Characteristics of spatial use and importance of landscape features for recovering populations of Eurasian lynx (*Lynx lynx*)

Značilnosti rabe prostora in pomen krajinskih značilnosti za ponovno naseljene populacije Evrazijskega risa (*Lynx lynx*)

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Abstract: Following the extirpation from Central and Southeastern Europe by the end of the 19th century, Eurasian lynx (*Lynx lynx*) was reintroduced in the Alps and Dinarics. The recovering population sizes fluctuated over the years; however, they remained relatively small and isolated since their distribution after the establishment has not significantly expanded by natural colonization. One of the most radical changes to the landscape of Europe over the past centuries has been the creation of vast urban and agricultural areas and subsequent extension of infrastructure, causing increasingly fragmented landscape, especially for weak dispersers like lynx. There is a pressing need to establish greater connectivity between the genetically isolated populations, particularly throughout the Alps and Dinarics, to achieve a viable meta-population structure. In the paper, we review scientific knowledge on Eurasian lynx spatial requirements and behaviour, and critically evaluate the methods used. Apart from habitat suitability and connectivity studies, we also provide a review of lynx home range sizes and movement activity, including dispersal. We present habitat suitability model constructed to examine suitable habitat for recovering Dinaric - SE Alpine population and compare home range sizes of lynx from Dinarics in Slovenia with other lynx populations in Europe. Future considerations for lynx conservation should include the impact of climate change, protection of corridor areas, reducing impact of barriers and, if needed, "complement" dispersal via translocations to achieve viable pan-European lynx metapopulation in the future.

Keywords: connectivity, conservation management, dispersal, Eurasian lynx, fragmentation, habitat suitability, home range, *Lynx lynx*

Izvleček: Po izumrtju evrazijskega risa (*Lynx lynx*) v srednji in jugovzhodni Evropi ob koncu 19. stoletja, so rise v 70. in 80. letih prejšnjega stoletja ponovno naselili v Alpe in Dinaride, čemur je v zadnjih dveh desetletjih sledilo še nekaj nadaljnjih naselitev. Vzpostavile so se razmeroma majhne in izolirane populacije, saj se njihova prostorska razširjenost z naravno kolonizacijo ni bistveno povečala. V preteklih stoletjih se je pokrajina v Evropi najbolj temeljito spremenila zaradi širjenja obsežnih urbanih in kmetijskih površin ter posledično širjenja prometne infrastrukture. To je povzročilo vse večjo razdrobljenost življenjskega prostora, zlasti za šibke dispergerje, kot je ris. Zato se vse bolj povečuje potreba po večji povezljivosti genetsko izoliranih populacij,

zlasti v Alpah in Dinaridih, s čimer bi vzpostavili viabilno metapopulacijsko strukturo. V prispevku predstavljamo pregled obstoječega poznavanja prostorskih zahtev in vedenja evrazijskega risa ter izpostavljamo prednosti in slabosti uporabljenih metod proučevanja. Poleg študij primernosti in povezljivosti habitata za risa je v prispevku predstavljen tudi pregled značilnosti domačih okolišev in gibanja risov, vključno z disperzijo. V prispevku predstavljamo model primernosti prostora za risa, ki je bil izdelan za širše območje dinarske - jugovzhodno alpske populacije in primerjavo velikosti domačih okolišev risov iz Slovenskega dela Dinaridov z drugimi populacijami risov v Evropi. Prihodnji vidiki ohranjanja evrazijskega risa v Evropi bi morali vključevati vpliv podnebnih sprememb, varovanje območij koridorjev med habitatnimi krpami, zmanjševanje vpliva (zlasti) linijskih ovir (npr. avtoceste) in po potrebi »dopolnjevati« disperzijo s premestitvami oziroma translokacijami osebkov, s čimer bi lahko v prihodnosti vzpostavili viabilno panevropsko metapopulacijo.

Ključne besede: disperzija, domači okoliš, Evrazijski ris, fragmentacija, *Lynx lynx,* povezljivost prostora, primernost prostora, varstveno upravljanje

Introduction

One of the most radical changes to the landscape of Europe over the past centuries has been the creation of vast urban and agricultural areas and subsequent extension of infrastructure networks, and after more than 5000 years of intense human activities only 2% of original prime forest remains (Iuell et al. 2003).

The Eurasian lynx, once widespread throughout Europe, disappeared from Central and Southern Europe and many other parts of the continent during the 18th and 19th centuries, as a consequence of direct persecution, habitat loss through forest destruction, expansion of cultivated land, and the excessive reduction of wild ungulates (Breitenmoser 1998, Schadt et al. 2002, Zimmermann 2003, Potočnik et al. 2009). Since the end of the nineteenth century, forests have regenerated in many mountainous regions of Europe (Breitenmoser 1998, Zimmermann 2004), and the wild ungulate populations have recovered quickly (Apollonio et al. 2010). The improvement of the ecological conditions as well as protective legislation was favourable for the return of large carnivores as lynx populations reintroduced in the Central Europe in the 1970s and 1980s still persist in the Swiss Jura Mountains, Northwest Swiss Alps, Dinarics, French Vosges and Chartreuse Alps mountains (Breitenmoser 1998, Chapron et al. 2014).

The population sizes have fluctuated over the years, but distribution has not significantly expanded by natural colonization. Following the first reintroductions, lynx were translocated to Northeastern Switzerland in 2001 (Ryser et al. 2004), and to the Kalkalpen (Austria) in 2011-2013. Lynx' current distribution in Central and Southeastern Europe seems to be mainly limited to sites that were used for reintroductions and translocations where they were successful.

One of these reintroduced populations is Dinaric - SE Alpine lynx population, which formally/administatively belong to the Alpine and Dinaric populations (Kaczensky et al. 2013), however they are both demographically and genetically the same population since the SE Alps have been colonized by lynx from Slovenia. As such, the lynx in Dinaric - SE Alpine population represent a genetically continuous unit, which is however presently divided in two distinct subpopulations: the larger Dinaric and the smaller SE Alpine subpopulation. This population plays an important role as the "stepping stone" that connects lynx populations in the southeastern Europe (Albania/Kosovo/North Macedonia) with the reintroduced populations in the northwestern and eastern Alps in Switzerland, France and Austria (Kalkalpen).

The reintroduced/translocated populations in Europe are relatively isolated, and only limited movement occurs between some of them (Zimmermann and Breitenmoser 2007). In the human dominated and highly fragmented landscape

of Europe, dispersal is constrained by natural (e.g. rivers, deep valleys) and anthropogenic barriers such as vast urban and agricultural areas and subsequent extension of traffic infrastructure networks (Potočnik et al. 2019a). Furthermore, dispersing sub-adult lynx show a strong tendency to establish home ranges in territories adjacent to conspecifics (Zimmermann et al. 2005). Thus, the combination of environmental and ecological factors make it unlikely that lynx will spontaneously colonize new areas in the Alps. It is therefore a conservation priority to link the existing lynx populations in the Alps to the Jura and Dinaric Mountains (Molinari-Jobin et al. 2003), potentially to the Vosges, Bohemian-Black Forest and Balkan populations, and in long-term possibly even to Carpathian populations (European Commission 2013). Natural dispersal alone likely would be insufficient to establish this interconnectivity, making translocations and reintroductions necessary (e.g. Zimmermann and Breitenmoser 2007, Molinari-Jobin et al. 2010).

Here we review scientific knowledge on Eurasian lynx spatial requirements and behavior as well as to examine the advantages and weaknesses of the methods used. It is crucial to assess and mitigate the negative effect of habitat fragmentation on lynx populations and facilitate genetic exchange among isolated (sub)-populations or demes in Central and Southeastern Europe. Knowledge on amount and distribution of suitable habitat available to particular lynx population and to the obstacles it is exposed to is important for improvement of our understanding of lynx population connectivity within each population and across habitat patches at the metapopulation level. Apart from habitat suitability and connectivity studies, we provide also information on lynx home range size and movement activity, including dispersion, as a critical part of its ability to occupy sufficient interconnected areas to compensate for demographic variations and subsequently support genetic exchange between (sub)-populations, ensuring viability of the metapopulation. We also present lynx habitat suitability model we constructed for Dinaric Mountains - SE Alps and adjacent regions as well as preliminary data on home range sizes of GPS-collared lynx in Dinaric Mountains in Slovenia between 2003 and 2020.

