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Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation?

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Abstract

Eurasian lynx are slowly recovering in Germany after an absence of about 100 years, and additional reintroduction programs have been launched. However, suitable habitat is patchily distributed in Germany, and whether patches could host a viable population or contribute to the potential spread of lynx is uncertain. We combined demographic scenarios with a spatially explicit population simulation model to evaluate the viability and colonization success of lynx in the different patches, the aim being to conclude guidelines for reintroductions. The spatial basis of our model is a validated habitat model for the lynx in Germany. The dispersal module stems from a calibrated dispersal model, while the demographic module uses plausible published information on the lynx' life history. The results indicate that (1) a viable population is possible, but that (2) source patches are not interconnected except along the German–Czech border, and that (3) from a demographic viewpoint at least 10 females and 5 males are required for a start that will develop into a viable population with an extinction probability of less than 5% in 50 years. The survival rate of resident adults was the most sensitive parameter, and the best management strategy for the success of reintroduction would be to reduce the mortality of residents in the source patches. Nevertheless, the extremely low probability of connectivity between suitable patches makes most of the reintroduction plans isolated efforts, and they are therefore questionable in the long run. With such a model, the suitability of the single habitat patches can be assessed and the most appropriate management scheme applied. This study shows that simulation models are useful tools for establishing the comparative effectiveness of reintroduction plans aimed at increasing the viability of the species.
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1. Introduction

Species reintroduction is being increasingly regarded as a valuable tool for conservation schemes, for example to save species from extinction or to reinstate species that have become locally extinct. Due to a change in public attitudes towards wildlife in the mid-20th century, species reintroductions have been increasingly considered (Leaper et al., 1999; South et al., 2000; Sarrazin and Legendre, 2000; Breitenmoser et al., 2001; O'Toole et al., 2002). In human-dominated landscapes of Germany, reintroductions of lynx *Lynx lynx* have been the subject of intense, controversial debate since the 1970s (see Schadt et al., 2002a,b). A recent example is the

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release of lynx into the Harz Forest in 2000 (Wotschi-kowsky et al., 2001). Lynx are also slowly recolonizing the Bavarian Forest and the adjacent low mountain ranges following a reintroduction of lynx in the Czech Bohemian Forest (Fig. 1; Wölfl et al., 2001).

Carnivore reintroductions in particular are extremely lengthy, costly and complex processes, and so they evidently need to be made more efficient (Breitenmoser et al., 2001). The future development of a reintroduced lynx population and the success of potential reintroduction initiatives are difficult to assess because of the large spatial requirements of a lynx population and because the dynamics of small expanding populations in fragmented landscapes are not well understood. Questions such as the minimum number of individuals that should be released and the influence of factors leading to higher mortality on population development remain unanswered. For example, although the higher deaths caused

by humans in fragmented landscapes due to habitat contraction and modification as well as poaching and road mortality are major factors contributing to the failure of reintroductions (Kaczensky et al., 1996; Trombulak and Frissell, 2000; Ferreras et al., 2001), their consequences for population dynamics are inherently difficult to assess.

Models as assessment tools for reintroductions and management have been used for a variety of species (Howells and Edward-Jones, 1997; Letcher et al., 1998; Bustamante, 1998; Leaper et al., 1999; Merrill et al., 1999; South et al., 2000; Ebenhard, 2000; Mathews and Macdonald, 2001; Ellner and Fieberg, 2003; Steury and Murray, 2004; Posillico et al., 2004). The assessment of human impact on the survival of species, such as fragmentation due to roads, is increasingly relying on population viability analyses (PVA), which use demographic models incorporating various aspects of the ecology and behaviour of the species concerned (Boyce, 1992;
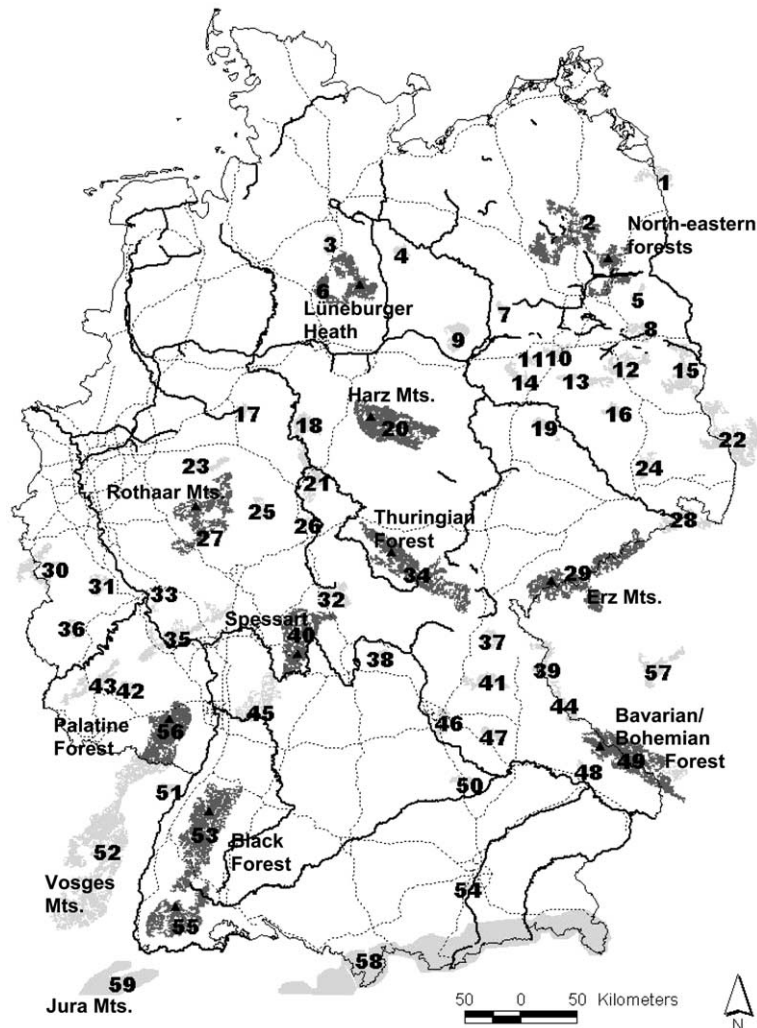

