The reintroduced Dinaric lynx population dynamics in PVA simulation,

The 30 years retrospection and the future viability

Modeli razvoja in analiza viabilnosti re-introducirane dinarske populacije risa,

30-letni pogled nazaj ter možnosti preživetja v prihodnosti

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Abstract. In the study, we modelled population dynamics of the reintroduced Dinaric lynx population. We used data obtained by monitoring to estimate population dynamics – spatial expansion, abundance estimates, and mortalities – since the reintroduction in 1973 and up to the present day, and then looked for demographic and habitat parameters that would provide the best fit of a lynx population model to this data. We tried to evaluate the importance of these parameters for future population dynamics and viability (PVA) of this lynx population. We constructed a number of 100-year simulations using a range of demographic parameters, different prey availabilities and simulating other potential human related factors that might affect the lynx population. We found that the reintroduced lynx population must have had high fecundity rates with more than 1.6 kittens survived per female and per litter to reach abundances over 100 individuals despite the high human related mortality. The elasticity analysis revealed that adult survival is by far the most important demographic parameter for the lynx population dynamics. PVA highlighted two important factors that had a major impact on population growth dynamics and related risk of population extinction: changes in the survival rates of subadult and adult individuals and, especially, the quality of habitat with regard to prey availability. Survival rates of subadult and adult lynx are directly influenced by human activities, mainly manifested through illegal shooting, and are difficult to control. Quite opposite to that, the quality of habitat with regard to prey availability can be directly influenced through management. Since habitat quality can have a significant role for the lynx population dynamic and viability, even in presence of minor, difficult to control changes in survival rates of subadults and adults, adequate prey species management might be one of the most important short-term conservation priorities.

Keywords. Eurasian lynx, *Lynx lynx*, population dynamics, PVA simulation, reintroduction, Dinaric region

Izvleček. V raziskavi smo zgradili modele populacijske dinamike ponovno naseljene populacije risa v Dinaridih. Pri oblikovanju modelov smo uporabili podatke, ki so bili pridobljeni pri spremljanju razvoja populacije od leta 1973 kot so: prostorsko širjenje, ocena številčnosti in smrtnost ter nato poiskali ustrezne demografske in prostorske parametre s katerimi smo dobili populacijski model, ki v največji meri ustreza zbranim podatkom. Poskušali smo oceniti pomen teh parametrov za razvoj in viabilnost populacije v prihodnje. Pripravili smo serijo simulacij 100 letne populacijske dinamike risa pri čemer smo variirali demografske parametre, razpoložljivost plena ter odsimulirali druge antropogene dejavnike, ki bi lahko vplivali na populacijo risa. Ugotovili smo, da je morala biti stopnja rodnosti ponovno naseljene populacije visoka z več kot 1.6

preživelih mladičev na samico. Le tako bi lahko populacija dosegla številčnost preko 100 osebkov ob hkratni visoki antropogeni smrtnosti risov. Analiza elastičnosti populacije je pokazala, da je preživetje odraslih osebkov daleč najpomembnejši demografski parameter, ki v največji meri vpliva na populacijsko dinamiko. Z analizo populacijske viabilnosti (PVA) smo ugotovili dva pomembna dejavnika, ki imata največji vpliv na dinamiko populacijske rasti in z njo povezana tveganja za izumrtje populacije. To sta preživetje doraščajočih in odraslih osebkov ter kvaliteta risovega habitata z vidika razpoložljivosti (gostote) plena. Na spreminjanje stopnje preživetja ima največji vpliv človek s svojim neposrednim vplivom (zakoniti in nezakoniti lov, promet), ki ga je težko regulirati. Ravno nasprotno pa lahko upravljalci z ustreznim upravljanjem s plenskimi vrstami v veliki meri vplivajo na kvaliteto risovega prostora z vidika dostopnosti hrane. Zato je lahko zadnje eden izmed najpomembnejših kratkoročnih varstvenih ukrepov pri upravljanju s populacijo risa v Sloveniji v prihodnje.

Ključne besede. Evrazijski ris, *Lynx lynx*, populacijska dinamika, PVA simulacija, reintrodukcija, dinarska regija

Introduction

The reintroduction of individual animals of a certain species to an area where the species has become extinct in the recent past has become one of the most important, albeit controversial, approaches to conservation of threatened species over the last few decades (Breitenmoser & al. 2001, Bekoff 2001). The current presence of the Eurasian lynx (*Lynx lynx*) in Slovenia is a direct result of a successful reintroduction. The reintroduction project was started in 1972, when experiences with carnivore recovery programs were still very limited. Considering the contemporary requirements that such reintroduction projects should meet (IUCN/SSC, 1998), the reintroduction program had many deficiencies, especially from valuational and organisational point of view. However, the reintroduction was performed with consent and cooperation of hunters, the most important interest group that had the power to directly affect the success of the reintroduction. This was of great importance, since review analyses show that in successful reintroductions a human – carnivore conflict either did not exist, or had been reasonably solved (Reading & Clark 1996, Wolf & al. 1996, Breitenmoser & al. 2001). Besides, the newly established population had favourable habitat and prey conditions (Čop 1994), which can be considered of key importance for the reintroduction's success. Since only three pairs of lynx were introduced, there can be no doubt that the population experienced the founder effect through the genetic drift (Breitenmoser-Würsten & Obexer-Ruff 2003), a reduction of heterozygosity, a loss of alleles and a further de-

pletion of its gene pool through inbreeding. These negative predispositions aside, the monitoring of the population shows that the population has undergone a rapid expansion into Croatia and Bosnia and Herzegovina, and also expansion towards the north into Austria and towards the northwest into Italy. The long term monitoring effort has been initiated soon after the reintroduction, and several comprehensive papers and internal reports have been published (eg. Čop 1994, 1997, Čop & Frković 1998, Frković 2003, Staniša & al. 2001, Jonozovič 2004). However, the monitoring has been mainly oriented in collection of spatial distribution of lynx signs of presence and on recording of killed (culled) lynxes. According to these, the expansion into the unoccupied areas came to a halt in the early nineties.

Although the monitoring effort is very important, other population studies should also be considered. Telemetry (Huber & al. 1995), population modelling and population viability analysis (PVA) may prove to be of great value for management of the Dinaric lynx population, since we still cannot be confident in its long-term survival.

In general, population viability analysis is a useful tool for identification of variables important for population growth and the resulting viability of reintroduced or other small populations. We performed the analysis in two parts. In the first part, we used the monitoring data to estimate population dynamics of the Dinaric lynx population (spatial expansion, abundance estimates, and mortalities) since the reintroduction up to the present day, and then looked for demographic and habitat parameters that would provide the best

fit of a lynx population model to this data. We applied different scenarios in modelling of population dynamics of the re-introduced lynx from 1973 to 2003, using different demographic and/or environmental parameters. In the second part of the analysis we tried to evaluate the importance of the same parameters for future population dynamics and viability (PVA) of such a lynx population. We constructed a number of 100-year simulations using a range of demographic parameters, different prey availabilities and simulating other potential human related factors that might affect the lynx population.