Habitat suitability

Top predators are generally not very sensitive to a particular habitat structure, vegetation or ecosystem type (Mladenoff et al. 1995). But among the European large carnivores, Eurasian lynx is certainly the one with the most specific demands regarding habitat and prey (Breitenmoser 1998). However, lynx can adapt to semi-natural landscape and their permanent disturbances (Breitenmoser-Würsten et al. 2001). The Eurasian lynx is present in large continuous lowland forest areas with more than 50% of forest cover. It is linked to forest areas with high amount of forest fringe (Breitenmoser et al. 2000). The Eurasian lynx can also tolerate interruptions by open land habitat patches and land use types such as pastures or agriculture. Telemetry studies in 1990s in the Swiss Alps (Breitenmoser-Würsten et al. 2001) showed that re-introduced lynx originating from highly forested Carpathian Mountains, already adapted to open areas, when compared to the first telemetry studies in the early 1970s (Haller and Breitenmoser 1986). Intensive land use is tolerated as long as there is enough connected forest area for retreat (Breitenmoser 1998, Schadt et al. 2002).

Presence and availability of food/prey sources is important parameter determining habitat suitability for animal species. Lynx diet varies greatly depending on prey availability and accessibility. Although other species within *Lynx* genus developed specializations for hunting lagomorphs, Eurasian lynx staple prey in Central Europe are roe deer (*Capreolus capreolus*) and Alpine chamois (*Rupicapra rupicapra*) as well as other ungulate species like red deer (*Cervus elaphus*) and European mouflon (*Ovis aries musimon*). In other parts of its distribution, it can also prey on semi-domestic reindeer (*Rangifer tarandus*) and white-tailed deer (*Odocoileus virgianus*). In areas with low roe deer density Eurasian lynx diet can seasonally shift to other types of prey like rodents and birds (Krofel et al. 2012). In a research of lynx diet in Dinaric forests with low density of ungulates, rodents represented considerable part of the diet (7.7%) at peaks of their population dynamics. This proves that Eurasian lynx is able to adapt to various food sources. Given present high population densities of ungulate species across Europe (e.g. Apollonio at al. 2010) it is

assumed that prey availability is not a limiting factor for its habitat suitability in Central and Southern Europe.

Habitat suitability modeling has become a common conservation management tool to analyze and predict suitable habitat for a range of species including mammals, other vertebrates and invertebrates as well as plants and other organisms (Guisan et al. 2013, Morrison et al. 2012). Various modeling methods exist (e.g. Maxent, ENFA, GARP etc.), but in general, they all involve evaluating the potential habitat of one or more species based on known occurrences (presence-only), sometimes absence data (presence-absence), and environmental conditions at those locations, to identify additional areas of suitable habitat with similar environmental conditions (Elith and Leathwick 2009).

One of the first habitat suitability models for lynx has been developed by Zimmermann and Breitenmoser (2002) using probability model for distribution in Swiss Jura Mountains. Later they adapted it and extended it over entire Jura Mountains (Zimmermann and Breitenmoser 2007). Schadt et al. (2002) used a new approach in habitat suitability modelling. They prepared habitat model using presence-absence data and logistic regression to formalize the relationship between environmental conditions and species habitat requirements in quantifying the amount of potential habitat. They generated a home range suitability model based on local radio-tracking data obtained from lynx in the French and Swiss Jura Mountains (a landscape similar to the Central Europe low mountain ranges in fragmentation and population density) and extrapolated the model to Germany. Zimmermann (2004) used Ecological Niche Factor Analysis (ENFA) modelling to predict the potential distribution of lynx in the Alps. The first factor, called marginality, accounted for 29 % of the total specialization and showed that lynx preferred forest, shrubs and herbaceous vegetation, but avoided areas of heterogeneous agriculture. The other three factors accounted for more specialization, mostly regarding distance to towns, heterogeneous agriculture, forest and open space frequencies.

Signer (2010) used an adapted habitat suitability model by Zimmermann and Breitenmoser (2007) for the Jura Mountains and extrapolated it over the Alps, which have a different relief and other environmental characteristics. Hence, the validity of the model for the Alps is questionable (Graf et al. 2006).

Skrbinšek (2004) made a habitat suitability model for Slovenian Alps and Dinaric mountains which we extrapolated (this paper) over entire range of Slovenia, Croatia, Bosnia and Herce-govina, NE Italy and border area with Austria (Fig. 1). The area encompasses the entire areal of re-introduced Dinaric population that is now recognized as Dinaric - SE Alpine population. We generated a home range suitability model based on methodology used by Schadt et al. (2002). They used telemetry data obtained from lynx in the French and Swiss Jura Mountains and evaluated with independent radio-tracking data from the low mountain range along the German-Czech border (Bufka et al. 2000) and from the Dinaric mountain range of southern Slovenia (Staniša and Huber 1997). We adapted the model to the updated environmental data and validated it with GPS and VHF telemetry data from Dinarics, as well as C1 and C2 data from lynx monitoring in Slovenia using Boyce index method (Boyce et al. 2002, Hirzel 2001, Hirzel et al. 2001, Hirzel et al. 2006) modified by (Skrbinšek, unpublished data). Our results indicate 16.300 km^2 of study area as high-quality habitat and additional 20.900 km^2 as still suitable habitat. Dinaric Mountains and SE Alps represent 11.400 km^2 and 9.500 km^2 of suitable habitat, respectfully.

Becker (2013) constructed lynx habitat suitability model using Maximum Entropy Species Distribution Modeling software (Maxent), a popular modeling software using a machine-learning algorithm to determine suitable habitat based on species occurrence and environmental data. This was first habitat suitability study that combined lynx presence data from the Jura Mountains and six locations in the Alps to assess suitable habitat for lynx throughout the entire Alpine region (Fig. 2). She used data of 102 different lynx from seven different study areas. She found that approximately 103.600 km^2 of suitable lynx habitat exists in the Alps, covering approximately 54% of the total Alpine Convention area and identified 22 patches of suitable habitat ranging from 400 to over 17.000 km^2, representing potential individual lynx subpopulations.
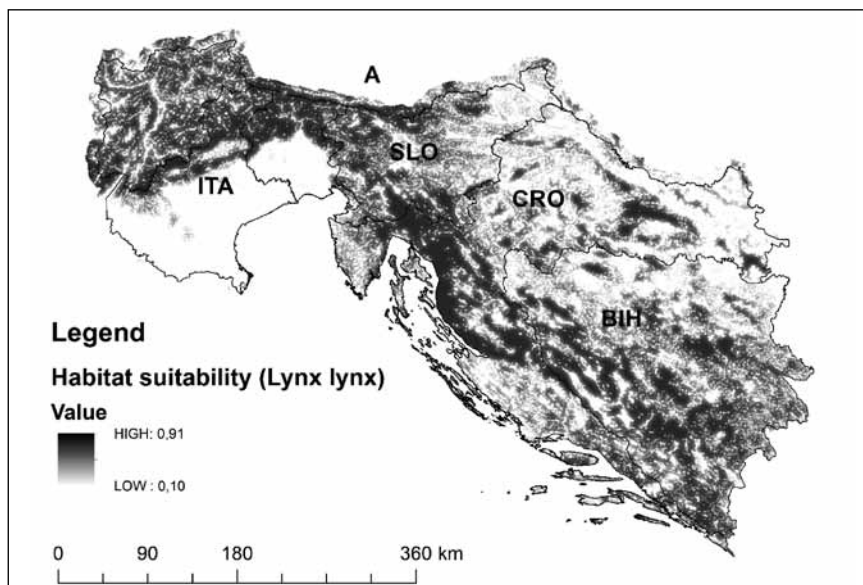
Figure 1: Habitat (home range) suitability map based on logistic regression model (after Schadt et al. 2002) and validated with GPS and VHF telemetry data from Dinarics in Slovenia, along with C1 and C2 presence data from lynx monitoring in Slovenia (SCALP methodology).

Slika 1: Karta primernosti habitata izračunana s pomočjo modela logistične regresije (po Schadt in sod. 2002), validiranega s podatki GPS in VHF telemetrično spremljanih risov iz Dinaridov v Sloveniji ter C1 in C2 podatki monitoringa risa v Sloveniji (po metodologiji SCALP).
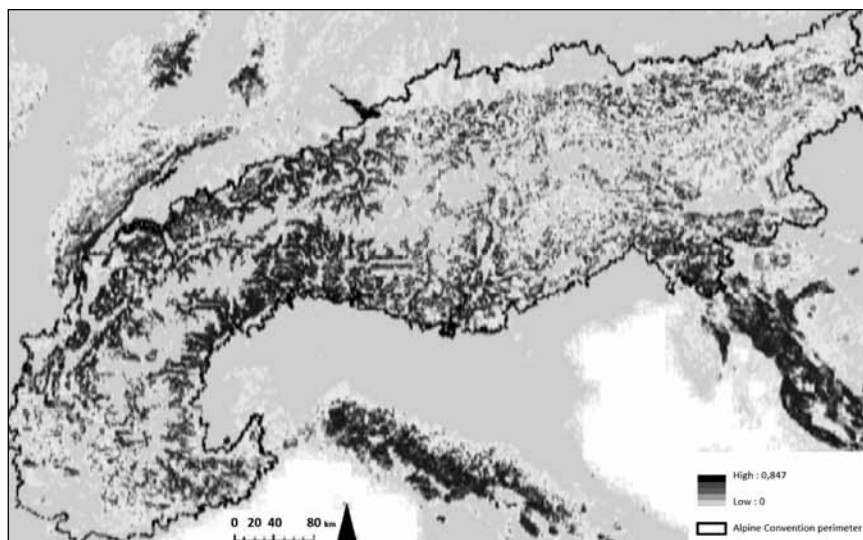
Figure 2: Lynx habitat suitability map for the Alps and adjacent regions based on Maxent model by Becker (2013). Dark colour, highly suitable habitat; light colour, unsuitable habitat.

