2 95% KDE (href*0.7), while the female’s 95% MCP and KDE (href*0.7) are similar — 119.20 km^2 and 108.50 km^2 respectively (Tab. 1, Fig. 2). On average a difference of 27% and 37% is observed for the 95% of 0.7 reference and ‘biological’ Kernel method for males and the female respectively (Tab. 1). The overlap of the territories of the two males (M05 and M06) that were tracked simultaneously in 2019, is 112 km^2 for 100% MCP (32% overlap) and 40 km^2 for href*0.7 95% KDE (17% overlap) (Fig. 2). The overlap of the territories for M04 with the territories for both M02 and M03 which were not tracked at the same time is 44% for 100% MCP between M04 and M03 (53% overlap for href*0.7 95% KDE); and 68% overlap for 100% MCP between M04 and M02 (65% overlap for href*0.7 95% KDE) (Fig. 2).

Minimum and maximum straight-line distances for males ranged from 0 to 24.8 km, whereas the female displacement ranged from 0 to maximum of 13 km per day. On average, males’ displacement was around 4 km/d throughout the year while the female’s average is 2.4 km/d. Season-wise, males’ furthest displacement was in the winter months (January–March) with 5.09 km/d, and lowest from July

Table 2 – Predation of the Balkan lynx including number of identified kill sites, interval between consecutive ungulate kills, kill rate, feeding time and search time for the next kill. Interval between kills was calculated via three approaches: using only consecutive kills confirmed in the field or using all telemetry data with either corrected or uncorrected GLC-based values (see Methods section for details). We regarded the corrected GLC-based values as most reliable and used them for calculating number of ungulates killed annually per lynx in total and per area according to each lynx's home-range (95% MCP). Feeding, search time and the average distance between consecutive kills were also calculated according to the corrected GLC-based estimates.

Lynx ID	No. of kills found in the field/ identified by GLC*	Interval between kills (days)			Ungulates killed/ year	Ungulates killed/ year/km^2	Feeding time	Search time	Average distance between consecutive kills (m)
		Field-checked estimate	GLC-based uncorrected values	GLC-based corrected values					
M01	25/26	11.37	11.24	11.87	30.80	0.11	2.76 ± 1.21	9.89 ± 5.43	8075
M02	25/31	7.41	8.37	8.50	42.90	0.12	3.33 ± 1.19	5.10 ± 4.46	9848
M03	16/21	7.32	9.03	9.82	37.20	0.09	3.40 ± 1.11	6.44 ± 4.95	10 391
M04	15/23	8.49	6.45	7.12	51.30	0.08	2.78 ± 1.72	4.60 ± 3.91	13 473
M05	18/26	17.00	14.50	18.34	19.9	0.08	3.48 ± 2.27	19.11 ± 19.35	7783
M06	24/40	7.50	9.30	9.72	36.0	0.13	3.22 ± 1.47	7.01 ± 5.46	7502
Average males	20.5/27.83	9.85	9.81	10.89	36.35	0.1	3.16 ± 1.49	7.02 ± 7.26	9512
F01 total	31/61	13.29	9.17	11.20	32.60	0.27	3.83 ± 1.58	8.23 ± 7.40	5534
F01 alone	26/47	13.80	9.82	11.48	31.80	0.27	4.02 ± 1.68	8.41 ± 7.58	5999
F01 with kitten	5/14	9.70	7.97	10.19	35.80	0.30	3.15 ± 0.89	7.54 ± 7.07	5104
Average females	20.47/40.67	12.26	8.99	10.96	33.40	0.28	3.67 ± 1.38	8.06 ± 7.35	5545

* Also includes kill sites with small prey

to September, 3.18 km/d (Fig. 4). The lowest displacement of F01 was from April to June, averaging 1.7 km per day (Fig. 4).