Fig. 1. Source and target patches for measuring the connectivity of the German landscape. Dark grey indicates source patches, which are larger than 1000 km^2; light grey shows target patches, which are larger than 100 km^2. Dotted lines show highways; black lines mark main rivers. The triangles indicate the starting points of the simulated animals. Connectivity between the patches for the different scenarios and the numbers of released lynx pairs are given in the Appendix.

Akcakaya and Raphael, 1998). Conservation efforts of other carnivores in fragmented landscapes using PVA have, for example, been made for the Iberian lynx in Spain (Gaona et al., 1998; Revilla et al., 2004). Despite a few drawbacks (Beissinger and Westphal, 1998; but see Wiegand et al., 2004), spatially explicit population simulation models are virtually the only means to answer certain specific questions of population development under different landscape and demographic scenarios (Brook et al., 2002) and should therefore be integrated into the recovery planning process (Morris et al., 2002). Often, generic population viability analysis tools are too unspecific for this purpose (Possingham and Davies, 1995; Akcakaya, 1995) and specifically constructed models are required (Wiegand et al., 1998; Brook et al., 2000; Reed et al., 2002).

We perform a PVA with a specifically constructed, spatially explicit population simulation model that summarizes the available data on the Eurasian lynx. The model consists of three submodels: a landscape submodel for entire Germany and some surrounding areas with a resolution of 1 km^2, an individual-based dispersal submodel which describes dispersal of lynx in this landscape, and a population submodel which includes a territory selection module allocating female and male home ranges (which may comprise areas on average 100 km^2) after dispersal in this landscape as well as a demographic module including mortality and reproduction. In a previous publication (Schadt et al., 2002b) we constructed and validated a habitat model for the lynx in Germany. Based on this map we defined four landscape categories: barriers, matrix, dispersal and breeding habitat, which we assigned to each 1 km^2 pixel of the landscape. The habitat model showed that a pixel of breeding habitat was always part of a connected and undisturbed area, mainly forests, of the size of an average female home range of about 100 km^2 (i.e., the habitat model included a variable which operated at a scale larger than the pixel of the landscape). We therefore refer to the areas with breeding habitat >100 km^2 as possibly suitable patches. Additionally, we refer to 'source patches', when the area identified as suitable is larger than 1000 km^2 (Schadt et al., 2002b). We then identify the scenarios under which a lynx population would be viable in Germany.

The aim of our study is to formulate management strategies and to provide guidelines for evaluating suitable habitat patches before animals are released in order to improve species reintroductions. To this end, we test the impact of demographic scenarios (i.e., different mortality scenarios) on the development of the population and hence on reintroduction success. In this context, questions such as the requirements for successful spreading (e.g., the size of suitable habitat, the numbers and sex of individuals, connectivity among populations) are of particular interest. Our specific questions are: (1) Can the suitable habitat patches sustain a viable lynx popula-

tion? (2) If so, what would be the minimum release population? (3) What would be the most efficient (economic) ratio of females to males? (4) And can other patches be colonized? We answer these questions explicitly for Germany. We are especially interested in population development in the Harz Forest, and whether there is a possible linkage via the Thuringian Forest with the population in the Bavarian Forest. Additionally, we assess the population development in other patches considered suitable, such as the Black Forest and the Palatine Forest (Fig. 1).

2. Methods

We use an individual-based, spatially explicit model to simulate the spatiotemporal population dynamics of lynx in Germany and to test the viability of reintroduced populations under the different demographic scenarios. The model basically consists of a landscape model, an individual-based dispersal model, a home range selection model, and a demographic model. The landscape model is based on a GIS habitat suitability map for Germany (Schadt et al., 2002b), and the dispersal model was developed in Kramer-Schadt et al. (2004). Model rules and parameters are derived from published data of lynx demography in Europe (Table 1). Sensitivity analysis was conducted to assess the influence of model parameters on the model results against a realistic reference scenario. Sensitivity was considered to be high whenever deviation from the reference scenario exceeded 20% (Huth et al., 1998).

2.1. Life history of Eurasian lynx

In central Europe, lynx are mostly bound to forested habitat and their main prey are ungulates, especially roe deer. Apart from females with the current year's offspring, lynx are solitary living animals. Their territories are intrasexually exclusive, and holding a territory seems to be a condition for adults to reproduce (Ferreras et al., 1997; Breitenmoser et al., 2000). Adult males generally occupy large territories, often sharing them with one or two females.

Mating takes place in spring and the average litter size is two kittens (Breitenmoser-Würsten et al., 2001). Subadults leave their natal territory at the age of about 10 months to search for their own territories (Zimmermann, 1998). Adults can also disperse if breeding areas are saturated (Gaona et al., 1998). Mortality during dispersal is higher than for resident individuals, the total annual mortality rate being about 0.5 (Ferreras et al., 1992, 2001; Gaona et al., 1998; Breitenmoser-Würsten et al., 2001).