Methods

PVA software and model parameters

The data on demographic attributes for the Dinaric lynx population are scarce, if not non-existent. To be able to model the development of the Dinaric lynx population, we estimated its population parameters from knowledge of lynx biology from other parts of the species' range.The simulations were performed using the RAMAS Metapop® software package (Applied Biomathematics, USA). All analyses and models were produced for the Dinaric lynx population as a whole and in its entire geographic range (Slovenia, Croatia and Bosnia and Herzegovina), since doing population dynamics and viability for individual parts of the population doesn't make much sense. Each scenario used for modelling of the population dynamics was run with 1000 iterations. The birth sex ratio used for the modelling was 1:1, since the sex structure in stable lynx populations shows a balanced ratio between males and females (Kvam 1991). We designed a post-reproductive Leslie matrix for both, males and females in seven separate stages, three for females and four for males. For both, we applied three age categories: yearlings, subadults and adults. Male subadults were placed in two stages. Although they can become sexually mature at the end of their second year of life, it is unlikely for them to breed until the end of their third year. The age at first reproduction is the demographic parameter that significantly affects the population dynamics (Akcakaya 2002). Histological analysis of testi-

cles in the Norwegian lynx population has shown that 50% of males reach sexual maturity at the age of 21 months (Kvam 1990). However it is unlikely that young males would participate in mating, since they are being chased away from females by older males. This probably means that they can mate only a year later, when they are almost 3 years old (Kvam 1991). The females in captivity reach sexual maturity at 21 months (Lindeman 1955, Henriksen & al. 2005). A similar result was obtained in Norway through analysis of ovulation or presence of corpora lutea, where most females also reached sexual maturity by the age of approximately 21 months. However, roughly half of the females were sexually mature already at the age of 7.5–11.5 months (Kvam 1990).

Reproductive success of a lynx population depends primarily on the feeding conditions in the environment, usually the density of roe deer, *Capreolus capreolus,* (Jedrzejewski & al. 1996, Okarma & al. 1997). When they become sexually mature, Eurasian lynx females usually mate until the high age of 12–13 years (Stehlik 1984, Stahl & Vandel 1998, Henriksen & al. 2005). In a radio-telemetric study in Scandinavia they found that 55% of two-year old females and 72% of older females were with kittens (Andren & al. 1998, 2002). In the model, we defined this proportion of females as reproductively active. Subadult (1 year old) females were defined as non-reproductive.

Many European studies of lynx reproduction found that the number of kittens per female at the end of their first year of life was between 1.6 and 1.2 (Kvam 1991, Pulliainen 1995, Jedrzejewski & al. 1996, Andren & al. 1998, 2002, Okarma & al. 1997, Jedrzejewska & Jedrzejewski 1998, Andersen & al. 2003, Henriksen & al. 2005). Deviating from this are data from Switzerland, where they found only 0.69 kittens per female in the studied animals (Breitenmoser & al. 1993). Reasons for this may be in different methodologies used to assess recruitment, or due to lower survival of kittens. We chose to use fecundities $F = 1.2$ and $F = 1.6$ for the model, referred to as the high and the low reproduction. In RAMAS Metapop®, fecundity is defined as the number of offspring that survive to the end of their first year of life per female.

Pre-dispersal and dispersal mortalities have been researched for many felid species, and they seem to vary between species (BREITENMOSER & al. 1993). Survival rates of dispersing or subadult lynx in Europe range from 36 % to 62 % (STEHLIK 1984, BREITENMOSER & al. 1993, ANDREN & al. 1998, HENRIKSEN & al. 2005). Although there are some data on survival rates of resident lynx in Europe (JEDRZEJEWSKI & al. 1996, KRAMER-SCHADT & al. 2005, ANDREN & al. 1998, 2006), the rather low statistical power of the data is common for all the studies. For the model, we used survival rates of subadult and adult lynx obtained from the survival data of 245 animals radio-tracked in the Scandinavian Lynx Project (ANDREN & al. 1998, 2006). The survival rates used were 62% for subadult males and females (one to two years old), 81% for two to three years old females and 83% for the males of the same age.

We are fully aware that these values might be biased due to small sample size and the limited time of the study. Additionally, these data are from the boreal region found in the northern part of the lynx areal in Europe, and we are using them to model population dynamics in a mountainous region of mixed forests in the southern part of the species' areal. However, all the values used in the model are rather high, since they should represent only background survival rates without the influence of human-related mortality which was modelled separately. We must consider that population models and PVA require information on many variables that are difficult to estimate for low-density populations (BEISSINGER & WESTPHAL 1998).

Even the simplest deterministic models need information regarding age structure, breeding schedule, and vital rates (MCKELVEY & al. 2000). These models assume that demographic rates are constant, which is certainly not true for lynx. Small populations are more sensitive to stochastic events, which usually make them more vulnerable to various detrimental factors and can significantly decrease their viability. Demographic and environmental stochasticity were included in our model to simulate variation in population size under natural conditions. Accordingly, we modelled lynx population dynamics stochastically by generating random annual lynx vital rates from the normal distribution curve according to the values defined above, using the coefficient of variability (*CV*) of 0.2 for fecundities and 0.1 for survival rates, which covers a substantial part of the variation in lynx vital rates known from the literature considered above.

Modelling historical 30-year population dynamics

In January 1973, three adult male and three adult female lynx were transferred to a quarantine enclosure in Slovenia from a quarantine enclosure in the Stromovka Zoo near Ostrava (in today's Slovak Republic). After 46 days they spent there separated in pairs, the lynx were released into the wild. According to direct observations and observations of signs of presence (ČOP 1994), none of the animals exhibited homing behaviour. Snow tracking of presumably all six animals was reported in November 1973. Thus, as the initial population size, three adult females and three adult males were modelled in our model.

In the years that followed the population grew and expanded. The initial development of the population showed a low mortality of individuals (KOS & KROFEL 2004). We can assume this to be of key importance for survival of the newly established population through the initial phase (KOS & KROFEL 2004). The population continued to grow despite legal culling of lynx being introduced in 1978, and also expanded in the northwestern direction towards Italy and the Alps (ČOP 1994). It seems that the rapid spatial expansion of the population that took place until the middle of the eighties of the previous century slowed down by the end of the decade, and came to a halt in the beginning of the 90s (ČOP 1997, ČOP & FRKOVIĆ 1998, FRKOVIĆ 2003). To be able to model the development of the population, we had to determine the population ceiling (*K*). The ceiling in RAMAS Metapop® is the population size above which all individuals are killed or have died, and it does not act like usually an environmental carrying capacity would act. We defined the ceiling as the population size at its highest point in the last 30 years, which was most likely reached at the end of the spatial expansion (17 to 18 years after reintroduction).

Effects of recorded human-related mortality

Two scenarios were applied for simulation of the thirty year population growth of the Dinaric lynx population using the ceiling growth model: (1) a population with high reproduction ($F = 1.6$) and (2) a population with low reproduction ($F = 1.2$). Deterministic growth rate (lambda) and elasticity analysis were performed for each of the fecundity values. Additionally, human-related mortality was included as a relative decrease of annual vital rates, determined as a percentage of killed lynx with regard to the mean population sizes in particular years with no additional mortality modelled. Thirty percent of the decreases were modelled as decreases of fecundities, and 70% as decreases of survival rates. This corresponds to the ratio between kittens and older animals killed in this population between 1973 and 2003 (FRKOVIĆ 2003). During this period, there are 375 lynx recorded as harvested, poached, and killed in traffic accidents or found dead in Slovenia, Croatia, and Bosnia and Herzegovina (POTOČNIK 2004).