Slika 2: Model primernosti habitata za risa na območju Alp in okoliških regij izdelan po metodi Maxent (Becker 2013). Temna barva, zelo primeren habitat; svetla barva, neprimeren habitat.
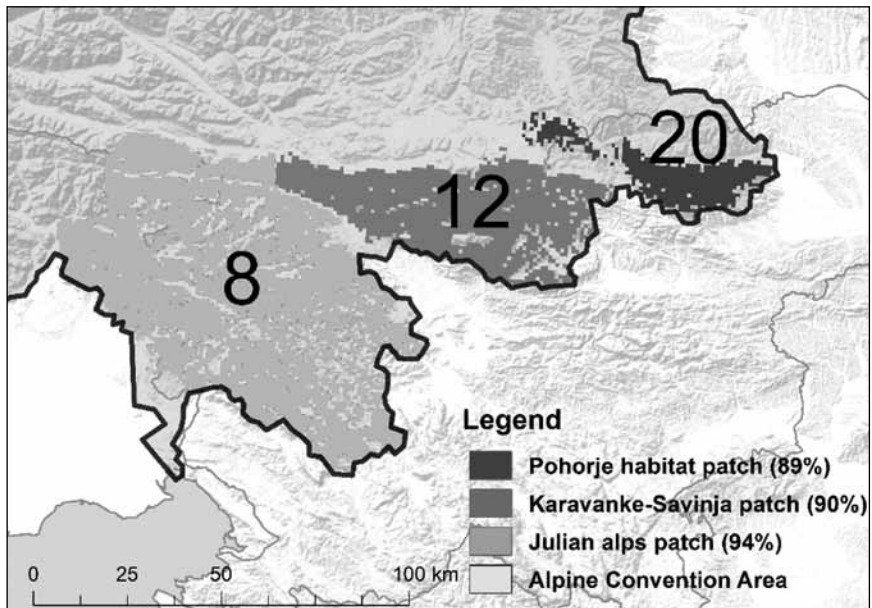
Figure 3: Relative size of three habitat patches of suitable lynx habitat from Slovenian Alpine area according to our model compared to the sizes from MaxEnt model (Becker 2013) for the same habitat patches numbered 8, 12 and 20. The patches cover regions of Julian Alps (Nr. 8), Karavanke - Savinja Alps (Nr. 12) and Pohorje (Nr. 20). The sizes of suitable habitat in our model corresponds to 94%, 90% and 89% of the Becker's (2013) habitat patch sizes.

Slika 3: Relativna velikost območij, kjer je primeren habitat za risa v slovenskem alpskem prostoru po našem modelu v primerjavi z modelom MaxEnt (Becker 2013) za iste habitatne krpe označene s številkami 8, 12 in 20. Habitatne krpe pokrivajo območja Julijskih Alp (št. 8), Karavank - Savinjskih Alp (št. 12) in Pohorja (št. 20). Velikosti primernega habitata v našem modelu ustrezajo 94 %, 90 % in 89 % velikosti habitatnih krp habitatnega modela, ki ga je izdelala Becker (2013).

The model shows very similar pattern of lynx suitable habitat areas with hotspots in Dinaric Mountains and in the Alpine area (Becker 2013) to our habitat suitability model. We also compared the sizes of three suitable lynx habitat patches stretching into the Slovenian Alps with sizes of corresponding areas in our model (Fig. 3). The patches cover regions of Julian Alps (Nr. 8), Karavanke - Savinja Alps (Nr. 12) and Pohorje (Nr. 20). The sizes of suitable habitat in our model corresponds to 94%, 90 and 89% of the Becker's habitat patch sizes, which indicates similar results of both models, however, slightly smaller size of suitable habitat seems our model a bit more conservative.

Habitat connectivity

Habitat loss and excessive fragmentation is a well-documented threat to wildlife (e.g. Andrén 1994, Hagan et al. 1996). As habitat is reduced, wildlife populations decrease in size and become more isolated. The extinction risks may be reduced by rescue effect due to dispersal between local populations (Hanski et al. 1996). Connectivity between suitable habitat patches depends on the number of dispersers available in the population, the distance between the source and the target populations, and the dispersal ability of the species under consideration (Wiens 1997).

The Central and South-Eastern European lynx populations are relatively isolated, and only limited movement occurs between some populations (Zimmermann and Breitenmoser 2007, Potočnik et

al. 2009). In the fragmented mountainous regions of the Alps and Dinarics dispersal is constrained by barriers including high mountain peaks, deep valleys, canyons and glaciers, fenced highways, large rivers as well as settlements, agricultural, industrial and other urban areas. The ongoing refugee crisis in Europe has seen many countries rush to construct border security fencing to divert or control the flow of people (Linnel et al. 2016). The process of border fencing can represent an important additional threat to wildlife because it can cause additional fragmentation of habitat, reducing its connectivity and lower effective population size.

Several studies have modeled lynx habitat connectivity in central Europe, using different methodologies (e.g. Zimmermann 2003, Schadt et al. 2004, Zimmerman 2004, Becker 2013, Magg et al. 2016). Zimmermann (2003, 2004) evaluated the habitat connectivity for the lynx in the Alps in order to reveal the suitable habitat patches (subpopulations), their potential size and connections between them. Connectivity was calculated in the GIS using a friction grid and a cost distance function. The results of the cost distance analysis showed that all 37 patches were within the range of dispersal cost of subadult lynx moving through unfavourable habitat. However, experience suggests that only few dispersers will cross unsuitable areas and anthropogenic linear barriers such as fenced highways.

Becker (2013) also evaluated habitat connectivity for lynx in the Alps. Firstly, she created a map of suitable habitat in Maxent and used ArcGIS RegionGroup to assign each cell to a connected region (see Becker (2013) for more details). Secondly, based on assumed barriers including major highways, rivers, and areas of high elevation she divided these regions into 32 habitat patches. Lastly, patches smaller than 400 km2 were discarded, resulting in 22 patches considered large enough to support lynx subpopulations.

Similar to Zimmermann (2004), Magg et al. (2016) calculated least-cost paths based on a resistance (friction) grid to assess the connectivity between suitable habitat patches in Bohemian - Bavarian lynx population. They assigned resistance grid values within the range of the inverse habitat suitability. Generally, the biggest anthropogenic barriers between different lynx habitat patches

were highways followed by other large urban settlements, main roads, and municipal roads. They pointed out that not habitat suitability, but habitat connectivity is limiting distribution of the Bohemian-Bavarian lynx population.

Kramer-Schadt et al. (2004) introduced an individual-based spatially explicit dispersal model to assess the probability of a dispersing lynx reaching another suitable patch in the complex heterogeneous German landscape. Results of the modeling revealed that most of the suitable patches could be interconnected by movements of dispersing lynx within 10 years of reintroduction or recolonization. However, when realistic levels of mortality risks on roads were applied, most patches became isolated except ones along the German-Czech border. Consequently, patch connectivity was limited not so much by the distribution of dispersal habitat but by the high mortality of dispersing lynx. Accordingly, they suggest that rather than solely investing in habitat restoration, management efforts should try to reduce road mortality, too.

Movement

Movement is one of the most studied yet least understood concepts in ecology and evolutionary biology. It has been considered as a glue cementing subpopulations and allowing connections between usually isolated populations (Waser et al. 2001, Wiens 2001). Movements have consequences for individuals as well as for populations and communities, and their effects on inclusive fitness are ultimately the selecting forces for dispersal, migration, exploration, and other types of movement that affect the distribution, abundance, and dispersion of individuals (Clobert and Wolff 2001).

Understanding animal movement is fundamental to interpret spatial-temporal patterns of habitat selection, foraging behavior, and the interactions between predator and prey (Bell 1990). Animal movements are influenced by intrinsic physiological factors (e.g., hunger and reproduction) and the sensory capabilities of organisms. Spatial structure also influences movement as long as there is a perceived difference in quality of the varying cover types as individuals search for resources such as food, mates, or den sites or use different

cover types to avoid intraspecific and interspecific agonistic encounters (Zollner and Lima 1997).

Eurasian lynx movements are related to the needs of foraging, mating and rearing of young. Despite its relatively small size, this species uses large home ranges, therefore their moving paths are longer, too (Schmidt et al. 1997). The movement paths of an individual arise from sequential decisions regarding their needs and perceptions of the surrounding habitat, and it is these decisions that ultimately give rise to the functional connectivity of the landscape (Tracey et al. 2013). Eurasian lynx is highly territorial species and if individuals are to maintain their rights to a territory, they need to move fast and widely enough to advertise their presence over as much area and in as short intervals as possible.