Females are usually mature at the age of two years. Lynx can be sexually active throughout their lifetime, which can be up to 17 years in the wild (Breitenmoser et al., 2000). Lynx suffer high mortality rates due to

Table 1
Model parameters for each submodel. The mortality probabilities for each model step are given in each submodel and were assessed with indirect parameter adjustment to reflect published data on annual mortality rates

Submodel	Symbol	Published value	Model parameter value or range
Demographic submodel			
• Non-overlapping core area size of female home ranges	CA_f	70 (SD ± 30) km[2a]	70–100 km^2
• Males overlapping females	RES_m	1 or more[a], 1–2[b,c]	Up to 3
• Surviving subadults starting to disperse per reproductive female	N_{sub}	1.6[d], 1.0–1.1[c]	1–2
• Sex ratio of kittens	$Ratio_s$	1:1[d,c]	1:1
• Reproduction rate (=prob. of giving birth)	P_{birth}	0.75[d], 0.88[c] 0.6 ± 0.12 SD; 0.8 ± 0.12 SD [e]	0.5, 0.75, 0.95
• Annual mortality rates of residents	MR_{res}	12%[d], 10–30%[e], 13%[c] Jura Mts., 22–28%[c] Alps	0.07, 0.18, 0.25 (results p.a. see Table 2)
• Number of released males and females	N_{rel}	–	1–18, 20, 22, 25, 30
Dispersal submodel			
• Correlation factor (dispersal)	P_C	[f]	0.5
• Probability of stepping into matrix	P_{matrix}	[f]	0.03
• Maximum number of intraday steps	s_{max}	[f]	45
• Exponent of step distribution of Eq. (2)	x	[f]	11
• Annual mortality rates of dispersers	MR_{disp}	55%[e], 44%[c] Jura Mts., 56–60%[c] Alps	(results p.a. see Table 2)
• Daily mortality rate of dispersers	M_{basic}	[f]	0.0001, 0.0006, 0.0014
• Mortality rate per crossing event of motorway/main river	$M_{highway}$	[f]	0, 0.09, 0.14
main road	M_{road}	[f]	0, 0.0009, 0.0019

[a] Breitenmoser et al. (1993).
[b] Breitenmoser et al. (2000).
[c] The authors state that their statistics concerning annual mortality rates are very weak due to small sample sizes (Breitenmoser-Würsten et al., 2001).
[d] Jedrzejewski et al. (1996).
[e] Gaona et al. (1998).
[f] Kramer-Schadt et al. (2004).

human-related factors such as poaching and road casualties, resulting in total annual mortality rates of 0.2–0.3. In protected areas, mortality rates for residents average about 0.1 (Ferreras et al., 1992; Jedrzejewski et al., 1996; Zimmermann, 1998; Ferreras, 2001; Breitenmoser-Würsten et al., 2001).

2.2. Study area

Germany has an area of about 358,000 km^2 and an average human population density of 230 inhabitants per km^2, dropping to about 100 inhabitants per km^2 in areas such as low mountain ranges (e.g., the Black Forest, Palatine Forest and Thuringian Forest). About 30% of Germany is forested, including plantations, albeit with large local variations (e.g., Hessen has 41% forest, compared to about 10% in Schleswig-Holstein). The forests are clustered in areas formerly unsuitable for agricultural activity in the low mountain ranges and in areas with poor soils in the north-east. Two point five per cent of German territory is protected by National Park status. Germany has a very dense road network consisting of 11,000 km of motorways and more than 50,000 km of interstate or main roads. We included connected neighbouring forest areas in Poland, the Czech Republic (e.g., the Bohemian Forest), France (e.g., the

northern Vosges Mountains) and Belgium in our large-scale study area (Fig. 1).

2.3. Data resolution and scales of the submodels

Our aim requires a model which operates at a spatial scale of entire Germany (358,000 km^2), the size of 'source patches' (i.e., the spatial unit of a population) is larger than 1000 km^2, a female lynx home range (i.e., the spatial unit of an individual lynx) is on average 100 km^2, and lynx disperse on average distances of 42 km (Kramer-Schadt et al., 2004). Our model therefore needs to balance between inclusion of detail in the description of the landscape given through the habitat suitability model, the spatial resolution of our data and the typical scales at which the important processes of the model take place.

For constructing the habitat suitability model with data from Switzerland, Germany, Czech Republic and Slovenia, Schadt et al. (2002b) used only one uniform data source, the CORINE land use data (European Topic Center on Land Cover, Environment Satellite Data Center, Kiruna, Sweden), which classify the following land use types on a 250-m grid. The CORINE classification names are provided in parentheses when different: (i) Urban areas (artificial territories); (ii) agricultural

land (strongly artificial vegetated areas); (iii) pasture (less artificial vegetated areas); (iv) forests; (v) non-wooded semi-natural areas, e.g., heathland; (vi) wetlands; (vii) water surfaces. There was no further breakdown of these land cover types to more detailed classes (e.g., deciduous forest etc.) available for all countries. The accuracy of the telemetry location data used to construct the habitat suitability map was 1 km^2, which was selected as the spatial resolution of the habitat suitability model. Of course, small scale features, such as dense understorey, may influence habitat selection (Fernandez et al., 2003), but given home ranges of 100–400 km^2, we can assume that within such a large area the lynx will find appropriate structures for its needs. This is in accordance with other very detailed habitat models in fragmented landscapes (Zimmermann, 2004).