Effects of prey density

Following conclusion of the spatial expansion, and re-adaptation of the prey to the new predator, is the second phase of population dynamics, with a decrease in population density and the end of population growth (BREITENMOSER & HALLER 1987, 1993). In this phase, if there are no other direct factors like hunting and poaching, the density of prey becomes the most important factor, affecting mainly the survival rate of the young, and trough it directly the reproductive success of the lynx population (BRAND & KEITH 1979, KVAM 1991, JEDRZEJEWSKI & al. 1996, OKARMA & al. 1997, FULLER & SIEVERT 2001, STEURY & MURRAY 2004). Although there are a number of carnivore species, especially those with cyclical populations, like for example the Canadian lynx (*Lynx canadensis*) for which we have a good understanding of the effects the food/prey has on demography (e.g. MCCORD & CARDOZA 1982, BREITENMOSER & al. 1993, SLOUGH & MOWAT 1996, O'DONOGHUE & al. 1997, MOWAT & al. 2000), such knowledge is surprisingly poor for the Eurasian lynx. Data exist from Poland, where

a deliberate reduction of roe deer (35 – 40%) and red deer, *Cervus elaphus,* (30%) densities in Bialowieza forest by game managers resulted in a 50% reduction of the reproductive success of the lynx (OKARMA & al. 1997, JEDRZEJEWSKA & JEDRZEJEWSKI 1998).

Effects of illegal hunting

The lynx has never been protected in Bosnia and Herzegovina. In the Serbian Republic of Bosnia and Herzegovina it used to be listed as a protected species between 1994 and 2001, but the effectiveness of the legal protection in the post-war political situation is questionable. According to reports, lynx are hunted whenever seen (SOLDO 2001). Until 2001, 25 lynx have been killed, with the first lynx killed in 1983 (SOLDO 2001). This represents 7% of all killed lynx reported for the entire Dinaric population. We can assume that Bosnia and Herzegovina represents a sink area with a low population density. In 1993, Slovenia passed a Decree on the Protection of Endangered Animal and Plant Species, and the lynx received the status of a species under strict protection. In 1998 it received a complete legal protection in Croatia as well. A year before that a new Hunting Act was passed in Croatia, introducing a leasing system for hunting grounds and effectively making hunting primarily an economic activity. Because of the complete legal protection the lynx lost its trophy value for hunters, which was possibly an important mechanism of the so-called active protection. All this made predators, especially the large carnivores, indirectly characterized as economic pests. A sentiment that there is no influence or control over the population size of a predator, and consequently no control over the effects it has on the prey species, certainly bears negative consequences for conservation of the predator. This is most often manifested through an increase of illegal hunting of the predator (BREITENMOSER & al. 2001, ČERVENY 2002). Illegal shooting of lynx is a considerable mortality factor and a threat to a small population (BREITENMOSER & al., 1998). The data on illegal hunting or poaching of lynx in Switzerland and Poland confirm this, as poaching in Poland contributed to 75% of all known lynx mortality and posed the most important mortality

factor in Switzerland (BREITENMOSER & al. 1993, SCHMIDT-POSTHAUS & al. 2002, JEDRZEJEWSKI & al. 1996, OKARMA & al. 1997).

Prey density and additional mortality as important factors for future viability

As a theoretical starting point for the Dinaric lynx PVA, we can use the estimate that the current lynx population numbers 100 individuals that live in an area of 20,000 km² (FRKOVIĆ 2003, FIRŠT & al., 2003, KOS & al., 2004). The initial population size used in the model was 100 individuals, with a stage structure equal to the calculated stable stage structure rounded to the closest integer. The population was limited just above the initial population size with a ceiling at $K = 110$ ($SD \pm 20$). Allee effects in RAMAS Met&apop® were determined by the function $N/(N+A)$, representing a relative decrease in fecundity with regard to the population size. A value of $A = 2$ was chosen, which decreased the vital rates for more than 5% when the population fell below the density of 1 individual per 500 km², which was double the size of an adult male home range radio-tracked in the region (HUBER & al. 1995).

Results

Modelling historical 30-year population dynamics

We ran simulations of an exponential population growth for 17 and 18 model years. We included effects of recorded human-caused mortality (ČOP 1997, ČOP & FRKOVIĆ 1998, FRKOVIĆ 2003, POTOČNIK 2004), modelled as a removal of the specific number of individuals per each year.

The simulated population reached mean sizes between 90 and 130 individuals. Therefore, we determined the population ceiling at $K = 110$ with a standard error (SE +/– 20) to simulate variation due to environmental stochasticity. These results are supported by estimations from the population monitoring reports of Slovenian Forest Service and FRKOVIĆ (2003). Judging by the results of simulations of potential inbreeding coefficients expected in the Dinaric lynx population 30 years after the reintroduction (POTOČNIK 2005), the inbreeding depression is not expected to have an important role in population dynamics during that period. However, for the simulations the founder animals were assumed unrelated and with a random choice of reproductive mates which is unlikely. So far there has been no evidence of the inbreeding depression (beside population decline), so we didn't include it in the models. However, since there is definitely inbreeding in the population, and there is recent genetic data to confirm it (MAJIĆ & al. unpubl.), this factor should be included in future modelling exercises as it can soon become of major importance for viability of the Dinaric lynx population.

Effects of recorded human-related mortality

Values obtained for lambda at high and low reproduction were 1.2 and 1.15, respectively. The elasticity analysis showed survival of adult individuals to be the most important parameter, with proportional contributions to population growth rates of 0.46 and 0.49 (Table 1).

Simulations showed that the modelled population with high reproduction would grow relatively fast until the year 1991. Afterwards, the population growth slows down, reaching

Table 1:   Elasticity, the relative contribution of demographic parameters to the population growth.

Tabela 1:   Elastičnost demografskih parametrov modela populacijske dinamike risa pri visokem oziroma nizkem reprodukcijskem uspehu.

Demographic parameter	Elasticity	
	high reproduction $F = 1.6$	low reproduction $F = 1.2$
fecundity (kitten recruitment)	0.19	0.18
survival of 1 - 2 year old individuals	0.17	0.16
survival of 2 - 3 year old individuals	0.18	0.17
survival of adults	0.46	0.49

the ceiling in 2003 (Figure 1). As a contrast, the population with low reproduction would grow slowly until 1991, and would not reach

HALLER 1992). We can assume that the first phase, the rapid expansion of the Dinaric lynx population, took place until the end of the eighties or the
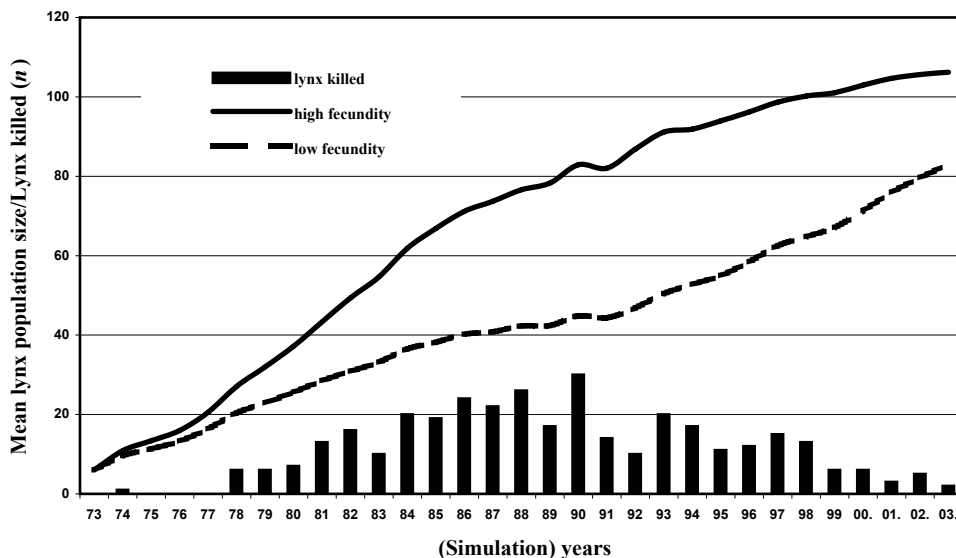

Fig. 1: Stochastic population growth models over a 30–year period with an initial population of three adult females and three adult males, taking into account the recorded lynx mortality.