Predation

We identified 228 GPS clusters as potential kill sites (feeding time >24 hours), of which we were able to find prey remains of 153 kills (Tab. 2, Fig. 1) belonging to five different species: roe deer (n=107), chamois (n=11), brown hare (*Lepus europaeus*) (n=27), red fox (*Vulpes vulpes*) (n=4) and marten (*Martes foina/martes*) (n=4) (Tab. S4). The mean corrected kill interval between consecutive ungulate kills was 10.81 days (SD=8.57 days, range=0.8–64.50 days, n=153), which corresponds to 33.80 ungulates killed per year per lynx. According to the ratio among found ungulate prey remains (107 roe deer and 11 chamois) this corresponds to an average of 30.4 roe deer and 3.2 chamois killed per year per lynx. Mean female kill interval (10.96) was similar to those of males (10.89) (W=2229, n_{female}=42, n_{males}=112, p=0.62) and was somewhat higher when she was accompanied by single kitten, although the difference was not significant (Tab. 2; W=169, $n_{singlefemale}$=33, $n_{withkitten}$=9, p=0.55). Corrected GLC-based kill rate estimate was 10.5% lower than the field-checked kill rate estimate and 10.3% lower compared to uncorrected GLC-based kill rate estimate (Tab. 2).

Table 3 – Grouped habitat types and the representation of prey found in each of them. Area % refers to how much of the particular group can be found in the area of interest (grouped MCPs); number of documented preys found in each of the habitat types; their percentage; and the Resource Selection Index (RSI).

CORINE grouped habitats	Area %	No. of prey	Prey %	RSI
Agriculture with significant areas of natural vegetation	4.59	1	0.65	4.10
Grassland, heathland and moors	23.72	12	7.79	4.10
Forests: broadleaf, mixed and coniferous	53.18	116	75.97	41.44
Transitional woodland-shrub	10.27	22	14.29	40.36
OTHER: cropland, urban areas, sparsely vegetated land and water	8.24	2	1.30	4.57

Based on the corrected GLC-based estimates lynx on average fed on ungulate prey for 3.54 days (SD=1.53, range=0.6–8.1 days, n=120). Feeding time of the female was longer compared to the males (3.67 vs 3.16, Tab. 2, W=2070, n_{female}=46, n_{males}=119, p=0.02), but this was mainly related to the period when female was alone (W=2771, $n_{singlefemale}$=36, n_{males}=119, p=0.008). When female was accompanied by the kitten, her feeding times were similar to males (3.15 vs 3.16, Tab. 2, W=557, n_{family}=10, n_{males}=119, p=0.74; Tab. 2). Mean search time lasted 7.99 days, around 7 days for males and 8 for the female (SD=8.10, range:0–62.5 days, n=116) and was similar for the female compared to the males (W=2386, n_{female}=42, n_{males}=117, p=0.78; Tab. 2). Average distance between consecutive ungulate kills for all males is 8944 m, while the female's average kill distance is 5534 m, with noticeable difference when being with kitten (5104 m) and without (5999 m) (Tab. 2).

Transitional woodland shrubs and forests are dominating the habitats where lynx prefer to hunt with 41.39 and 41.08 of the resource selection indices, respectively (Tab. 3 and Tab. S5). The mean distance to populated urban places was 13.19 km, and to rural, 1.84 km (Tab. 4, Fig. 1). However, the lynx M02 stands out from the others with kill sites at less than a kilometre away from rural and less than 10 km away from urban settlements (Tab. 4). The average altitude where kills are made is 1239 m (Fig. 1, Tab. 4) which is below the average of the area of interest (1308 m). The topography of the terrain revealed that Balkan lynx hunt on medium rugged terrain where we documented almost 45% of the prey (Tab. 5). High ruggedness is preferred in almost 15% of the cases, whereas the last ≈15% is shared between the two extremes of mild and extremely rugged terrain (Tab. 5). Regarding the aspect where kills were found, it is evident that lynx M02, M03 and especially M05 and F01 hunted much more in the southern exposition (Fig. 5). Prey made by M01 were more facing north, whereas the difference of the aspect of prey for M04 and M06 are negligible.