Considering the different spatial scales given above, which resolution would be appropriate for our model? Since lynx perceive forest fragments less than 1 km apart as connected (Haller and Breitenmoser, 1986), they may respond during dispersal to spatial structures of 1 km^2. In order not to loose detail of this process we used the original grain of the habitat suitability model also as the grain of our model landscape. Based on the habitat suitability map we defined the four landscape categories breeding habitat, dispersal habitat, matrix and barriers (see below). Thus, our landscape consists of a grid of 860×680 cells, each representing 1 km^2 and containing information about its suitability for lynx (e.g., dispersal habitat, matrix etc.).

In the dispersal model (see Section 2.6; Kramer-Schadt et al., 2004), the individuals directly search for the next movement steps based on the information the neighbouring 1 km^2 grid cells contain. In the population model (see Section 2.5), we upscale in terms of home range occupancy, i.e., each female that wants to settle and reproduce needs to collect a certain amount of contagious cells of non-occupied breeding habitat, whereas males search for cells that are already occupied by females (see below). The other scales automatically emerge from the behaviour of the individuals in the model in response to the landscape map and their demographic parameters. Individuals settling in a given source patch may (or may not) form a viable (sub)population, and the connectivity between source patches automatically emerges due to the behavioural rules of dispersing lynx. Thus, we use the same landscape model for all submodels, but in the submodels we address it in different ways to account for the different spatial scales involved.

2.4. Landscape submodel

We obtained the habitat suitability map for resident individuals by logistic regression with a mesh size of 1 km^2 as described in Schadt et al. (2002b). The model contained just one variable: the proportion of area used extensively by humans, such as forests and heathland, in a 5 km circular neighbourhood. The habitat types can be summarized as breeding, dispersal, matrix and barrier habitat. Breeding habitat refers to areas with non-fragmented forest and other natural and semi-natural land use types with a *P*-value above 0.5 as calculated in the logistic regression model. All forested area and breeding habitat is dispersal habitat (Kramer-Schadt et al., 2004). Barriers consist of urban areas and lakes, and are never used. The remaining areas, such as pasture and agricultural land, are summarized as matrix which, although not strictly avoided by dispersing lynx, is only used occasionally.

To simulate the effects of road mortality and crossing large rivers, we created a second map containing linear elements such as main roads (2–4 lanes), motorways ($\geqslant$4 high speed lanes) and main rivers (>100 m wide, e.g., the Rhine and the Danube). To integrate the assessment of connectivity between patches into our model, we define source patches as the main patches of special management interest (>1000 km^2) and target patches as each suitable area >100 km^2 (Fig. 1), which is the average home range size of a female lynx in the Swiss Jura Mountains (Breitenmoser et al., 1993). Patches separated by gaps of 1 km were considered as single patches, as this is thought to be the distance that lynx can perceive as connected (Haller and Breitenmoser, 1986). Altogether, we obtained 59 patches, of which 11 are source patches ((2) North-Eastern Forests, (6) Lüneburger Heath, (20) Harz Forest, (27) Rothaar Mountains, (29) Erz Mountains, (34) Thuringian Forest, (40) Spessart, (49) Bavarian Forest, (53) Northern Black Forest, (55) Southern Black Forest, (56) Palatine Forest; the numbers in parentheses refer to the patches shown in Fig. 1). Animals leaving the study area in the simulations are deleted because once they have emigrated they have no further influence on population development; the re-immigration of these individuals is not considered either.

2.5. Population submodel

One simulation run. At the beginning of each model time step (year), we determine the number of resident males and females and the number of dispersers. All non-residents older than one year disperse (Rule 1) and search for home ranges (Rule 2). The spatially explicit processes of dispersal and territory selection in the model depend upon local habitat quality as perceived by individual lynx as they move through the landscape. Consequently, these processes are determined by a set of rules which take into account the habitat type of the eight cells surrounding the location of the individual. If dispersing individuals survive, they settle or continue dispersal in the following year. Next, we decide for each

resident female to reproduce (Rule 3). In the final step, we update the demographic variables for each surviving individual (age and status, i.e., disperser or resident). Each parameter set is simulated 100 times to obtain a stabilized standard deviation (<1% variability).

Plausible parameter ranges. The demographic parameters of the model are mainly based on published data from Switzerland, Spain and Poland. These data were derived from long-term field studies of reintroduced Eurasian lynx populations in the Swiss Jura Mountains (Breitenmoser et al., 1993) and the Swiss Alps (Haller and Breitenmoser, 1986; Breitenmoser-Würsten et al., 2001) as well as a native population of Eurasian lynx in the Białowieża Primeval Forest (Jedrzejewski et al., 1996). Data from Spain are also based on long-term field studies of the Iberian lynx *Lynx pardinus* (Gaona et al., 1998; Ferreras et al., 2001). Although this is a different species, we use published information to constitute the range of the model parameters. Model rules include detailed information about life-history attributes, family structure, mortality rates and reproduction.

Mortality rates are influenced by the status of the animal. We introduce three different schemes in which a simulated individual may die (mortality scheme) to realistically reflect the effect of the fragmented landscape: (1) a daily mortality probability for dispersing lynx; (2) a mortality probability per linear barrier (road, motorway, river) crossing event for dispersers, and (3) an annual mortality probability per resident individual.

Mortality parameters for each scheme were adjusted for the Harz Forest with indirect parameter assessment to produce a plausible range for annual mortality rates as known from the literature (Table 1). We test 9 different mortality scenarios (low (~10%), medium (~20%) and high (~30%) total annual mortality for residents and low (~30%), medium (~50%) and high (~70%) total annual mortality rates for dispersers each, i.e., the combined effect of daily and road traffic mortality) (Table 2). Note that for dispersers the mortality rates may vary due to differing densities of motorways and other roads in the different patches.