Slika 1: Stohastični modeli populacijske dinamike risa v 30–letnem obdobju z začetno populacijo treh odraslih samcev in treh samic, upoštevajoč vpliv znanih izgub na celotnem območju.

the ceiling within 30 years despite faster growth in the years that follow. Thus, the population dynamics of the population with high reproduction was closer to the dynamics observed in the monitoring reports, and although the model did not include some mechanisms that are important for reintroduced populations, it was retained for further analysis.

These mechanisms were studied during expansion of a reintroduced lynx population in Switzerland (BREITENMOSER & HALLER 1987, HALLER 1992, BREITENMOSER & al. 1993). The mechanisms affecting population dynamics of a reintroduced lynx population can be divided into two phases. The dispersion of young animals is an important factor in the first phase of population growth, enabling a high survival rate and rapid spatial expansion of the population. It is a simple mathematical phenomenon, additionally amplified by naive prey that is not adapted to the new predator (BREITENMOSER & HALLER 1987,

beginning of the nineties of the previous century, when it slowed down or stopped.

Effects of prey density

To simulate the effects of prey density and availability on reproductive success of the Dinaric lynx population, we included the data on roe deer harvest in the model as a prey density parameter for the years after 1993, when the lynx expansion presumably stopped. We can assume that the harvest of roe deer population decreased with a decrease in roe deer population. The reasons for the decrease are various, including the effects of the presumable increase of the wolf population as well as the significant change in sex structure of the harvest with a much larger proportion of females being harvested. According to the Slovenian Forest Service and the Slovenian Hunters Association's harvest data, there was 40% decrease in the roe deer population size

between 1993 and 2003. Following the results from Bialowieza, we modelled the effects of prey density as a reduction in fecundity relative to the decrease in the harvest in a particular year with regard to the harvest in 1993. The maximum reduction of fecundity was down to 60% of the initial fecundity when the reduction of roe deer population was 40%. Simulations of population

1 to 10% and from 1 to 15% (Figure 2). In both simulations the populations started declining in a year when progressive effect of illegal hunting reached a 5% decrease in survival rates of all age and sex categories (Figure 2). Obtained mean population sizes at the end of simulations were 81 and 91 lynx, respectively. On basis of the available lynx monitoring data the Slovenian Forest
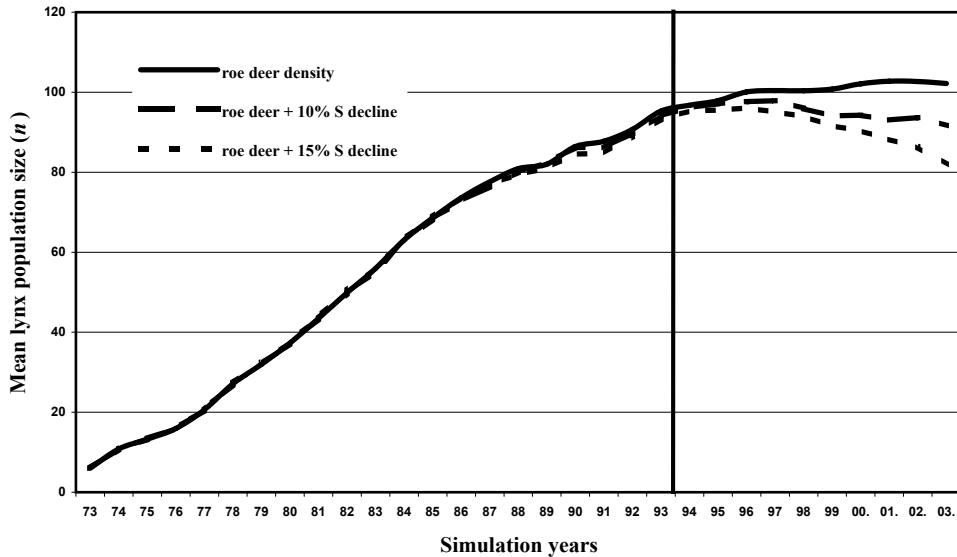

Fig. 2:   Stochastic lynx population growth models over a 30–year period with high reproduction, taking into account changes in roe deer abundance (roe deer density) and a gradual decrease in survival rates (S decline) caused by increased human related mortality in the last 10 years.

Slika 2:   Stohastični modeli populacijske dinamike risa v 30–letnem obdobju ob visoki reprodukciji, upoštevajoč spreminjanje številčnosti srnjadi (roe deer density) in postopno zmanjševanje preživetvene stopnje (S decline) risov zaradi povečane antropogene smrtnosti v zadnjih 10. letih.

dynamics that included the effects of prey density showed that the population would stop growing after 1993 at a mean population size of approximately 100 individuals (Figure 2).

Effects of illegal hunting

In contrast to the prey density, the illegal hunting is very difficult to measure or estimate. However, we assume that the strict protection of the lynx and the new hunting legislation in Slovenia and Croatia have caused a progressive increase in illegal hunting of this species. The effect was modelled, in addition to the prey density effect, as a 10–year linear decrease of survival rates from

Service estimated the number of lynx in Slovenia in 2003 to be approximately 45 individuals. The estimate for Croatia is 50 individuals (FRKOVIĆ 2003, FIRŠT & al. 2003). The data available on the recent population status of lynx in Bosnia and Herzegovina are scarce. Since the number of recorded dead lynx is low (% of all recorded losses in the Dinaric population) despite extremely relaxed hunting regulations, we believe the estimate of 40 individuals, from the country report (cf. VON ARX & al. 2004) to be quite exaggerated. With all that in mind and, despite the constructed model is being a simplified description of relations in the real population, we assume that it can be used as

a helpful basis for population viability analysis for the Dinaric lynx population.

Prey density and additional mortality as important factors for future viability

In simulations of population dynamics and viability analysis for the next 100 years, we exposed the population to different situations in the environment: (1) an environment with high prey density, simulated as high fecundity ($F = 1.6$), (2) an environment with medium prey density, simulated as medium fecundity ($F = 1.2$, –25%), and (3) an environment where prey density is low, simulated as low fecundity ($F = 1.0$, –40%). In all three cases we studied the effects of the decrease in lynx survival rates resulting from additional mortality (Figure 3) on the associated risks of population extinction over a 100-year period (Figure 3). To determine the acceptable, non-detrimental level of additional mortality, in the model considered as the effect of culling (illegal shooting), the population was considered viable if the risk of its extinction over a 100 years period was below 5% (SHAFFER 1981).