Jędrzejewski et al. (2002) made a research on Eurasian lynx movement patterns in Białowieża Primeval Forest (Poland). A total of 18 lynx (6 adult males, 5 adult females, 2 subadult males 1 subadult female and 4 kittens) were captured and radio collared.

Adult males moved the longest distances, whereas non-reproductive females moved the shortest distances (Tab. 1). Females with kittens moved significantly longer distances than single females. The longest uninterrupted movement of lynx (male) covered 31 km during which it covered up approximately 18% of its home range only (Jędrzejewski et al. 2002). The ratio between straight-line distances (SLD) and daily

median distances (DMD) was significantly higher in males than in females with kittens, which indicates that males moved in a different manner than females. Males moved more directly as they covered longer routes than females, which moved more intensively, but their movements were more concentrated and they stayed relatively close to the place visited on a previous day (Jędrzejewski et al. 2002). Compared to solitary male lynx, females must encounter more prey to meet their energy demands and those of their kittens, which accompanied them on 100% of movement paths (Fuller et al. 2010). Okarma et al. (1997) reported that males were on average killing 1,5 times fewer deer per time unit than females with kittens.

There is much evidence that predators adjust their circadian rhythm of activity to that of their main prey (Curio 1976, Ferguson, et al. 1988). The synchronization of predator and prey activity would occur more closely in species that rely on small or medium-sized prey which rest hidden in burrows. This prey is detectable mainly when moving outside the burrows. Lynx main prey are ungulates, which do not use burrows to rest. In Białowieża Primeval Forest, snow-tracking revealed lynx's successful attacks on both feeding or lying roe deer (Jędrzejewski et al. 1993). Thus, it is not the pattern of prey activity but the conditions that increase its vulnerability (Schmidt 1999).

GPS tracking in Dinaric mountains revealed movements of the lynx were primarily affected by daytime period, time since the last kill/den

Table 1: Daily movement distances (DMD) and straight-line distances (SLD) for radio-tracked *Lynx lynx* in Białowieża Primeval Forest. N, number of individuals; SD, standard deviation. (Jędrzejewski et al. 2002).

Tabela 1: Skupna dnevna prepotovana razdalja (DMD) in dnevni premik (SLD) evrazijskih risov v gozdu Białowieża. N, število osebkov; SD, standardna deviacija. (Jędrzejewski in sod. 2002).

	DMD (km)		SLD (km)	
Sex/age group of lynx	Mean ± SD	(min-max)	Mean ± SD	(min-max)
Adult males (N = 5)	9.0 ± 7.0	0 – 24.8	3.3 ± 3.2	0.7 – 2.5
Females with kittens (N = 4)	6.8 ± 4.3	0 – 18.6	1.5 ± 1.8	0.4 – 1.7
Females (N = 3)	3.7 ± 4.1	0 – 11.8	1.4 ± 1.6	0.8 – 1.9
Subadult males (N = 2)	7.4 ± 4.6	0 – 18.4	2.0 ± 2.1	0.5 – 2.0
Kittens (N = 3)	5.8 ± 2.9	0.9 – 10.3	1.9 ± 1.8	0.7 – 1.4
All lynx (N = 17)	7.2 ± 5.6	0 – 24.8	2.3 ± 2.7	0.4 – 2.5

translocation, lynx demographic category, and their interactions (Krofel et al. 2013). The lynx tended to stay closer to the prey immediately after the kill, but were found increasingly further away, especially during the day, as the time progressed. This effect was especially pronounced in the females with immobile kittens, but was practically nonexistent in the subadult male. There was a notable difference in movement pattern of female lynx during consumption process in period of denning (Krofel et al. 2013). While their kittens were immobile, the females were frequently found further away from the kill compared to when they were alone or had mobile kittens, as they kept regularly returning to the den site. This was particularly the case during daytime, when the females spent a lot of time at the den site.

Jędrzejewski et al. (1993) recorded longest lynx distances (mean 14 km, SD = 3,4 km) during the days when they made no kill. The distances in all consecutive days after making a kill were significantly shorter. Straight-line distances between consecutively killed prey varied from 2.9 km in reproducing female lynx to 6.4 km in adult males. In male lynx these distances were longer in mating season, whereas in females they were longer during the period of kitten's high mobility.

The influence of snow on Eurasian lynx movements is not clear, although there is information that snow conditions could affect their movements and subsequent predation success and distribution, especially for adult females with kittens (Pullianen 1995, Pulliainen and Hyypiä 1975, Haglund 1966), as it shown in Canada lynx (Murray and Boutin 1991, Stenseth et al. 2004).

Home range

A home range is the area in which an animal lives and moves on a periodic basis. It is among the most basic of ecological parameters that is regularly described for a given species. An understanding of the requirements for use of space is fundamental for species management and conservation (Schwartz 1999). Furthermore, home

Table 2: Minimum Convex Polygon (100%) home range estimates for adult Eurasian lynx in different sites in Europe. Some authors also provided 95% Kernel method home range estimates.
Tabela 2: Velikost domačih okolišev evrazijskega risa različnih območjih v Evropi ocenjena z metodo minimalnega konveksnega poligona z uporabo vseh lokacij (100% MCP) in kernelsko metodo (95% Kernel).

Study site	No. of animals		100% MCP home range size [km²]		95% Kernel home range size [km²]		Reference
	Male	Female	Male	Female	Male	Female	
Sarek, Sweden	8	21	709	407	431	251	Linnell et al. 2001
Northwestern Alps, Switzerland	11	12	159	106	/	/	Breitenmoser-Wursten et al. 2001
Hedmark, Norway	7	10	1456	832	886	535	Herfindal et al. 2004
Białowieża Primeval forest, Poland	5	3	248	133	235	152	Schmidt et al. 1997
Swiss Jura, Switzerland	3	5	264	168	/	/	Breitenmoser et al. 1993
French Jura, France	3	5	258	150	/	/	Stahl et al. 2002
Nord-Trøndelag, Norway	3	2	1515	561	1719	235	Linnell et al. 2001, Sunde et al. 2000
Akershus, Norway	2	2	812	350	/	/	Herfindal et al. 2004
Bergslagen, Sweden	4	1	632	307	305	97	Linnell et al. 2001
Vosges mountains, France	3	1	235	516	/	/	Schmidt et al. 1997
Kočevje, Slovenia	2	2	200	177	/	/	Huber et al. 1995
Slovenian Dinarics	3	7	222	178	306	217	This study
Average			562	313			

range size is one of the most important parameters in producing population estimates. It is important to know how much space individuals need when estimating potential carrying capacities to plan conservation or recovery programs (Schmidt et al. 1997). Home range size is not easy to determine. One big problem is that home ranges vary greatly between interspecific and intraspecific samples. While some interspecific variations in home range can be explained in body mass and feeding styles (Guarino, 2002) in many cases patterns of space-use within species vary by factors of 10 to 1000 (Gompper and Gittleman 1991). Another problem is variety of concepts, methodologies and estimators used to determine home ranges within and between species. The simplest estimator of a home range from a set of location data is the minimum convex polygon (MCP) (Mohr 1947) that has been widely used in Eurasian lynx studies, although it has many drawbacks including often overestimating the size of home ranges (Burgman and Fox 2003). The other estimators, especially in more recent studies, that have been frequently employed for constructing utilization distribution home ranges in lynx are the so-called (fixed or adaptive) kernel density estimators (Worton 1989, Burgman and Fox 2003). We collected these estimators for lynx home range data from different studies across Europe and added lynx home range size estimates obtained in our previous studies and conservation projects in Dinarics in Slovenia (Tab. 2). In 2003 we equipped first lynx with GPS collar in the Dinaric region. Since then we collared 8 more lynx (3 males and 5 females) in Slovenian Dinarics.

Schmidt et al. (1997) obtained data on home range sizes of different demographic categories of Eurasian lynx in Białowieża Primeval forest, Poland. They studied the effects of different parameters like age, sex, season and sociality on home range variation (Tab. 3). They therefore divided monitored individuals into four groups: (1) adult males (body mass > 19 kg), (2) adult females (only females with kittens), (3) subadult males of known age < 2.5 years (Kvam 1991) or body mass < 15 kg, and (4) subadult females less than 2 years old (Kvam 1991) or weighing up to 15 kg and not accompanied by kittens.