Rule 1: *Dispersal.* By definition, starting animals are dispersers as long as they do not occupy a territory (see Rule 2); otherwise dispersal starts in the second year after separation from the mother. The same dispersal rules are applied to males and females. For movement rules see below (Section 2.6).

Rule 2: *Settlement.* We use two different territory selection mechanisms for males and females. Females are the basic unit in the model that react to the landscape structure, i.e., the arrangement of the different grid cells of breeding habitat, dispersal habitat, matrix and barriers, because they have more stringent objectives for territory selection (i.e., no motorways or rivers inside), as is known for other large carnivores (e.g. Kaczensky et al., 1996). Males overlap contiguous female territories, i.e., in the model they search for occupied female territories. We applied the procedures for territory selection to dispersing individuals for each time step (day).

Once a dispersing female has found a cell of breeding habitat, it searches the surrounding area for contagious cells of non-occupied breeding habitat. If it finds at least 70–100 cells (=km^2), it can occupy a territory (Table 1). To include stochasticity in territory size we draw for each female a random number of cells from a uniform distribution between 70 and 100 cells. The simulated female then has to use this amount of cells as her territory. Once occupied, territory cells cannot be used by other females. In unoccupied areas the female that 'comes first' has the best chance of occupying a territory. The possibility of territories shifting was not considered in the model as lynx normally have fixed territories (Breitenmoser et al., 1993).

The male search strategy is for occupied territory cells of neighbouring females. Once a male has occupied a territory belonging to a female, this female is not available to other males (owing to the intrasexual exclusivity of territories; Breitenmoser et al., 1993). Males can overlap up to three neighboured females in the model.

Rule 3: *Reproduction.* The probability of reproduction of each female per year is 0.75 (Jedrzejewski et al., 1996). Only females occupying a territory (age ≥ 2) and overlapped by a male can reproduce. Field studies show that the litter size can be up to 4 cubs, although kitten mortality is at least 50% (Breitenmoser et al., 1993; Jedrzejewski et al., 1996). Thus, about one

Table 2
Simulated mortality rates resulting from the different mortality scenarios for the Harz Forest Mountains under given landscape conditions when more than 8 females and 8 males are released

Scenario	1	2	3	4	5	6	7	8	9
Total annual mortality rates (±SD) [%]									
Residents	12.0 (±0.2)	19.8 (±0.7)	28.6 (±0.7)	10.8 (±0.1)	20.4 (±0.5)	29.2 (±1.2)	10.6 (±0.1)	20.7 (±0.8)	29.2 (±1.1)
Dispersers	19.1 (±0.2)	21.5 (±1.0)	25.0 (±1.7)	47.2 (±0.6)	54.0 (±1.5)	55.0 (±1.3)	63.2 (±0.3)	69.0 (±1.0)	69.6 (±1.5)
Total	15.7	21.2	26.8	29.6	36.9	42.2	37.5	44.6	49.6

Birth probability was set to 0.75. Scenario 5 for example with a total annual mortality rate of 37% resembles a realistic mortality scenario known from Poland or Spain, where poaching and road casualties occur.

or two subadults per reproductive female start dispersal in their second year (Table 1). We therefore set the probability of having one or two dispersers starting to 0.5 and the sex ratio to 1:1 (Jedrzejewski et al., 1996).

We did not include environmental stochasticity, e.g., good years with a higher birth probability and vice versa, as the roe deer density – the main food resource of Eurasian lynx (Breitenmoser and Haller, 1993; Okarma et al., 1997; Jobin et al., 2000) – in Germany is very high. Hence it is assumed that food limitation does not feature in population dynamics (Schadt et al., 2002b).

2.6. Dispersal submodel

The movement rules and parameters were taken from a calibrated dispersal model for the Eurasian lynx (Kramer-Schadt et al., 2004; Table 1). The smallest spatial unit in our dispersal model is one movement step. We assume that individuals survey their eight-cell neighbourhood and that their movement steps are based on this information. The next cell is chosen based on the preference for dispersal habitat and the avoidance of matrix. If the neighbourhood of a dispersing lynx, comprising the origin cell and its 8 neighbours, contains only matrix or dispersal habitat cells, the probability of choosing one of these cells is random (i.e., 1/9). However, if the neighbourhood is a mixture of dispersal habitat and matrix, we consider the preference for dispersal habitat as follows: The number of matrix cells n_{mat} within the neighbourhood is counted. The probability of leaving dispersal habitat P_{leave} is then dependent on the number of matrix cells around the origin cell multiplied by a factor P_{matrix} (ranging from total avoidance of matrix [$P_{matrix} = 0$] to randomly choosing any surrounding cell [$P_{matrix} = 1/(9 - n_{barr})$], where n_{barr} is the amount of barrier cells)

$$P_{leave} = n_{mat} \cdot P_{matrix}.$$

We included a correlation factor P_c of maintaining direction within a day, which gives the probability of the next cell being in the same direction of movement. The hierarchy is preference of dispersal habitat over correlation in movement direction. The first direction of every day is chosen randomly (Revilla et al., 2004).

Each day, we assign a dispersing lynx a certain amount of movement steps s based on a probability $P(s)$ using the power function

$$P(s) = \varphi \cdot \left(1 - \left(\frac{s - 1}{s_{max} - 1}\right)\right)^x,$$

with an exponent x, giving the probability to move many or few steps per day, and parameter s_{max} that gives the maximum number of steps that a dispersing lynx can cover during one day and a normalization factor φ scaling $P(s)$ between 0 and 1. $P(s)$ is a good descriptor of the empirical distribution of daily movement distances.