In different prey density scenarios, the simulations showed substantial differences in the decline of survival rates. There was no extinction risk in any of the scenarios when no additional mortality was included in the model. That means that in the absence of additional mortality a decline in fecundities as severe as 40% would not pose a threat to the Dinaric lynx population. On the other hand, the prey density had a drastic influence on the extinction risk dynamics in presence of progressive decreases of survival rates. In the high prey density scenario, the limit of the population viability was reached at a 10.5% decrease in survival rates. On the contrary in the medium and the low prey density conditions the risk of extinction reached the threshold of viability at 6% and 3%, respectively (Figure 3). Results of the model indicate that the population is much more sensitive to even minimal changes in survival rates of adults and subadults (as a result of additional human related mortality) under the low prey density conditions than when the prey density is high.
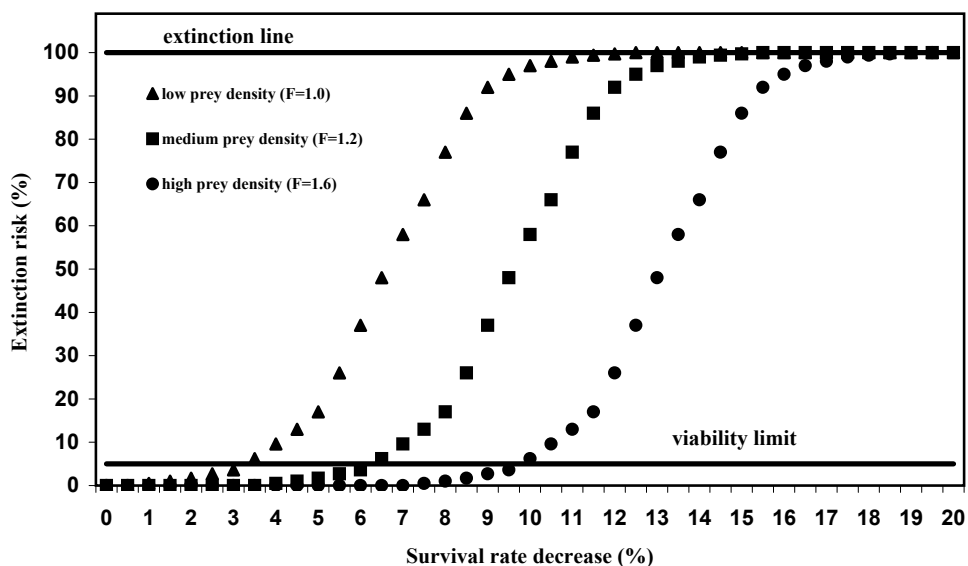

Fig. 3: Extinction risk dynamics influenced by decreasing survival rates caused by human related mortality in subadult and adult lynx at different fecundities, simulating different prey densities.

Slika 3: Dinamika tveganja za izumrtje populacije ob zmanjševanju stopnje preživetja doraščajočih in odraslih risov, kot posledice povečane antropogene smrtnosti ob različni reproduktivni uspešnosti s katero smo simulirali različno gostoto plena v okolju.

Discussion

Carnivores, especially lynx, are elusive animals, and to monitor the progress and the success of a reintroduction programme is a difficult, expensive and long lasting task (BREITENMOSER *& al.* 2001). There is a clear need to improve the efficiency of reintroductions. By simulating population dynamics and viability of the Dinaric lynx population we tried to contribute to understanding of the reintroduction mechanisms. The thirty year retrospective models simulating the Dinaric lynx population growth indicate that the reintroduced population must have had high fecundity rates (F > 1.6) to reach abundances over 100 individuals despite the high human related mortality. The high human related mortality, especially in Bosnia and Herzegovina, might be one of the reasons for the slow down of lynx expansion (VON ARX *& al.* 2004) or probably low dispersion to the southern Dinaric Mountains. An expansion toward north and northwest into the Alps in Slovenia has been probably slowed down due to significant spatial obstacles (traffic infrastructure, urban areas, open habitat) separating the Alps from the Dinaric region (SKRBINŠEK 2004). In Slovenia, no reproduction has been recorded in the Alps (STANIŠA &al. 2001). We can assume these obstacles to have an important effect on local oscillations in population size and may obstruct the population flow. This would have a d&rimental effect on viability of the entire population and increase the risk of local extinctions. The effect of the matrix obstacle increases when a dispersion pressure from the core area of the population is decreased.

Approximately 20 years after the reintroduction, when the intensive expansion of the population into new, unoccupied habitats came to an end, the population probably culminated and habitat quality parameters, like the prey density, became important density dependant factors. Changes in reproductive output are certainly a major potential response, and the relationship of nutrition and both reproduction and recruitment is well documented in mammals (SADLEIR 1969). Since recruitment to a population is a function of the proportion of productive females, litter size, and offspring survival, these demographic parameters should be higher when prey is relatively abundant (FULLER & SIEVERT 2001). Changes

in food abundance can drastically affect the survival of new-borns. Post-partum mortality of Canadian lynx kittens during a snowshoe hare, *Lepus americanus,* population decline was the main factor responsible for a lack of recruitment to the lynx population in Alberta (BRAND & KEITH 1979). A slower increase of home-range sizes with a decrease in prey density in female than in male lynx (HERFINDAL *& al.* 2005) might be, as an alternative to the SANDELL'S (1989) prediction of a change in the mating tactics of males, explained by a decreased reproductive output of females, resulting in lower food requirements during the low prey density. However, even considerable decline in prey density in the third decade after the lynx reintroduction in Slovenia, simulated as a up to 40% decrease in fecundity, i.e. production of only one kitten that survives until end of its first year per female, did not lead to a population decrease.

The elasticity analysis revealed that adult survival is by far the most important demographic parameter for the lynx population dynamics. This is not surprising, considering the fact that lynx have a relatively long reproductive period (STEHLIK 1984). Therefore, even minor decreases in survival rates could cause a decrease in population. Throughout history, carnivores have been perceived as man's competitors for prey and consequently directly persecuted (SILLERO-ZUBIRI & LAURENSON 2001). We presume that the controlled harvest of lynx as a trophy animal produced relatively positive attitudes of hunters toward the lynx in Slovenia and Croatia, which probably changed after its strict protection was put in place, and especially after the new hunting legislation has been adopted in Croatia.

Conclusions

Our 30–year simulations revealed that the reintroduced lynx population started declining when its survival rates were gradually decreased for 5%, simulating increased human related mortality in that period. BREITENMOSER *& al.* (1999) believe that in Switzerland the expansion of lynx after reintroduction has ceased due to illegal killings. Even insignificant decreases in game densities or minor losses of livestock caused by lynx can make illegal killing the most important

mortality factor, as has probably happened in the case of the lynx in the Swiss Alps (BREITENMOSER & al., 1998).

The hypothetical models of lynx population dynamics over a 100–year period highlighted two important factors that had a major impact on population growth dynamics and the related risk of population extinction: (1) changes in the survival rates of subadult and adult individuals in the population that are directly influenced by human activities and are difficult to control, and (2) the quality of habitat with regard to prey availability (density), which is relatively controllable parameter trough management of prey species in the lynx areal. The changes in the survival rate are by and large governed by the direct influence of man (legal hunting, illegal hunting, traffic mortality). Of these factors, legal hunting is the only one over that we can exert direct control or management. The other two factors, especially illegal hunting, can be affected only indirectly through long-term education and actions that decrease predator-caused conflicts.

Effects of habitat quality can have a major impact even when there is a minimal change in the survival rate of subadults and adults in the population. The most important factor affecting prey availability is the regulation of population size of prey species by man. Natural competitors for food, especially wolves (JEDRZEJEWSKI & al. 1993), also affect prey availability. Quite opposite to the adult survival parameter, the quality of habitat with regard to prey availability can be directly influenced through management. Since habitat quality can have a significant role for the lynx population dynamics and viability, in presence of even minor changes in survival rate of subadults and adults in a population, we must consider an adequate prey species management to be one of the most important short-term conservation priorities. Many values used for the PVA model are quite arbitrary, since there are no or few hard data for Dinaric lynx population and such an approach is the only choice. Therefore, the results should be used with caution, as some future simulations with new/better data may show different results.