The results showed that sex of lynx was most important variable affecting home range size, following by time of monitoring, and number of localizations. In adult males, a notable growth in the utilized area was found in December-January, i.e. the pre-mating season (increase by 94% compared to October-November range) and February-March, i.e. the mating season (increase by 36%). There were no data for subadults in December-March, when the increase of the adult's home ranges was largest. In reproducing adult females, the most conspicuous change occurred in May -June, when the area utilized decreased by 81% in comparison to November-December. Female home ranges were largest in January-February (39% increase) (Schmidt et al. 1997). Lynx is territorial species, so one of important parameters defining home range size is the social status of individuals. Schmid et al. (1997) studied overlap of home ranges and identifying parameters that influence it. The results showed that home range overlap among lynx depended mainly on

Table 3: Minimum Convex Polygon (100%) average yearly and seasonal home range estimates for different Eurasian lynx age groups in Białowieża Primeval forest, Poland.
Tabela 3: Povprečna velikost celoletnih in sezonskih domačih okolišev evrazijskega risa v pragozdu Białowieża na Poljskem. Velikost je ocenjena z metodo MCP (100 %).

| | Home range [km²] | | |
	Average	Autumn/Winter	Spring/Summer
Adult male	248	165	143
Adult female	133	94	56
Subadult male	199	65	67
Subadult female	85	65	71

the age and sex of the individuals. The average overlap of home range among males was 30%. The most extensive overlap (75%) was between the home ranges of adult and subadult males. The average home range overlap between adult females was 29%. Except for females with kittens, the lynx usually avoided contact with conspecifics. Adult males were always found > 1km away from each other. The average distance between simultaneously radio-tracked males was 11.6 km, however the distance between females was shorter (8.1 km). The nearest females were 0.5 km apart (Schmidt et al. 1997).

Many authors suggest that intraspecific variation in home range size is highly correlated with food/prey availability (Sandell 1989, Powel et al. 1997, Girgione et al. 2002). However, estimating the availability of food and prey can be both difficult and expensive in the field and it is desirable to employ indirect methods that could explain some of the existing variation in home range size (Herfindal et al. 2005). Throughout their range in Europe home range sizes of lynx vary by a factor of 10 (Linnell et al. 2001, Jedrzejewski et al. 2002). In initial attempts to compare home range size between populations, researchers generally used latitude as a simple measure of variation in environmental productivity (Buskirk and McDonald 1989, Gompper and Gittleman 1991). However, Herfindal et al. (2005) stressed that this is not the best method, as it does not take the effect of altitude and oceanic influence into account. They tried to explain variations in home range using FPAR index. It reflects the fraction of incident photosynthetically active radiation absorbed by the green leaves and has been used as a measure of net primary production (Sellers et al. 1997). Herfindal et al. (2005) study was trying to explain this variation in terms of available indices of prey density and environmental productivity. On the individual level they explored Eurasian lynx home range variations compared to roe deer density in south-eastern Norway, which is rarely demonstrated through quantification of prey density within home ranges for carnivore species. They used hunting statistics as an index of variation in prey density assuming that roe deer harvest reflected population density. Results showed significant decrease in home range size of lynx with increasing roe deer density. On a European level, they related home range sizes of 111 lynx from 10 study sites to estimates derived from remote sensing of environmental productivity and seasonality. Results of multivariate regression models indicated a clear relationship between lynx home range size and study area productivity. Although there is no independent data that relates productivity directly to prey density one can reasonably assume that such relationship exists.

The analyses also revealed that for a given prey density/productivity, males had larger home ranges than females (Herfindal et al. 2005). It probably reflects both the larger body size of the male lynx and the predicted sex differences in reproductive strategies of the sexes (Sandell 1989). Sandell (1989) also predicted that female home range size should closely follow prey density, but that at some point male home range size should increase more rapidly due to a change in mating tactics and abandon territoriality. However, lynx males remained territorial at any point of density of prey or female lynx (Herfindal et al. 2005).

Dispersal

Dispersal is any movement of individual organisms in which they leave their home area, sometimes establishing a new home area. It is a crucial parameter in population dynamics, especially in threatened subpopulations within a meta-population (Levins 1970, Hanski 1999). Dispersal alone can help a population recover, if the reasons for the decline were demographic or genetic. Ultimate mechanisms that most likely affect dispersal are environmental variation and demographic structure. The proximate mechanisms include genetics, competition, individual fitness, and (breeding) habitat selection. These act via the fitness traits of survival and reproduction. If dispersal enhances these functions, it will be selected for independently of whatever proximate factors may serve to trigger it (Shields 1982). Another evolutionary issue is the fitness that often follows successful colonization of empty habitat or the discovery of new habitat beyond the species' current range. Possibility of inbreeding or outbreeding depression are also potential concerns (Shields 1982). A final evolutionary issue concerns the maintenance of an appropriate level

of genetic variability in a population (e.g. Cooper and Kaplan 1982). This is often considered a population level process involving the long-term probability of demic survival and reproduction. We can distinguish breeding dispersal i.e. the subsequent movement between sites or groups and natal dispersal i.e. the movement an individual makes from its birth site or previous breeding site to the site where it potentially reproduces (Zimmermann 2004). Ultimate factors are the selective forces that shape the evolution of the behavior. Main factors that drive individual into a dispersal are: genetic predisposition to disperse, local population density, habitat change, age of individual, reproductive status and perturbation (Zimmermann 2004). The decision to stop dispersal may involve various elements of habitat selection or patch choice, such as conspecific attraction, habitat quality or physiological factors (Wiens 2001).

The chances for successful dispersal depend on the connectivity of the landscape and is consequently decreased in intensively used landscapes i.e. matrix by barriers mostly imposed by humans, such as transportation infrastructure and the loss of suitable habitat (Schadt et.al. 2004). Dispersal allows a species to recolonize former habitats after severe range depression. Natal dispersal rate and dispersal distances are generally male biased in mammals and female biased in birds (Greenwood 1980, Dobson 1982, Clarke et al. 1997). However, the significance of dispersal for the spread of a population is less obvious in felids. Natal dispersal patterns are generally male biased for large solitary felids (Smith 1993, Beier 1995, Maehr et al. 2002), whereas the patterns are less clear among the four species of the *Lynx* genus, with no clear patterns within species and findings ranging from male biased dispersal (Mowat and Slough 1998, Mowat et al. 2000, Schmidt 1998, Janečka et al. 2007) to male and female lynx dispersing equally far and with equal frequency (O'Donoghue et al. 1997, O'Donoghue et al. 1998, Ferreras et al. 2004, Zimmermann et al. 2005, Campbell and Strobeck 2006).

A study comparing dispersing lynx from populations in the Nordics, Baltics, and Dinaric Mountains as well as Central Europe found that the mean dispersal distance was 39 kilometers, and 68% of dispersing lynx settled within

50 kilometers (Molinari-Jobin et al. 2010). Lynx tend to establish home ranges adjacent to those of other lynx (Zimmermann et al. 2005), which affects their likelihood of establishing new colonies. Thus, while a lynx population may expand in spatial size, solitary lynx are unlikely to disperse and establish entirely new, separate populations (Zimmermann et al. 2007).

A comprehensive research on the spatio-temporal behaviour of subadult lynx in two re-introduced populations was carried out in Switzerland between 1988 and 2001 (Zimmermann 2004, Zimmermann et al. 2005, Zimmermann et al. 2007). The study was based on telemetry and other data for 39 juvenile lynx; 22 in the north-west Swiss Alps and 17 lynx in Jura Mountains. The lynx became independent at the age range from 9.3 – 10.6 months (there was no significant difference between males and females). Subadult lynx separated from their mother 91 - 100 days after the beginning of the year (first decade in April). Mothers mostly left their kittens at the edge of their territory by undertaking excursions on the other side of their territories or even out of their home range. In most cases the mother seemed to have left the juveniles. The cause of separation may be the sense of the female that she is not able to kill enough prey for her kittens (Molinari and Molinari-Jobin 2001). Different aspects of the spatio-temporal behavior suggest that disintegration of litters of the free-ranging lynx is not caused by female parent aggression as pointed out by Stroganov (1962) and later by Jonsson (1984). After the separation, the subadults usually stayed a few days close to the place where the separation occurred and then moved on (Zimmermann 2004). The mean distance made by lynx that completed dispersion was 68.8 km (N = 7) in the one study area and 21.4 (N = 12) in the other. In both areas no difference between sexes was observed for centroid, total or maximum dispersal distances whichever dispersal category was considered (Zimmermann et al. 2007).

Dispersing lynx were recovered mean = 41.2 km (N = 14) (in Jura Mountains) and mean = 24.3 km (N = 13) (in North Western Swiss Alps) away from their point of origin. However, expressed in relative units as the mean circular resident female's and male's home range diameters, the median recovery distance in the North-West Swiss Alps was

2.0 (range 0.4-5.6) times the mean circular resident female's home range diameter and 1.4 (range 0.3-3.8) times the mean circular resident male's home range diameter. In the Jura Mountains, it was 2.0- (range 0.1-6.6) and 1.5- (range 0.1-5.1) times the respective means (Zimmermann et al. 2007). For some subadults (N = 5) the researchers were able to document a transient home range but most subadults established a definitive home range directly after their dispersal. Subadults from the north-west Swiss Alps and the Jura Mountains appeared to have the same dispersal potential as there were no observed differences between the two areas in the total and maximum distances dispersed. However, a larger proportion of individuals in the north-west Swiss Alps, all males, moved through unfavourable habitat but all stopped at fenced highways and turned back, except one male, which left the area. The apparent

reduced ability of subadults to cross barriers led to circular dispersal (Zimmermann et al. 2007). Within the study, they did not detect any positive density dependent effects in lynx dispersal and hence could not confirm the hypothesis that high population density encourages the expansion of the population.