2.7. Population scenarios

We release lynx in the patches considered for reintroductions (the Black Forest (53), Palatine Forest (56), Bavarian Forest (49), Harz Mountains (20), North-Eastern Forests (2) and Thuringian Forest (34); Fig. 1). Our goal is to assess the minimum number of female and male lynx required for successful reintroduction under the different mortality scenarios, and also the connectivity between these patches.

Assessing the minimum release population. We define the 'minimum release population' (MRP) as the population size whose chances of survival are >95%, measured as the percentage of extinction $P_{ext} < 5\%$, if it were to survive at least 50 years. As females are the basic unit, we increase the number of females and keep the number of males fixed to the amount of released females (Table 1). To assess the minimum number of males needed for an MRP, we use the obtained minimum amount of females necessary for an MRP as a fixed parameter and vary the number of males.

Isolation or connectivity of the patches. We define connectivity as the probability P_{col} of settling and reproducing in other patches. Population development in other patches is measured as the arithmetic mean of the observed exponential rate of increase $\bar{r}$ during the population persistence time T_P of all simulation runs n, t is time (years), N_{t+1} is the number of animals (residents + newborns) in a certain patch in the current year, and N_t the number of animals of the previous year in the same patch. Within the time of population persistence, we calculated the geometric mean of r (Caughley, 1980)

$$\bar{r} = \frac{\sum_1^n \frac{\sum_t^{T_P} \ln\left(\frac{N_{t+1}}{N_t}\right)}{T_P}}{n}.$$

We only considered residents and newborns to assess whether individuals (e.g., immigrants) have settled in these patches. Thus, the influence of this year's dispersers on population development was neglected and we could ensure that population growth was due to reproduction and settlement. When $\bar{\lambda} > 1$, where

$$\bar{\lambda} = \overline{e^r}$$

the population has increased. We used the z-score to calculate the proportion of the one-tailed normal curve that lies beyond (i.e., is more extreme than) a given normal deviate, where $Z = (\bar{r} - \mu)/\sigma$ (Zar, 1999); in this case it is the proportion of the curve that lies beyond the stable state of population development (i.e., $\mu = 0$, no growth). We distinguish different probability classes of increasing population trend P_{col}, i.e., (1) >0.75, (2) >0.5 and <0.75, (3) >25 and <0.5, (4) >0.05 and <0.25, (5) >0.01 and <0.05 and (6) <0.01. For example, probability classes of (2) have a positive population trend in more than 50% of cases. Probability classes of

(6) indicate that at least one female in 50 years and 100 repeated simulations settles in the patch ($P = 0.0002$). Note that these are extreme cases. We define patches linked with a probability class of at least (6) as connected.

3. Results

3.1. Model sensitivity

For the sensitivity analysis we simulated an increasing amount of females and males in the Harz Forest with different parameter values for reproduction and for the nine mortality scenarios (Table 1). We chose the Harz Forest to highlight the applied nature of our study, as lynx have been released there recently. We took mortality Scenario 5 ($P_{birth} = 0.75$, $MR_{res} = 0.2$, $MR_{disp} = 0.5$; Table 2) as the reference scenario because it yielded the current knowledge on overall mortality rates (see below: 'Plausible parameter ranges').

Deviations from the 20% envelope occur with different mortality rates for resident individuals and different birth rates. If more than five females and males are released in our reference scenario, the mortality rate of dispersers plays a crucial role for the survival of the whole population (Fig. 2). Dispersers have to fill the gaps in the reproducing part of the population, especially when birth probability is low or resident mortality high.

A higher birth probability of 0.95 affects the minimum number of females needed to establish a viable population. It is decreased to 6 females (Fig. 2(c)). For a birth probability of 0.5, only mortality scenarios with very low mortality rates for residents and dispersers show a trend to reach the MRP with at least 10–20 females, depending on dispersal mortality. As expected, we can therefore state that the survival of residents is the most important factor for establishing a viable population, which was also predicted to be important for other species of predators, such as Iberian lynx *Lynx pardinus*, cheetahs *Acinonyx jubatus*, badgers *Meles meles*, vultures *Gyps fulvus* or brown bears *Ursus arctos* (Crooks et al., 1998; Wiegand et al., 1998; Van Appeldoorn et al., 1998; Gaona et al., 1998; Sarrazin and Legendre, 2000).
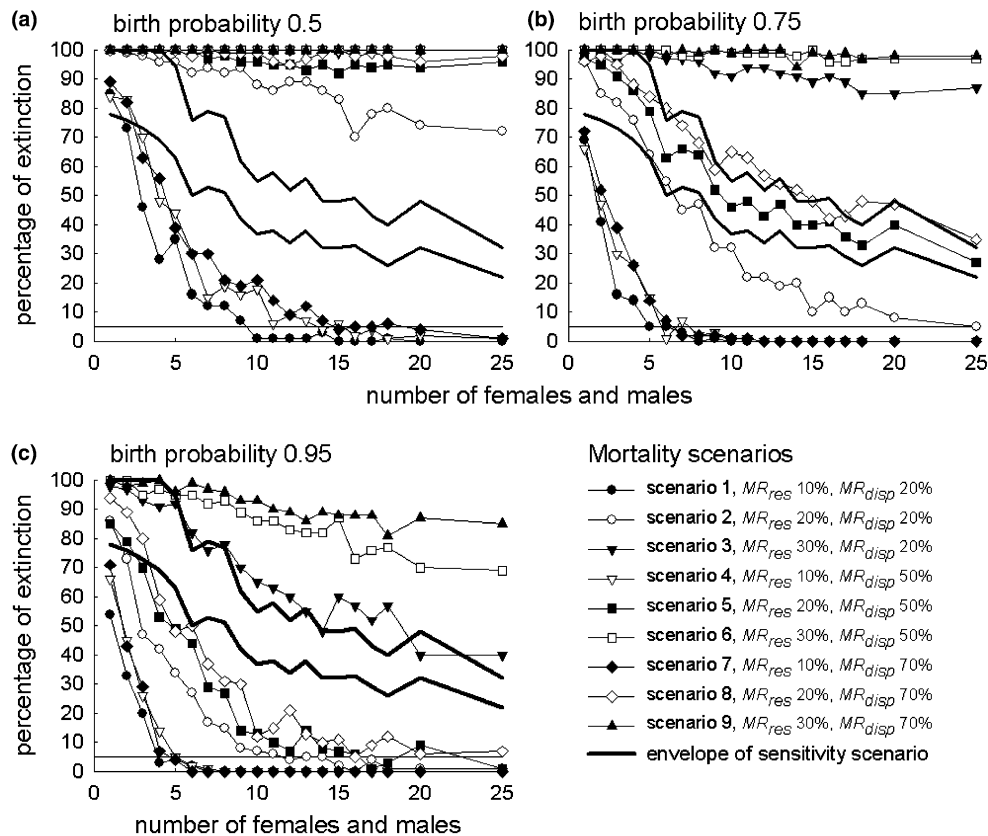