Discussion

The size of the home-range is usually a trade-off between the available resources and the effort maintaining them. Territorial mammals such as the Eurasian lynx have to make this trade-off in order to find enough food, shelter and partners for reproduction. Up to present, the techniques that are used for home-range estimation are clustered in two basic groups: the geometric, such as the minimum convex polygons,

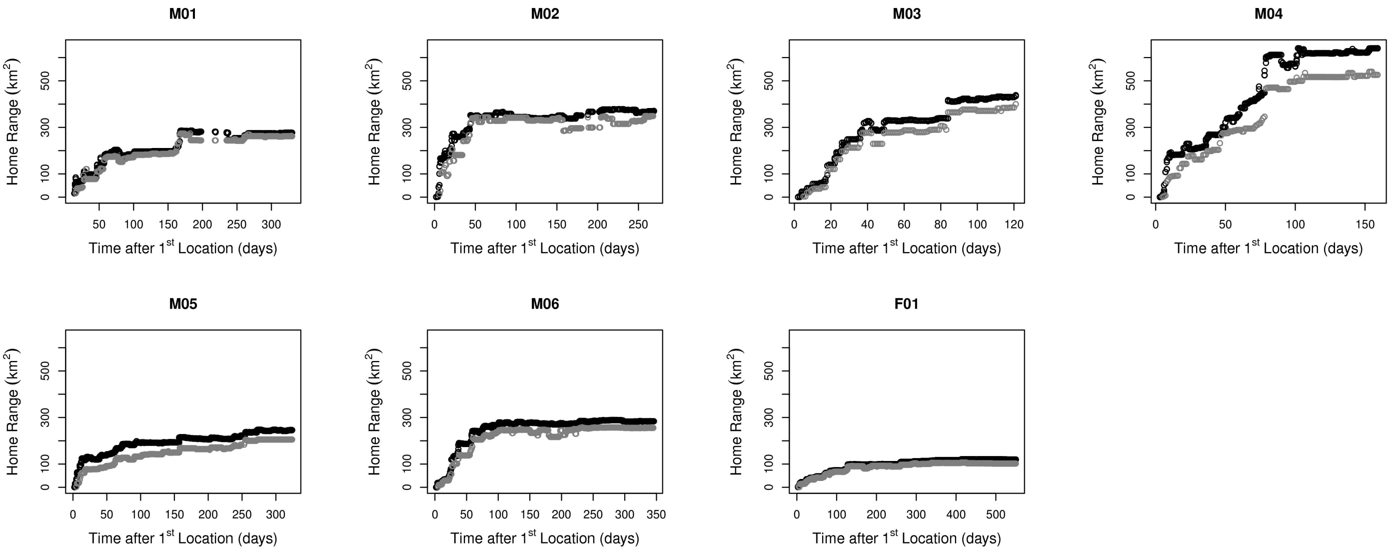

Figure 3 – Cumulative home-range of each lynx individual using one location per day (grey dots) and all locations obtained within the tracking period (black dots).

Table 4 – Distance of lynx kills to the closest urban and rural settlements (in km), average altitude (in m) of sites where kills were found for each lynx.

	Urban	Rural	Altitude
M01	13.48	1.37	1299
M02	8.67	0.97	1086
M03	15.69	2.23	1163
M04	13.07	2.02	1308
M05	18.91	1.65	1311
M06	11.74	1.58	1257
F01	15.05	2.59	1383
Average	13.80	1.77	1258

Table 5 – Terrain ruggedness on kill sites and comparison with the terrain ruggedness distribution of the grouped MCPs of all seven lynxes.

Ruggedness description (indices)	No. of prey	Ruggedness	
		Prey%	Grouped MCPs%
Mild (0–3)	13	8.44	17.77
Small (4–6)	40	25.97	30.06
Medium (7–10)	68	44.81	33.73
High (11–15)	23	14.94	14.56
Extreme (>15)	9	5.84	3.88