Similar study of various aspects of lynx natal dispersal was carried out in Scandinavia by comparing dispersal patterns of 120 radio-marked lynx in two study areas in Sweden (Sarek and Bergslagen areas) and two study areas in Norway (Hedmark and Akershus areas, Samelius et al. 2012). They found, contrary to the Swiss study, that male lynx dispersed farther than female lynx with mean dispersal distances of 148 and 47 km for male and female lynx that were followed to the age of 18 months or older. In fact, female lynx often established home ranges that overlapped or

Table 4: Mean age at separation from mothers and mean dispersal distance for lynx in Jura Mountains, North-western Alps (CH), Sarek and Bergslagen (SWE), Hedmark and Akershus (NOR). Date of the birth in Jura Mountain and Northwestern Alps was estimated as the mean birth date of all known births, while 1ˢᵗ of June was assumed as date of the birth for other study areas. Researchers used the arithmetic center of the area for starting and finishing point to calculate the distance of dispersal.

Tabela 4: Povprečna starost mladičev ob ločitvi od samice in povprečna dolžina disperzijske poti risov v Jurskem pogorju, Severozahodnih Alpah (CH), Sareku in Bergslagnu (SWE), ter Hedmarku in Akershusu (NOR). Datum kotitve risov v Jurskem Pogorju in Severnozahodnih Alpah je podan kot povprečje vseh znanih datumov iz predhodnjih raziskav, za ostala območja pa je datum kotitve 1. junij. Raziskovalci so za lokacijo začetka in konca disperzije določili središče domačega območja.

Lynx pop.	Gender	Age at separation from mother [days]	Dispersal distance [km]	Reference
Jura Mountain (CHE)	M + F	330.9 (N = 14)	41.2 (N = 14)	Zimmermann et al. 2005
Northwestern Alps (CHE)	M + F	413.6 (N = 13)	24.3 (N = 14)	Zimmermann et al. 2005
Sarek, Sweden	M	303 (N = 14)	130 ± 82 (N=11)	Samelius et al. 2012
Sarek, Sweden	F	276 (N = 10)	47 ± 19 (N=21)	Samelius et al. 2012
Hedmark, Norway	M	288 (N = 7)	136 ± 72 (N = 5)	Samelius et al. 2012
Hedmark, Norway	F	297 (N = 8)	69 ± 107 (N = 5)	Samelius et al. 2012
Akershus, Norway	M	285 (N = 2)	83 ± 34 (N = 4)	Samelius et al. 2012
Akershus, Norway	F	300 (N = 1)	15 ± 23 (N = 4)	Samelius et al. 2012
Bergslagen, Sweden	M	255 (N = 4)	205 ± 69 (N = 9)	Samelius et al. 2012
Bergslagen, Sweden	F	249 (N = 11)	47 ± 19 (N = 19)	Samelius et al. 2012
Mean	M	282.75 (N = 27)	138.5 (N = 29)	
Mean	F	280.5 (N = 30)	44.5 (N = 49)	
Mean		299.75	79.75	

partly overlapped that of their mothers. Similarly, the dispersal rate was greater among male lynx than among female lynx, with 100% of the males dispersing compared with 65% of the females dispersing.

The central and south-eastern European lynx populations are relatively isolated, and only limited movement occurs between some populations (Zimmermann and Breitenmoser 2007, Potočnik et al. 2009). In the fragmented mountainous regions of the Alps and Dinarics dispersal is constrained by barriers including high mountain peaks, deep valleys, canyons and glaciers, fenced highways, large rivers as well as settlements, agricultural, industrial and other urban areas. The ongoing refugee crisis in Europe has seen many countries rush to construct border security fencing to divert or control the flow of people (Linnel et al. 2016). The process of border fencing can represent an

important additional threat to wildlife because it can cause additional fragmentation of habitat, thus reduce its connectivity and lower effective population size.

Among Eurasian lynx re-introduction pro-grams in Europe in the 1970s, three male and three female lynx were translocated from Slovakia and released in the northwestern Dinarics in Slo-venia in 1973. Although little experience and no guidelines were available for carnivore recovery programs (Breitenmoser et al. 2001), data on signs of presence like sightings, reproduction events, scats, prey kills, attacks on domestic animals and mortalities were collected opportunistically but recorded systematically, both in Slovenia and Croatia (Čop and Frković 1988). Thus, the monitoring was mainly oriented in collection of spatial distribution of lynx signs of presence and on recording of dead (culled) lynxes. The founder
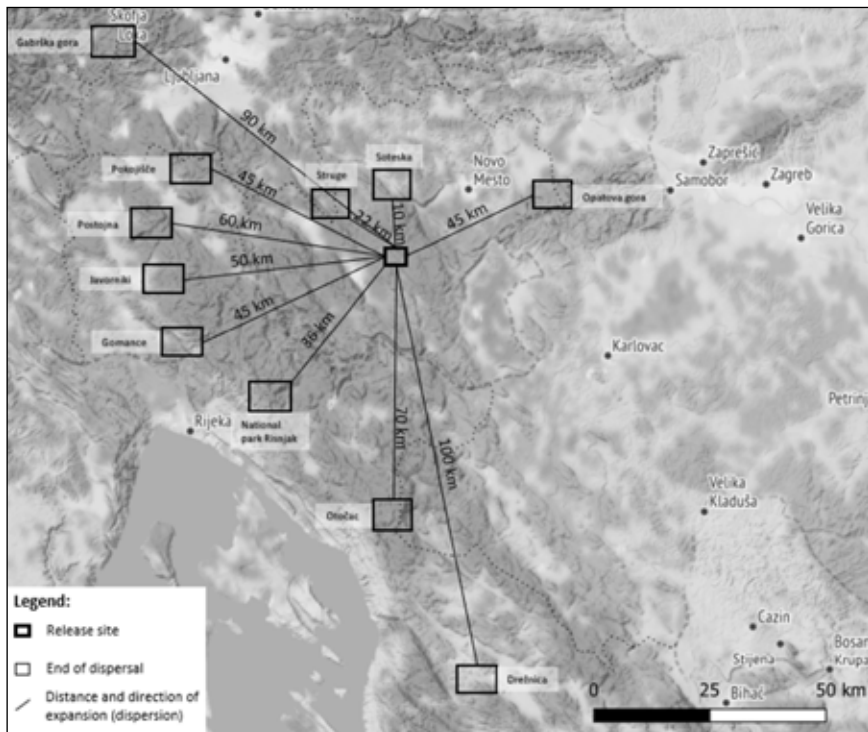
Figure 4: Dispersal of lynx released in Kočevski rog between 1973 and 1981 (modified after Čop and Frkovič 1988) (map source: © *Stamen Design).*
Slika 4:   Disperzija risov od mesta izpusta v Kočevskem Rogu med leti 1973 in 1981 (prirejeno po Čop in Frkovič 1988) (vir kartografskih podatkov: © *Stamen Design).*

individuals established territories near the release site. Second year after the release, young lynx started to disperse into neighboring areas (Čop and Frković 1988). The monitoring data made it possible to follow the forefront of the expansion of the growing population in subsequent years. Eight years after the reintroduction young dispersing lynx or adult territorial lynx were recorded in all directions (but mainly along the Dinaric Mountains, at distances from 36 to 100 km from the release site (Čop and Frkovič 1988) (Fig. 4). Four decades after the reintroduction, it seems that the lynx dispersal was more successful towards southeast, along the Dinaric Mountains in Croatia and Bosnia and Herccegovina (BiH), than toward northwest, into the southeastern Alps in Slovenia, Austria and Italy. The maximum distance of recorded area of presence of lynx in BiH from the release site is around 390 km, while from the northwest (NE Italy) is around 140 km. The proximate cause for that is not clear, yet; however, it is obvious that fenced highway Ljubljana - Trieste represents an extremely strong barrier for dispersing lynx (Skrbinšek 2004). Given the apparent reduced ability of subadults, especially females, to cross the highway in almost a half of century after the reintroduction, it is unlikely that lynx will be able to spontaneously establish new reproductive area towards the SE Alps.