Povzetek

Reintrodukcija oziroma ponovna naselitev osebkov določene vrste na območje, kjer je bila njena populacija v preteklosti iztrebljena (IUCN, 1995), je postala v zadnjih desetletjih ena izmed pomembnejših oblik upravljanja z ogroženimi živalskimi vrstami (READING & CLARK 1996, WOLF & al. 1996). Ponovno naselitev risa v Sloveniji leta 1973 lahko torej uvrščamo med pionirske naravovarstvene ukrepe, ki jih danes ciljno proučuje tudi varstvena biologija. Namen tega poglavja je predstaviti pomen posameznih demografskih parametrov ter njihov vpliv na populacijsko dinamiko in viabilnost dinarske populacije risa. Kljub relativno majhnemu številu populacijskih parametrov potrebnih za izdelavo osnovnih modelov populacijske dinamike je za dinarsko populacijo risa znanih le malo parametrov. Zato smo bili pri oblikovanju modelov prisiljeni uporabiti objavljene podatke o biologiji risa iz drugih evropskih populacij.

Za matematično modeliranje populacijske dinamike risa smo uporabili programski orodji RAMAS Metapop® (Applied Biomathematics, ZDA). Program omogoča oblikovanje in simulacijo (meta)populacijskih modelov s prostorsko strukturiranostjo. Vse analize in modeli so bili izdelani za dinarsko populacijo risa kot celoto na celotnem območju prisotnosti, saj populacijske dinamike in analize preživetvenih sposobnosti populacije ni mogoče obravnavati le za posamezen del populacije. Mehanizme, ki vplivajo na populacijsko dinamiko pri reintroduciranih populacijah risa delimo v dve fazi. V prvi fazi populacijske rasti je disperzija mladih osebkov pomemben dejavnik, ki omogoča visoko preživetje ter hitro prostorsko širjenje populacije. Gre za preprost matematični fenomen, ki ga dodatno ojači še naiven plen, ki nima izkušenj z novim plenilcem. Prva faza, hitro širjenje dinarske populacije risa, je najverjetneje potekalo do konca 80. oziroma začetka 90. let, ko se je upočasnilo oziroma ustavilo.

Po prenehanju prostorskega širjenja ter prilagoditvi plena na novega plenilca sledi druga faza populacijske dinamike, v kateri pride do zmanjšanje populacijske gostote oziroma ustavitve rasti populacije. V tej fazi je gostota plena, če niso prisotni drugi neposredni dejavniki, kot

so lov in krivolov, najpomembnejši dejavnik, ki vpliva predvsem na preživetje mladičev.

Deterministična stopnja rasti populacije je bila pri optimalni rasti lambda = 1,2, pri sub-optimalni pa 1,15. To pomeni, da se v prvem primeru populacija vsako leto teoretično poveča za 20%, v drugem pa za 15%. Analizirali smo elastičnost posameznih demografskih parametrov (Tabela 1). Ugotovili smo, podobno kot ANDREN & al. (1998), da je največji vpliv na populacijsko dinamiko imelo preživetje odraslih osebkov, saj je spreminjanje parametra preživetja odraslih osebkov prispevalo kar 46–49% k spreminjanju populacijske dinamike populacije ter kvaliteta prostora z vidika dostopnosti (gostote) plena, ki neposredno vpliva na produkcijo mladičev (Tabela 1, Slika 2). Na spreminjanje stopnje preživetja ima največji vpliv človek s svojim neposrednim vplivom (zakoniti lov, promet, nezakoniti lov). Pri tem je le zakoniti lov dejavnik, ki ga lahko neposredno kontroliramo oziroma uravnavamo. Na ostala dva dejavnika, predvsem na nezakoniti lov, lahko vplivamo le posredno z dolgoročnim izobraževanjem in ukrepi, ki zmanjšujejo konfliktnost plenilca. Učinki kvalitete prostora so lahko izrednega pomena že pri minimalnem spreminjanju stopnje preživetja doraščajočih in odraslih živali v populaciji.

S simulacijami populacijske dinamike smo predstavili teoretična izhodišča razvoja dinarske populacije risa in njihove potencialne posledice v prihodnjih 100 letih. Za izhodišče modela smo uporabili začetno velikost populacije 100 osebkov s starostno in spolno strukturo, ki je bila blizu izračunani stabilni populacijski strukturi. Pri tem smo uporabili enake populacijske parametre kot v prvem delu s povprečno produkcijo 1,6 mladiča/samico. V model smo vključili Aleejev efekt, katerega učinki bi se pokazali šele v primeru, ko bi številčnost risa padla pod 20 osebkov v populaciji. Populacijo smo omejevali pri povprečni številčnosti K = 110 osebkov s stohastičnimi nihanji +–20 osebkov. Pri simulacijah populacijske dinamike in analize viabilnosti smo populacijo izpostavili dvema različnima situacijama v okolju. V prvem primeru smo simulirali populacijsko dinamiko risa v okolju z visoko gostoto plena (srnjadi), ki se kaže z visoko produkcijo mladičev (OKARMA & al. 1997) (F = 1,6). V drugem primeru pa smo simulirali razmere v okolju z nizko gostoto plena v okolju, kjer smo v model vključili za 25% oziroma 40 % manjšo produkcijo oziroma preživetje mladičev. Za dane vrednosti smo ugotavljali učinke zmanjševanja stopnje preživetja risov (S), kot posledice dodatne smrtnosti, na populacijsko dinamiko in z njo povezana tveganja za izumrtje populacije v obdobju 100 let (Slika 3). V okolju z visoko gostoto plena (F = 1,6) se verjetnost izumrtja populacije risa pri zmanjšanju preživetja za do 10 odstotnih točk ni zmanjševala. Nasprotno pa se je verjetnost izumrtja naglo povečevala pri nadaljnem zmanjšanju preživetja risov kot posledice dodatne smrtnosti (Slika 3). Pri simulacijah populacijske dinamike v okolju z nižjimi gostotami plena (srnjadi) (F = 1,0 in 1,2) smo ugotovili, da bi se v okolju z nižjo gostoto plena številčnost populacije risa začela zmanjševati že pri zmanjšanju povprečne stopnje preživetja za 5 odstotnih točk, tveganje za njeno izumrtje v stoletnem obdobju pa bi se pri dodatnem zmanjševanju preživetja začelo hitro povečevati in bi pri zmanjšanju preživetja doraščajočih in odraslih osebkov za 15 odstotnih točk populacija zanesljivo izumrla v obdobju 45 let (Slika 3). Za razliko od parametra stopnje preživetja odraslih osebkov, lahko človek v veliki meri neposredno vpliva na parameter kvalitete prostora z vidika dostopnosti hrane. Zato je lahko primerno upravljanje s populacijami plenskih vrst eden izmed prioritenih varstvenih ukrepov pri pripravi strategij upravljanja z dinarsko populacijo risa na celotnem območju njene razširjenosti.

Literature

AKCAKAYA H.R. 2002: RAMAS Metapop®, Viability analysis for stage-structured metapopulations (version 4.0)., Applied Biomathematics, Setauket, New York, 205 pp.