and statistical techniques, such as kernel density estimators (Fleming et al., 2015). Most of the Eurasian lynx home-range studies focus on these two estimators which makes comparison fairly straightforward. Balkan lynx home-ranges are much smaller in comparison to the lynx that dwell in Scandinavia's vast natural and semi-natural habitats with scattered prey and conspecifics (Sunde et al., 2000a) reaching sizes of almost 2000 km^2 for males and more than 500 km^2 for females (100% MCP and 95% Kernel) (Bouyer et al., 2015; Linnell et al., 2001; Moa et al., 2001; Sunde et al., 2000a). Lynx that live in Białowieża primeval forest on the other hand reach densities of 5 ind/100 km^2 (Schmidt et al., 1997) with average home-ranges of 248 km^2 for males, and 133 km^2 for females (100% MCP and 95% Kernel) (Jędrzejewski et al., 1996; Schmidt et al., 1997). This implies a relatively small area with suitable habitat, which makes Białowieża act like an island. However, their home-ranges started expanding after the ungulate decline in the area (Schmidt, 2008). Balkan lynx data in our research (href*0.7 95% Kernel and 100% MCP) are more in line with the Central European populations. In the Swiss Alps, MCPs excluding outliers, revealed a home-range of 275 km^2 to 450 km^2 for males (n=3) and 96 km^2 to 135 km^2 for females (n=7) (Haller and Breitenmoser, 1986). In Slovenia, home-range size varieties from 72 km^2–598 km^2 (n=4 females and 2 males) (Krofel, 2012), whereas in Bohemian forest ecosystem the mean home-range is 445 km^2 for males and 122 km^2 for females (n=10) (Magg et al., 2016). It is important to note that the sample size of all the studies used for comparison of home-ranges is larger than the study presented here. Moreover, the technology gradually changed from VHF to GPS

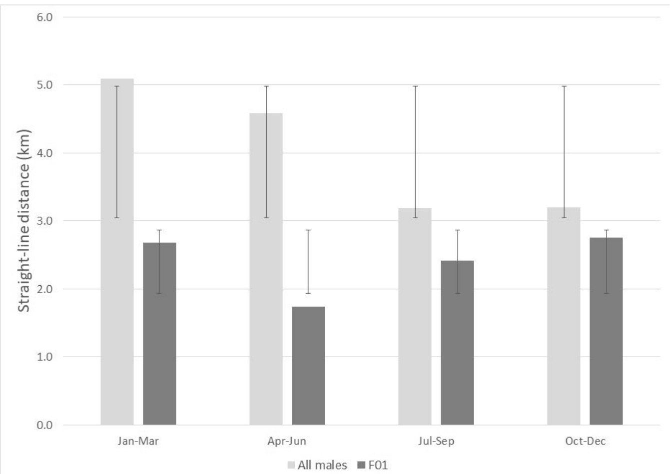

Figure 4 – Seasonal representation of the mean straight-line distance between consecutive daily locations of all male lynx and the female. We calculated the mean distance of each month for the female who was followed for more than one year.

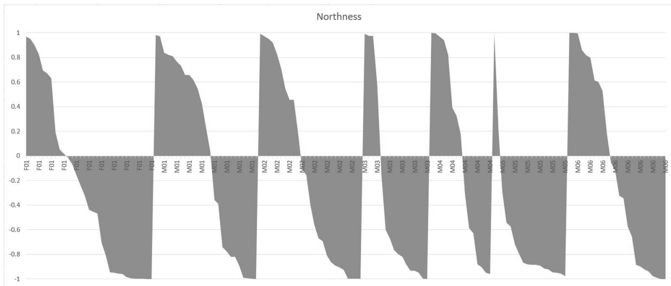

Figure 5 – Visual representation of the aspect where kills were found from all seven lynx. Values closer to 1 are facing North and -1 are facing South. Values closed to 0 are West and East-oriented slopes.

telemetry allowing for exceptional spatial and temporal resolution of the data (Hofman et al., 2019).

Despite the small sample size of seven individuals, using GPS telemetry, we provided first insight into the space use of this small population. In contrast to the female, most males were followed less than one year. Because of their large home-ranges, it is advisable that lynx are monitored over a longer period (6 to 12 months) in order to conclude the dynamics of their spacing (Breitenmoser et al., 1993). Our study showed that, on average, after 147 days the home-range of the Balkan lynx does not show any increase (taking both one and all locations per day). This, however, should be taken cautiously since the sample size is fairly small. Also, the males M03 and M04 were tracked for 4 and 5 months, respectively. The male M04 on the other hand had a home-range of 942 km^2 (95% Kernel) which he traversed in around 100 days. Using VHF-tracking only, Jędrzejewski et al. (2002) did similar measurement and concluded that after 31 days, male Eurasian lynx covered 45% of its total home-range, whereas a female with kittens took 29 days to cover 43% of her home-range. In similar fashion, Schmidt et al. (1997) concluded that more than one year of tracking is needed to know the full size of the home-range. The only female tracked in our study is pointing out that even after 14 months the home-range can grow or shift, which is a natural process, given the food availability, the fate of the conspecifics and the reproduction status of the individuals. It should be noted that if calculated on yearly basis a slight shift in the territory can be observed in resident animals (Breitenmoser-Würsten et al., 2007). In our case, the male M04 established a large territory which overlapped with the areas used by males M02 and M03. However, subsequent camera-trapping did not proof their presence in this area (unpublished data). Males M05 and M06 were followed simultaneously (Fig. 2). Their overlap of the 100% MCP (32%) is double than the study done in the Swiss Jura Mt. (16% male overlap of the total range (Breitenmoser-Würsten et al., 2007)). Being a solitary and territorial mammal, same-sex lynx overlap with their territories to a much lesser extent (Breitenmoser-Würsten et al., 2007) suggesting that males M02 and M03 have either abandoned their territory or are dead. In such case, male lynx tend to extend their territory in order to increase their reproductive and hunting success (Schmidt et al., 1997). Small sample size in relatively large time span limits our study to a certain degree. More data, especially female lynx, are needed to study the social organization and recruitment of the Balkan lynx, to learn more on the way they share the space.