Conclusions

Conservation biology and conservation management rarely get a straightforward and clear answers for all the problems we may want to address. That is also the case for the habitat suitability modelling. Regardless of which methods and concepts are used creating habitat suitability models, they often reveal more questions to ask than to answer them. Different habitat suitability modelling approaches have proved to be useful according to the evaluation criteria established, but there may be no single "best" model or modelling concept.

We should highlight the need to carefully consider models' parameters and data input, which could be even more important in the future. Especially considering the fact that the use of GPS telemetry data (that is often clustered) for study-ing animals' movements and use of resources is expected to increase (Cagnacci et al. 2010). For future models, it would be useful to include lynx presence data from different populations/areas, which might expand the range of environmental conditions that lynx occupy, and thus contribute to a more comprehensive model (Becker 2013).

Another option could be to assess suitable lynx habitat using other modelling methods, e.g. an ensemble approach combining multiple methods or a spatially explicit individual based movement model. As a subsequent step, we could combine the GIS models (habitat and land tenure system of the lynx) with population viability considerations into meta-population models, and hence bring such theoretical approaches closer to the real world (Zimmermann 2004).

Habitat restoration is of little concern for the conservation of the Eurasian lynx as forest and shrubs have continuously increased since the eradication of the species at the beginning of the 20th century and seem to further increase as a consequence of the economic changes. Prey base is not a limiting factor either since roe deer, red deer or chamois, lynx's main prey, have re-colonized almost all suitable habitat in the Alps and Dinarics and are more abundant than ever (Apolonio et al. 2010).

Due to contradicting results, available field studies (Zimmermann 2004, Zimmerman et al. 2007, Samelius et al. 2012) haven't provided clear answers about possible male biased dispersal rate and distance in lynx as predicted in mammals (Greenwood 1980) although the study from Swiss Jura and the Alps did not reveal any sex bias. Dispersal directions and distances were shaped by the surrounding habitat, topography, as well as linear barriers (e.g. highways) (Zimmermann 2004). These outcomes have consequences for the calibration of individual based dispersal models: not only road mortality should be considered (see Kramer-Schadt et al. 2004), but habitat-type specific mortalities as well as the effect of linear barriers should furthermore be included. Such models have several clear advantages: among others, they force one to develop explicit hypothesis, to organize existing knowledge, and to estimate values for unknown parameters.

For reintroduced, small or recovering populations like Dinaric - SE Alpine population a metapopulation management in the form of translocating lynx from one habitat patch to another may be an alternative conservation tool. Such a management, reproducing dispersal, may be necessary if proved natural colonisation is hindered in increasingly fragmented landscapes of Europe.

Future considerations about suitable habitat for lynx should also include the impact of climate change. Mountainous environments are considered particularly at high risk, with significantly reduced snow depth and duration of snow-cover (Beniston et al. 2003) upward shifts of flora (Gehrig-Fasel et al. 2007) and risks of shifts of areals of new/alien predator/competitor species like golden jackals (*Canis aureus*) (Potočnik et al. 2019b) could impact lynx's predation and the amount of available habitat. Influence of human activities, like forest exploitation, game management and direct disturbance through recreation in forest ecosystems, lynx main habitat, should be taken into account while setting nature conservation strategies. Conservation efforts to protect corridor areas or reduce the impact of barriers remain important for the establishment of a viable Pan-European lynx metapopulation.

Povzetek

Evrazijski ris (*Lynx lynx*), nekoč razširjen po vsej Evropi, je v 18. in 19. stoletju izginil iz srednje in južne Evrope ter mnogih drugih delov celine kot posledica neposrednega preganjanja, izgube življenjskega prostora ob izsekavanju gozdov, širjenja obdelovalne zemlje in izrazitega zmanjšanja številčnosti prostoživečih parkljarjev (Breitenmoser 1998, Schadt in sod. 2002, Zimmermann 2003, Potočnik in sod. 2009). Izboljšanje ekoloških razmer v začetku 20. stoletja je bilo ugodno za vrnitev velikih zveri, zato so v 70. letih prejšnjega stoletja izpeljali nekaj ponovnih naselitev na območju Alp, eno pa so leta 1973 izvedli tudi v Dinaridih v Sloveniji. Do danes so se od naselitev ohranile risje populacije Jurskem pogorju v Švici, severozahodnih švicarskih Alpah, Dinaridih in v francoskih Alpah na območju Vogezov in Chartreuse (Breitenmoser 1998).

Velikosti teh populacij so se skozi leta spreminjale, vendar se po vzpostavitvi populacij njihova razširjenost z naravno kolonizacijo ni bistveno povečevala. Po teh naselitvah so rise leta 2001 preselili še v severovzhodno Švico (Ryser et al. 2004) in v Apneniške Alpe v Avstriji (2011-2013). Zdi se, da je sedanja razširjenost risov v srednji in jugovzhodni Evropi večinoma posledica vzpostavitve populacij omejenih na območja uspešnih ponovnih naselitev oziroma translokacij risov v preteklih desetletjih. Zato je prednostna naloga njihovega ohranjanja povezati obstoječe populacije risov v Alpah s populacijami v Juri in Dinaridih (Molinari-Jobin et al. 2003), potencialno pa tudi s populacijami v Vogezih, ob češko-nemški meji in na Balkanu ter dolgoročno, morda celo s Karpatsko populacijo (Evropska komisija 2013).

V prispevku predstavljamo pregled obstoječega poznavanja prostorskih zahtev in vedenja evrazijskega risa ter izpostavljamo prednosti in slabosti uporabljenih metod proučevanja. Poleg študij primernosti in povezljivosti habitata za risa je v prispevku tudi pregled značilnosti domačih okolišev in gibanja risov, vključno z disperzijo. Predstavljamo model primernosti prostora za risa, ki je bil izdelan za širše območje dinarske - jugovzhodne alpske populacije in primerjavo velikosti domačih okolišev risov iz Dinaridov v Sloveniji, ki so bili GPS-telemetrično spremljani med leti 2003 in 2020 z drugimi populacijami risov v Evropi.

Modeliranje primernosti prostora za posamezne vrste je postalo običajno orodje za varstveno upravljanje, za analizo in napovedovanje primernega habitata za številne vrste, vključno s sesalci, drugimi vretenčarji in nevretenčarji ter rastlinskimi vrstami in združbami. Enega prvih modelov primernosti habitata za risa sta razvila Zimmermann in Breitenmoser (2002) z uporabo verjetnostnega modela za območje Jurskega pogorja v Švici. Kasneje sta ga dopolnila in razširila na celotno območje Jurskih Alp (Zimmermann in Breitenmoser 2007).

Skrbinšek (2004) je izdelal model primernosti habitata za območje Slovenije, ki smo ga za namen te študije ekstrapolirali na območje celotne Slovenije, Hrvaške, Bosne in Hercegovine, SV Italije ter obmejno območje z Avstrijo. Območje zajema celotno širše območje ponovno naseljene

dinarske populacije, ki jo danes prepoznavamo kot dinarsko - jugovzhodno alpsko populacijo. Model smo razvili na osnovi metodologije, ki so jo uporabili Schadt in sodelavci (2002). Uporabili so telemetrične podatke risov spremljanih v francoski in švicarski Juri, model pa nato ovrednotili z neodvisnimi telemetričnimi podatki risov iz območja vzdolž nemško-češke meje (Bufka in sod. 2000) in iz dinarskega območja južne Slovenije (Staniša 1998). Njihov model smo prilagodili novim okoljskim podatkom in ga evalvirali z GPS in VHF telemetričnimi podatki, kot tudi podatki C1 in C2 monitoringa risov v Sloveniji (po Molinari in sod. 2003).

Becker (2013) je z uporabo programskega paketa »Maximum Entropy Species Distribution Modelling Model« (Maxent) izdelala model primernosti habitata risa za celotno območje Alp, ter del Dinaridov in Apeninov. Ugotovila je, da v Alpah približno 103.600 km^2 primernega habitata za risa, ki pokriva približno 54 % celotnega območja Alpske konvencije, znotraj katerega je opredelila 22 krp primernega habitata v velikosti od 400 do več kot 17.000 km^2, ki predstavljajo območja potencialnih sub-populacij risov. Model kaže zelo podoben vzorec primernega habitata na območju Dinaridov kot habitatni model, ki smo ga izdelali mi za območje dinarske-jugovzhodno alpske populacije. Primerjali smo tudi velikosti treh habitatnih krp (Becker 2013), ki se raztezajo v slovenske Alpe, in velikosti ustreznih površin v našem modelu in sicer za območja Julijskih Alp, Karavank - Savinjskih Alp in Pohorja. Velikosti primernega habitata v našem modelu ustrezajo 94 %, 90 % in 89 % velikosti habitatnih krp Beckerjevega modela. To kaže na podobne rezultate obeh modelov, vendar nekoliko manjša velikost krp primernega habitata v našem modelu nakazuje na njegovo nekoliko bolj konzervativno opredeljevanje prostora primernega za risa.