Fig. 2. Extinction probability of the Harz population under different mortality scenarios and birth probabilities when the same number of females and males was released. Only scenarios with low mortality values for residents reach a viable population within a time horizon of 50 years. The envelope of our reference Scenario 5 (see (b)) shows that the most sensitive parameters are the birth rate and the mortality rate of residents. The lower the birth probability, the more important the initial number of released animals.

Table 3
Minimum number of females needed to establish a viable population under the mortality scenarios for the different source locations (Fig. 1)

Location (patch no.)	Patch size [km^2]	Occupied HR (SD)		Mortality scenario								
		Females	Males	1	2	3	4	5	6	7	8	9
Northern Black Forest (53)	1934	18 (3)	11 (2)	7	–	–	6	–	–	9	–	–
Bavarian Bohemian Forest (49)	1849	18 (3)	11 (2)	6	30	–	7	–	–	7	–	–
Palatine Forest (56)	5232[a]	13 (2)	8 (1)	8	–	–	9	–	–	9	–	–
Harz (20)	1566	15 (2)	9 (1)	7	–	–	8	–	–	7	–	–
North-Eastern Forests (2)	1721	11 (2)[b]	7 (1)	17	–	–	–	–	–	–	–	–
Thuringian Forests (34)	1676	16 (2)	10 (1)	7	–	–	8	–	–	10	–	–

Birth probability is 0.75 and the time horizon 50 years. We released the same amount of females and males in each patch. If an MRP is reached in a mortality scenario, the minimum number of females is given. Also shown is the maximum carrying capacity of resident lynx reached and the patch size. The number of occupied home ranges (HR) was measured for viable populations as the average number of home ranges after the first 20 years until the maximum time step of 50 years.

[a] Palatine and Vosges Mountains in France together. The size of the German part is 1354 km^2. Lynx emigrating into the Southern Vosges Mountains were deleted.

[b] The low number of occupied home ranges in comparison to the patch size indicates that not all the space was continuously occupied due to the increased mortality on the two highways intersecting the patch.

3.2. Population scenarios

Assessing the minimum release population. If an overlap of one to three female territories per male is assumed, the Harz Forest (20) has a carrying capacity of 15 ± 2 female resident lynx and 9 ± 1 male resident lynx. This results in a density of about 1 female resident lynx per 100 km^2 of breeding habitat, which also holds for the other source patches, with the exception of the North-Eastern Forests (2) (Table 3), which are fragmented by two motorways.

For low mortality rates of residents in the Harz Forest (mortality scenarios 1, 4, 7; Table 3) and a realistic annual birth probability of 0.75 per resident female, the probability of extinction drops relatively quickly below 0.05 with an increasing number of females, i.e., for at least 8 released females (and 8 released males) we reach the requirements for an MRP. Mortality rates of dispersers did not affect the viability of the population if the resident mortality was very low (Fig. 2(b)). Lynx pairs released in addition to 8 pairs had no effect on population development. The optimal sex ratio for scenarios reaching an MRP (Scenarios 1, 4, 7) was reached with about 8 females and 5 males in the Harz Forest (Fig. 3).

Assuming higher mortality rates of residents of about 0.2, which are realistic figures known from lynx populations in unprotected areas with poaching or expected road casualties (Jedrzejewski et al., 1996; Gaona et al., 1998; Ferreras et al., 2001), the requirements for an MRP are not met (Fig. 2(b)). However, the mean persistence time of a population with resident mortality of about 0.3 (Scenarios 3, 6 and 9) was about the life span of an individual lynx (in years ± SD: e.g., for the Harz Forest: 17 ± 7 in Scenario 3, 14 ± 5 in Scenario 6, 12 ± 4 in Scenario 9). This indicates that monitoring programs should be launched for a long period before
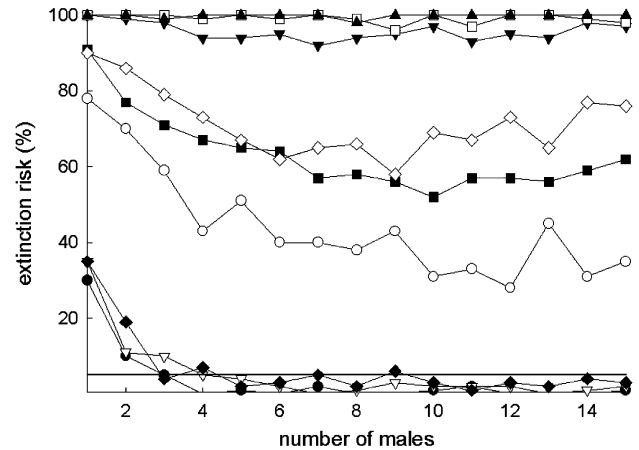