The smoothing parameter (bandwidth) is a crucial element in determining the outer contours (home-range estimate), but also affects the estimation of the utilisation distribution (Kie et al., 2010). Therefore, a biologically meaningful method in obtaining the bandwidth would imply more 'natural' home-range estimate. However, due to irregular daily intervals when fixes arrived in the males (mostly at dusk and night), as well as occasional interruption of the time-series due to unsuccessful fix acquisition, our result show oversmoothed polygons for arounds 30% compared to the 0.7 reference bandwidth. This, it turns, is a drawback of this method as it requires regular daily intervals and uninterrupted GPS communication.

The straight-line distance of the Balkan lynx are in line with its ecology, showing signs of increased movements during the mating season in the period January–March for males. The significant drop of movement in the period April–June for the female suggests maternal behaviour with limited movements during postnatal period (Fig. 2). Our results differ from the one of Breitenmoser-Würsten et al. (2007) with distance between daily locations of 2.51 km for males and 0.96 km for females, as well as with Jędrzejewski et al. (2002) (3.3 km for adult males and 1.5 km for females). The reason for the larger displacement of the Balkan lynx could suggest longer search for prey due to lower prey densities (see results for predation) or higher disturbance (not presented here). In respect to predation, Balkan lynx appears to have similar ecological role as elsewhere in Central Europe, i.e. as an apex predator of wild ungulates. Like in other populations, predation is not limited to ungulates and diet is supplemented with smaller prey, such as lagomorphs and smaller carnivores. Although the GPS telemetry method is used to determine the proportion of small prey in lynx diet, due to short feeding times, the effort in documenting the kills is huge (Vogt et al., 2018). Therefore, combination of GPS telemetry with scat analysis is advisable for this purpose (Krofel et al., 2011; Ivanov et al., 2018) and this will be an important task for future research on the Balkan lynx. In any case, GPS telemetry allows good understanding on the lynx kill rates on ungulates and their consumption process and provides room for comparison with lynx populations in other parts of Europe. In Slovenian and Croatian Dinaric Mountains the lynx population reintroduced from the Carpathian population on average killed 40–73 roe deer, chamois and red deer per year (Krofel et al., 2013), in German and Czech Bohemian forest 53–76 roe and red deer (Belotti et al., 2015), in Swiss Jura Mountains 56–72 roe deer and chamois (Molinari-Jobin et al., 2002), in Polish Białowieża forest 68 roe and red deer (Okarma et al., 1997), and in Scandinavia 33–73 roe deer and/or reindeer (Nilsen et al., 2009; Sunde et al., 2000b; Pedersen et al., 1999). Ungulate kill rates can differ considerably depending on lynx age, sex and social status, as well as season and prey species available (Mattisson et al., 2011). Nevertheless, the data collected for the Balkan lynx (on average 31–51 ungulates per year per lynx) suggest somewhat lower kill rates, which could be associated with relatively low ungulate densities in our study area (unpublished data), especially when compared with most of Central Europe. This is also suggested by relatively long search time (average of 7.2 days) when compared with Central European populations (typically 2–4 days). Especially notable is the low kill rate and long search times of one of the males (M05) and the female, who probably relied to a larger degree on smaller prey (martens, foxes and especially hares). Whether this is characteristic for Balkan lynx in general or specific to these individuals can only be answered with further research (ex. Ivanov et al., 2018). Higher use of smaller prey by females would not be unique, as for example remains of edible dormouse (*Glis glis*) were found in 50% of the stomachs of female lynx from the Dinaric population (Krofel et al., 2011).