ANDERSEN. R., J. D. C. LINNELL, J. ODDEN, H. ANDRÉN, B. E. SETHER, P. F. MOA, I. HERFINDAL, T. KVAM & H. BRYSETH 2003: Population dynamics, population development and harvest strategy for lynx. NINA Fagrapport **59**, pp. 1–28. (In Norwegian)

ANDRÉN H., J. D. C. LINNELL, O. LIBERG, P. AHLQVIST, R. ANDERSEN, A. DANELL, R. FRANZÉN, T. KVAM, J. ODDEN & P. SEGERSTRÖM 2002: Estimating total lynx (Lynx lynx) population size from censuses of family groups. Wild. Biol. **8**, 299–306.

ANDREN H., J. D. C. LINNELL, O. LIBERG, R. ANDERSEN, A. DANNELL, J. KARLSSON, J. ODDEN, P. F. MOA, P. AHLQVIST, T. KVAM, R. FRANZÉN & P. SEGESTRÖM 2006: Survival rates and causes of mortality in Eurasian lynx (Lynx lynx) in multi-use landscapes. Biol. Conserv. **35**, 234–254.

ANDRÉN H., P. AHLQVIST, R. ANDERSEN, T. KVAM, O. LIBERG, M. LINDÉN, J. ODDEN, K. OVERSKAUG, J. D. C. LINNELL & P. SEGERSTRÖM 1998: The Scandinavian lynx projects. Annual Report 1997. NINA Oppdragsmeldung **518**, pp. 1–11.

BEISSINGER S. R., M. I. WESTPHAL 1998: On the use of demographic models of population viablity in endangered species management. J. Wild. Managem. **62**, 821–841.

BEKOFF M. 2001: Human-carnivore interactions, adopting proactive strategies for complex problems. In: GITTLEMAN J. L., S. M. FUNK, D. MACDONALD, R. K. WAYNE (eds.): Carnivore conservation, Cambridge University Press, Cambridge, pp. 179–195.

BRAND C. J. & L. B. KEITH 1979: Lynx demography during snowshoe hare decline in Alberta. J. Wild. Managem., **43**: 927–849.

BREITENMOSER U., C. BREITENMOSER-WÜRSTEN & S. CAPT. 1998: Re-introduction and present status of the lynx in Switzerland. Hystrix **10**: 17–30.

BREITENMOSER U. & H. HALLER 1987: Nahrungsökologie des Luches *Lynx lynx* in den schweizerischen Nordalpen. Z. Säugetierk. **52**: 168–191.

BREITENMOSER U. & R. H. HALLER 1993: Patterns of predation in reintroduced European lynx in the Swiss Alps. J. Wild.Managem. **57**: 135–144.

BREITENMOSER U. 1998: Large predators in the Alps, The fall and rise of man's competitors. Biol. Conserv. **83**: 279–89.

BREITENMOSER U., C. BREITENMOSER-WÜRSTEN, A. RYSE , F. ZIMMERMAN, C. ANGST, P. OLSSON, H.J. BAUMGARTNER, A. SIEGENTHALER, P. MOLINARI, J. LAAS, A. BURRI, A. JOBIN & J.M. WEBER 1999: Lynx management problems in the Swiss Alps. Cat News, **30**: 16–18.

BREITENMOSER U., C. BREITENMOSER-WÜRSTEN, L. N. CARBYN, S.M. FUNK 2001: Human-carnivore interactions, adopting proactive strategies for complex problems. In: GITTLEMAN J. L., S.M. FUNK, D. MACDONALD, R. K. WAYNE (eds.): Carnivore conservation, Cambridge University Press, Cambridge, pp. 179–195.

BREITENMOSER U., P. KACZENSKY, M. DÖTTERER, C. BREITENMOSER-WÜRSTEN, S. CAPT, F. BERNHART & M. LIBEREK 1993: Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. J. Zool. (Lond.) **231**: 449–464.

BREITENMOSER-WÜRSTEN C. & G. OBEXER-RUFF 2003: Population and conservation genetics of two reintroduced lynx (*Lynx lynx*) populations in Switzerland – a molecular evaluation 30 years after translocation. SCALP Conference Proceedings, Amden, Switzerland, pp. 5–6.

ČERVENY J., P. KOUBEK & L. BUFKA 2002: Eurasian Lynx (*Lynx lynx*) and its chance for survival in Central Europe, The case of the Czech Republic. Acta Zoologica Lithuanica **12**: 362–366.

ČOP J. & A. FRKOVIĆ 1998: The reintroduction of the Lynx in Slovenia and its present status in Slovenia in Croatia. Hystrix **10**, 65–76.

ČOP J. 1994: Spremljanje naselitve risa (*Lynx lynx* L.) v Sloveniji 1973–1993. Research report. Forestry Institute of Slovenia, Ljubljana, pp. 1–85 (in Slovenian)

ČOP J. 1997: Die Raumverbreitung des Luchses nach der Wiedereinbürgerung 1973 in Kočevje, Slowenien, bis 1997. In: Der Luchs in Mitteleuropa, Scriftenreiche des Landesjagdverbandes Bayern, Band **5**, pp. 47–57.

FIRŠT B., A. FRKOVIĆ, T. GOMERČIĆ, M. GRUBEŠIĆ, Đ. HUBER, B. IVIČEK, Z. JAKŠIĆ, I. KOS, D. KOVAČIĆ, B. KULIĆ, B. LIPOVAC, A. MAJIĆ SKRBINŠEK, I. MARKOVINOVIĆ, M. MILAŠINOVIĆ, V. SOLDO, D. SPUDIĆ, Ž. ŠTAHAN, C. STANIŠA, M. STARČEVIĆ, A. ŠTEFAN & A. ŠTRBENAC 2005: Plan upravljanja risom u Hrvatskoj Ministarstvo zaštite okoliša i prostornog uređenja Republike Hrvatske, Croatia, Zagreb, pp. 1–52. (In Croatian)

Frković A. 2003: Ris u Hrvatskoj. Upravni odjel za gospodarski razvoj Primorsko-goranske županije, Lovački savez Primorsko Goranske županije, pp. 1–91.

Fuller T.K. & P.R. Sievert 2001: Carnivore demography and the consequences of changes in prey availability. In: Gittleman J.L., S.M. Funk, D. Macdonald, R.K. Wayne (eds.): Carnivore conservation, Cambridge University Press, Cambridge, pp. 163–178.

Haller H. 1992: Zur Ökologie des Luchses Lynx lynx im Verlauf seiner Wiederansiedlung in den Walliser Alpen. Mammalia Depicta 15: 1–62.

Henriksen H., R. Andersen, A. J. M. Hewison, J. M. Gaillard, M. Bronndal, S. Jonsson, J. D. C. Linnell & J. Odden 2005: Reproductive biology of captive Eurasian lynx Lynx lynx. Eur. J. Wildl. Res. 51, 151–156.

Herfindal I., J.D.C. Linnell, J. Odden, E. Birkeland Nilsen, R. Andersen 2005: Prey density, environmental productivity and home range size in the Eurasian lynx (Lynx lynx). J. Zool. (London) 265: 63–71.

Huber T., P. Kaczensky, C. Staniša, J. Čop & H. Gossow 1995: Luchs Telemetrie Projekt Kocevska, Slowenien. Final report, pp. 1–23.

IUCN/SSC Re-introduction Specialist Group 1998: IUCN Guidelines for reintroductions. IUCN, Gland, pp. 1–11.

Jedrzejewska B. & W. Jedrzejewski 1998: Predation in vertebrate communities, the Bialowieza Primeval Forest as a case study. Springer-Verlag Berlin Heidelberg, New York, Ecological studies, 135: pp. 1–450.