Povezljivost prostora za risa v srednji Evropi so modelirali v različnih študijah, v katerih so uporabljali različne metodološke pristope (npr. Zimmermann 2003, Schadt in sod. 2004, Zimmerman 2004, Becker 2013, Magg in sod. 2016). Zimmermann (2004) je povezljivost prostora za alpski prostor modeliral v GIS programskem orodju z uporabo frikcijskih rastrov (angl. friction grid) in funkcije stroškovnih razdalj (ang. Cost Distance Function). Rezultati analize

stroškovnih razdalj so pokazali, da je bilo vseh 37 evidentiranih habitatnih krp znotraj disperzijske razdalje odraščajočih risov, ki se gibljejo skozi neugoden življenjski prostor. Kljub temu pa so rezultati terenskih študij pokazali, da je v resnici povezljivost prostora veliko manjša, predvsem na račun linijskih barier (ograjenih avtocest), ki jih večina risov v disperziji ni uspela prečkati (Zimmermann in sod. 2007).

Prav tako je Becker (2013) je ocenila povezljivost prostora za risa v Alpah in opredelila 22 habitatnih krp. Povezljivost prostora je najprej izračunala s programskim orodjem ArcGIS RegionGroup, nato pa je večje habitatne krpe še subjektivno razdelila na več podregij na podlagi upoštevanja avtocest, velikih rek ali visokih gorskih grebenov kot razmejitvenih območij, ob predpostavki da bi risi tako velike ovire le redko prečkali.

Schadt in sod. (2004) so za preučevanje povezljivosti prostora in simulacijo uspešnosti disperzije risov uporabili individualni prostorsko eksplicitni model disperzije (IBSEDM), ki temelji na simulaciji verjetnosti posameznih osebkov v disperziji, da bodo dosegli sosednje primerne habitatne krpe. Model so aplicirali na kompleksno heterogeno nemško pokrajino. Ugotovili so, da bi risi, glede na svoje disperzijske sposobnosti večino primernega prostora kolonizirali v približno desetih letih. Ko pa so v modelu upoštevali tudi pričakovane stopnje smrtnosti risov ob prečkanju cest, je večina habitatnih krp ostala izoliranih, razen ob nemško-češki meji. Posledično se je izkazalo, da je bila povezljivost habitatnih krp bolj omejena z visoko smrtnostjo na cestah, kot z razdrobljenostjo in razpršenostjo primernega habitata. V skladu s tem so predlagali, naj se prizadevanja za varstveno upravljanje namesto zgolj v vlaganja v obnovo habitatov usmerijo tudi v ukrepe za zmanjšanje smrtnosti na cestah.

Gibanje risov v prostoru je povezano s potrebami po iskanju hrane, parjenju in vzreji mladičev. Kljub razmeroma majhni telesni velikosti pa ta vrsta uporablja velike domače okoliše, zato je tudi njihovo gibanje v prostoru zelo intenzivno (Schmidt in sod. 1997). Jędrzejewski in sod. (2002) so opravili raziskavo o vzorcih gibanja evrazijskih risov v pragozdnem območju Białowieża na Poljskem. Skupno so telemetrično spremljali 18 risov (6 odraslih samcev, 5 odraslih samic, 2 subadultna samca 1 subadultna samica

in 4 mladiči). Odrasli samci so se v povprečju premikali na največje razdalje, medtem ko so se samice, ki niso bile reproduktivne, premikale na najkrajših razdaljah. Samice z mladiči so se premakale na bistveno daljših razdaljah kot samice brez mladičev. Najdaljše neprekinjeno gibanje risjega samca je merilo 31 km, pri čemer je obhodil približno 18 % njegovega domačega okoliša (Jędrzejewski in sod. 2002).

Vpliv snega na gibanje evrazijskih risov ni jasen, čeprav obstajajo študije, ki nakazujejo, da bi snežne razmere lahko vplivale na njihovo gibanje ter na nadaljnji uspeh in razporeditev njihovega plenjenja, zlasti pri odraslih samicah z mladiči (Pullianen in sod. 1995, Pulliainen in Hyypiä 1975, Haglund 1966) Takšen vpliv snega je bil jasneje opažen pri kanadskem risu (*Lynx canadesis*) (Murray in Boutin 1991, Stenseth in sod. 2004).

Schmidt in sod. (1997) so pridobili podatke o velikosti domačih okolišev risov iz različnih demografskih kategorij (Białowieża, Poljska). Poskušali so prikazati učinke različnih parametrov, kot so starost, spol, sezona in socialnost na velikost in spreminjanje domačih okolišev. Izkazalo se je, da je spol risa najpomembnejša spremenljivka, ki vpliva na velikost domačih okolišev, temu je sledil čas spremljanja osebkov in število zbranih lokalizacij, ki so jih uporabili za izračun. V celotnem območju njihove razširjenosti v Evropi se velikosti domačih okolišev risov razlikujejo za faktor 10 (Linnell in sod. 2001; Jedrzejewski in sod. 2002) V začetnih poskusih primerjanja velikosti domačih okolišev med populacijami so raziskovalci na splošno uporabili zemljepisno širino kot preprost indikator gradienta okoljske produktivnosti (Buskirk in McDonald 1989, Gompper in Gittleman 1991). Kasneje so Herfindal in sod. (2004) pokazali, da ta spremenljivka ni ustrezna, saj ne upošteva vpliva nadmorske višine in regionalnih klimatskih pogojev. Njihovi rezultati multivariatnih regresijskih modelov so pokazali jasno povezavo med velikostjo domačega območja risa in produktivnostjo proučevanega območja. Čeprav ni neodvisnih podatkov, ki bi produktivnost okolja neposredno povezovali z gostoto plena, utemeljeno domnevajo, da takšna povezava obstaja.

Disperzija je vsako gibanje posameznega osebka, pri katerem zapusti domače območje, včasih pa ob tem vzpostavi novo domače območje (Levins 1970). Je ključni parameter v populacijski dinamiki, zlasti pri ogroženih subpopulacijah znotraj metapopulacije (Levins 1970, Hanski 1999).

Študija v kateri so primerjali disperzijske vzorce risov iz populacij v Nordijskih, Baltskih in Dinarskih gozdnih območjih ter iz srednje Evrope, je pokazala, da je bila povprečna disperzijska razdalja risov 39 kilometrov, 68 % risov, ki so dispergirali pa se je naselilo na območju znotraj 50 kilometrov (Molinari-Jobin in sod. 2010). Mladi risi tako pogosto vzpostavljajo domače okoliše na mestih, ki mejijo na območja drugih risov (Zimmermann in sod. 2005), kar pomembno vpliva na verjetnost vzpostavljanja populacij na novih območjih. Medtem ko se ob večanju populacija risov sicer lahko prostorsko širi, je verjetnost, da bodo posamezni risi dispergirali daleč stran in ustanovili povsem nove, ločene populacije zelo majhna (Zimmermann in sod. 2007).

Štiri desetletja po ponovni naselitvi risov v Dinaride v Sloveniji se zdi, da je bilo širjenje risov uspešnejše proti jugovzhodu, vzdolž Dinarska območja na Hrvaškem in v Bosni in Hercegovini (BiH), kot proti severozahodu, v jugovzhodne Alpe v Sloveniji, Avstriji in Italiji. Največja razdalja zabeleženega območja prisotnosti risa v BiH od mesta izpustov je približno 390 km, medtem ko je od severozahoda (SV Italija) približno 140 km. Zanesljivega odgovora za to sicer še nimamo; očitno pa je, da ograjena avtocesta Ljubljana - Trst predstavlja izjemno močno oviro za disperzijo risov iz dinarskega območja proti Alpam (Skrbinšek 2004).

Sodeč po dosedanjem poznavanju in izkušnjah bi morali v prihodnje vidike ohranjanja primernega življenjskega okolja risa vključevati tudi vpliv podnebnih sprememb. Gorska okolja veljajo za posebej ogrožena, pri čemer se globina in trajanje snežne odeje v zadnjih desetletjih močno zmanjšujeta (Beniston in sod. 2003), spreminja se naravna vegetacija (Gehrig-Fasel in sod. 2007) povečuje pa se tudi tveganje za spreminjanje in širjenje novih/tujerodnih plenilcev/kompetitorjev, kot je na primer evrazijski šakal (*Canis aureus*) (Potočnik in sod. 2019b). Vsi omenjeni dejavniki bi lahko pomembno vplivali tako na razpoložljivost prehranskih virov za rise, kot tudi na količino razpoložljivega ustreznega prostora zanje. Ne glede na to pa prizadevanja za ohranjanje območij in

koridorjev med habitatnimi krpami, zmanjševanje vpliva (zlasti) linijskih ovir (avtoceste) in, po potrebi, »imitacija« disperzije s premestitvami oziroma translokacijami osebkov ostajajo pomemben del varstvenih ukrepov za vzpostavljanje viabilne pan-evropske metapopulacije risa v Evropi.

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