Reliance of the Balkan lynx on wild ungulates demonstrated in the present study has several conservation and management implications. Firstly, it indicates importance of improving ungulate prey availability, especially roe deer. Eurasian lynx can adapt to lower ungulate prey densities by increasing their hunting effort and changing their spatial organisation (Schmidt, 2008), but this can have further negative demographic effects on the already critically endangered Balkan population. Therefore, wild ungulate management should be one of the priorities for future conservation efforts of the Balkan lynx. Next, lynx predation on ungulates should be taken into account by game managers when designing hunting plans, as failure to consider lynx predation pressure may result in an inappropriate hunting quota. Similarity between the foraging ecology of the Balkan lynx with other European populations should be taken into account when selecting suitable founders for future reintroduction or population reinforcement activities. For example, we suggest that since Balkan lynx are not available as a source population, other populations (e.g. Carpathian) could be considered as a suitable ecological replacement to perform the ecological function of the Balkan subspecies in its former range (e.g. in Dinaric Mts.).

Ecological parameters on where the prey species were found supplements the knowledge on the foraging ecology of the Balkan lynx. Although medium disturbed habitats are preferred by the Eurasian lynx (Bouyer et al., 2015), living in close proximity to populated settlements, caused the lynx M02 to complement his diet with fox and marten, probably due to lower abundance of roe deer (Tab. S4). This fact was supported by the average distance between each ungulate kill, resulting in shorter distances of kills for lynx that spent most of the time inside the protected area (M01, M05 and M06) and the ones that dwelled outside (M02, M03, M04). While our results suggest that more frequent hunting grounds are on the southern exposition with medium ruggedness, Filla et al. (2017) found that Eurasian lynx use more rugged terrain and with south and west aspect during winter nights. However, further research is needed in order to estimate the importance of these factors depending on the season or part of the day (as in Filla et al., 2017).

Conclusion

With the use of GPS telemetry, we provide the first reliable estimates of the home-range size, and the foraging ecology of the Balkan lynx. In contrast to statements of several previous authors (e.g. Bekavac, 2012; Mirić, 1981), we show that the spatial and foraging ecology of the Balkan lynx population actually appear similar to other European populations of this species, especially those from Central Europe (Breitenmoser and Breitenmoser-Würsten, 2008), with home-range sizes of several hundred square kilometres and hunting focused predominantly on wild ungulates. Although the sample size is small (7 individuals), results points to lower kill rates compared to the Central European populations, which may be owing to the low population density of ungulates in the study area, as indicated by the longer search time compared to Central European populations. In that respect, ungulate species management should be given priority when designing conservation measures. Additional factor to be considered is the occasional reliance on small prey, as seen in the foraging behaviour of the radio-collared female and one of the males. Such behaviour can be further elucidated by conducting scat analysis (Ivanov et al., 2018). To conclude, this investigation provides new insights into the ecological role of lynx in Southeast Europe, which will hopefully inform conservation measures in order to help this population bridge the extinction risk.

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Supplemental information

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

Table S1 Trapping effort. Number of activations represents the total number the traps were triggered, including lynx captures, by-catches, missed opportunities for lynx captures, as well as false triggers due to weather or trigger malfunction. M01 and M02 were captured with foot-snares 8 months after their initial capture.

Table S2 Age and biometric measurements of the radio-collared lynx. Age was estimated comparing the colour and tooth wear according to Marti and Ryser-Degiorgis (2018).

Table S3 Captures and the summary of the fixes of five GPS-collared Balkan lynx. Expected fixes column represents the total amount of GPS fix attempts from the deployment to the day when the GPS battery got exhausted. The "% of Success" column represents the relation between the Successful and Expected fixes.

Table S4 Number of documented prey species for each radio-collared lynx.

Table S5 Corine Land Cover (CLC) description of the habitat types with corresponding code and the grouped habitat types selected for the Resource Selection Index.