Jedrzejewski W., B. Jedrzejewski, H. Okarma, K. Schmidt, A. Bunevich & L. Milkowski 1996: Population dynamics (1869–1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland and Belarus). Ecography 19: 122–138.

Jedrzejewski W., K. Schmidt, L. Milkowski, B. Jedrzejewska & H. Okarma 1993: Foraging by lynx and its role in ungulate mortality, the local (Bialowieza Forest) and the Palaearctic viewpoints. A. Theriol. 38: 384–403.

Jonozovič M. 2004: Monitoring pojavljanja risa v Sloveniji. In: Kos I. (ed.): Lynx in Slovenia, background documents for conservation and management, University of Ljubljana, Biotechnical Faculty, Ljubljana, Slovenia, pp. 133–140. (in Slovenian with English summary)

Kos I. & M. Krofel 2004: Pojavaljanje risa na ozemlju Slovenije. In: Kos I. (ed.): Lynx in Slovenia, background documents for conservation and management, University of Ljubljana, Biotechnical Faculty, Ljubljana, Slovenia, pp. 69–74. (in Slovenian with English summary)

Kos I., H. Potočnik, T. Skrbinšek, A. Majić Skrbinšek, M. Jonozovič & M. Krofel 2004: Lynx in Slovenia, background documents for conservation and management, Kos I. (ed.), University of Ljubljana, Biotechnical Faculty, Ljubljana, Slovenia, pp. 1–239. (in Slovenian with English summary)

Kramer-Schadt S., E. Revilla & T. Wiegand 2005: Lynx reintroductions in fragmented landscapes of Germany, Projects with future or misunderstood wildlife conservation?. Biol. Conserv. 125(2): 169–182.

Kvam T. 1990: Ovulation rates in European lynx (Lynx lynx) from Norway. Z. Saügtierk. 55: 315–320.

Kvam T. 1991: Population biology of the European lynx (Lynx lynx) in Norway. Dissertation, University of Trondheim, Department of Zoology, Trondheim, pp. 1–45.

Lindemann W. 1955: Über die Jugend-entwicklungen beim Luchs (Lynx l. lynx, Kerr) und bei der Wildkatze (Felis s. silvestris, Schreber). Behaviour 8: 1–44.

McCord C.M. & J.E. Cardoza 1982: Bobcat and Lynx (Felis rufus anf F. Lynx). In: Chapman J.A. & G.A. Feldhammer (eds.): Wild mammals of North America, biology, management, and economics, John Hopkins University Press, Baltimore, pp.728–766.

McKelvey K.S., S.W. Buskirk, C.J. Krebs 2000: Theoretical insights into the population viability of lynx. In: Ruggiero L.F., B.A. Keith, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKel-

vey & J.R. Squires (eds.): Ecology and Conservation of Lynx in the United States, University of Colorado Press, Boulder, Colorado, pp. 21–38.

Mowat G., K. G. Poole & M. O'Donoghue 2000: Ecology of Lynx in Northern Canada and Alaska. In: Ruggiero L.F., B.A. Keith, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey & J.R. Squires (eds.): Ecology and Conservation of Lynx in the United States, University of Colorado Press, Boulder, Colorado, pp. 265–306.

O'Donoghue M., S. Boutin , C.J. Krebs & E.J. Hofer 1997: Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80: 150–162.

Okarma H., W. Jedrzejewski, K. Schmidt, R. Kowalczyk & B. Jedrzejewska 1997: Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. A. Theriol. 43: 203–224.

Potočnik H. 2004: Zgodovinski pregled vzrokov izumiranja risa v Evropi. In: Kos I. (ed.): Lynx in Slovenia, background documents for conservation and management, University of Ljubljana, Biotechnical Faculty, Ljubljana, Slovenia, pp. 69–74. (in Slovenian with English summary)

Potočnik H.: 2005. Modeli razvoja dinarske populacije risa. In: Kos I., H. Potočnik, T. Skrbinšek, A. Majić Skrbinšek, M. Jonozovič & M. Krofel: Lynx in Slovenia, background documents for conservation and management, Second edition, pp. 118–129. University of Ljubljana, Biotechnical Faculty, Ljubljana, Slovenia. (in Slovenian with English summary)

Pulliainen E., E. Lindgren & P.S. Tunkkari 1995: Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland. A. Theriol. 40: 181–196.

Reading R.P. & T.W. Clark: 1996. Carnivore reintroductions, an interdisciplinary examination. In: Gittleman J.L.(ed.): Carnivore behavior, Ecology and Evolution, Cornell University Press, Ithaca, New York, pp. 296–336.

Sadleir R.M.F.S. 1969: The role of nutrition in the reproduction of wild mammals. J. Repr. & Fert., Supplement 6: 29–48.

Sandell M. 1989: The mating tactics and spacing patterns of solitary carnivores. In: Gittleman J.L. (ed.): Carnivore behaviour, ecology and evolution, Chapman and Hall, London, pp. 164–182.

Schmidt-Posthaus H., C. Breitenmoser-Würsten, H. Posthaus, L. Bacciarini & U. Breitenmoser 2002: Causes of mortality in reintroduced eurasian lynx in Switzerland. J. Wild. Dieas. 38: 84–92.

Shaffer M.L. 1981: Minimum population sizes for species conservation. Bioscience 31: 131–134.

Sillero-Zubiri C. & M.K. Laurenson 2001: Interactions between carnivores and local communities: conflict or co-exsistence?. In: Gittleman J.L., S.M. Funk, D. Macdonald, R.K. Wayne (eds.): Carnivore conservation, Cambridge University Press, Cambridge, pp. 163–178.

Skrbinšek T. 2004: Model primernega prostora za risa v Sloveniji. In: Kos I. (ed.): Lynx in Slovenia, background documents for conservation and management, University of Ljubljana, Biotechnical Faculty, Ljubljana, Slovenia, pp. 92–111. (in Slovenian with English summary)

Slough B.G. & G.Mowat 1996: Lynx population dynamics in an untrapped refugium. J. Wild. Managem. 60: 946–961.

Soldo V. 2001: The lynx in Bosnia and Herzegovina. In: Breitenmoser-Würsten Ch. & U. Breitenmoser (eds.): The Balkan lynx history, recent knowledge on its status and conservation needs, Kora Bericht, 7, Muri, pp. 6—7.

Stahl P. & J-M. Vandel 1998: Le lynx Boreal. SFEPM, Encyclopedie des carnivores de France, 19, pp. 1–54.

Staniša C., I. Koren & M. Adamič 2001: Situation and distribution of the lynx (Lynx lynx) in Slovenia from 1995–1999. Hystrix, Italian Journal of Mammology 12: 43–51.

Stehlik J. 1984: Reproduction of the Lynx (Lynx lynx Linneaus, 1758) in captivity. Folia Venatoria 14: 163–159.

Steury T.D. & D.L. Murray 2004: Modeling the reintroduction of lynx to the southern portion of its range. Biol. Conserv. 117: 127–141.

VON ARX M., C. BREITENMOSER-WÜRSTEN, F. ZIMMERMANN & U. BREITENMOSER 2004: Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. Kora Report, 19e, Switzerland, Muri, pp. 246–251.

WOLF C.M., B. GRIFITH, C. REED & S.A. TEMPLE 1996: Avian and mammalian reintroductions, update and reanalysis of 1987 survey data. Cons. Biol. **10** (9): 1142–1154.