Fig. 3. Influence of an increasing number of male lynx on population development in the Harz Forest under different mortality scenarios. Eight females are fixed. For legend see Fig. 2.

the success of a species reintroduction can be assessed, and that care should be taken to keep adult mortality very low.

We obtain similar requirements for an MRP for the northern Black Forest (53), the Palatine Forest (56) and the Thuringian Forest (34). Six to ten females need to be released, and it is only the scenarios with low resident mortality that yield viable populations (Table 3). However, in the Bavarian Bohemian Forest (49) a viable population can even be obtained with a higher resident mortality, but only if the number of released females is high (Scenario 2, Table 3). By contrast, a viable population in the North-Eastern Forests (2) is only likely given a high number of initially released females and very low mortality rates of both residents and dispersers. The differences between these patches are explained by the different mortality rates of the dispersing animals (Table

Table 4
Total annual mortality rates [%] of dispersers in the different source patches due to different road and motorway densities under the different mortality scenarios

Location (patch no.)	Road density [km/km²]	Patch size [km²]	Length [km] of linear barriers			Mortality scenario								
			Main roads	Motorway	Main rivers	1	2	3	4	5	6	7	8	9
Northern Black Forest (53)	0.17	1934	336.8	26.1	–	36.7	40.7	41.4	61.8	65.7	65.0	72.9	74.9	75.0
Bavarian Forest (49)	0.01	1849	21.4[a]	–	–	9.3	11.1	12.9	27.2	31.3	33.6	47.2	52.1	52.2
Palatine Forest (56)	0.15	1354	196.5	21.5	–	26.7	33.8	36.1	44.2	54.7	56.6	53.3	63.3	66.2
Harz (20)	0.19	1566	303.7	–	–	19.1	21.5	25.0	47.2	54.0	55.0	63.2	69.0	69.6
North-Eastern Forests (2)	0.07	1721	125.1	74.8	35.3	58.2	61.6	61.7	77.0	78.3	78.4	83.8	84.4	83.9
Thuringian Forests (34)	0.13	1676	223.3	–	–									

The parameters for crossing linear barriers have been adjusted for the Harz Forest.

[a] Only the roads on the German side could be considered.

4). Even in the low dispersal mortality scenarios (Scenarios 1, 2, 3), the total annual mortality rates of dispersers are up to three times higher in the North-Eastern Forests (2) than in the Harz Forest (20) since the former are divided by two motorways and flanked by another (Fig. 1); the population in the North-Eastern Forests (2) could not spread because all the dispersers were killed on the motorways. Accordingly, the extinction risk of the whole source patch was much higher, and on average only 11 females occupied territories even though there was room for at least 17. By contrast, the road density in the Bavarian Bohemian Forest (49) is low, as is the annual mortality rates of dispersers (Table 4). This shows that dispersing lynx represent a buffer mechanism enhancing the viability of the whole population, because vacant territories can be occupied quickly (Grimm et al., 2005).

Patch connectivity. Generally speaking, connectivity to other patches (i.e., that at least one female settled in another patch in 50 years and 100 repeated simulation runs) occurs for each source patch and different mortality scenarios, and all the source patches are interconnected via target patches (Fig. 1; Appendix). The Thuringian Forest (34) would even be directly connected to the four source patches Harz Forest (20), Rothaar Mountains (27), Spessart (40) and Erz Mountains (29). However, sporadically arriving females are no guarantee of colonization.

The chances of an increasing population trend in the target patches due to migration from other patches are extremely low. Only the German–Czech border (49, 48, 41, 44, 39), the northern and southern Black Forest (55, 53), Palatine Forest and the Vosges Mountains (56, 52) and Thuringian Forest and the Rhön (32, 34) could be colonized permanently with a probability $P_{col} \geqslant 0.5$ within a time frame of 50 years. Patch connectivity mainly occurs for scenarios with low resident mortality (Scenarios 1, 4, 7). Population spread across Germany is very restricted, although occasional individual exchange is possible.

4. Discussion

PVA can be a valuable tool to support practical conservation and can be used to evaluate and design management methods (Ebenhard, 2000). The basic question of a PVA is 'What are the minimum conditions for the long-term persistence and adaptation of a species or population in a given place?' (Soulé, 1987). Population viability analysis has been a specific field of research in conservation biology since the mid-1980s and has been conducted for a variety of species (e.g. Gaona et al., 1998; Hansen et al., 1999; McCarthy et al., 2000, 2001; Penn et al., 2000; Kelly and Durant, 2000; Haight et al., 2002). Unfortunately, PVA has a few drawbacks linked to the parameterizing of models, making the results uncertain and unreliable (Beissinger and Westphal, 1998). PVA's significance and usefulness are rooted in its ability to compare different management options (Reed et al., 2002; Brooks et al., 2002), and we show an example of how different mortality scenarios affect the probability of the reintroduction of a lynx population succeeding.

One important advantage of modelling is that a model puts the data and knowledge on the system into a logical framework and allows exploring the consequences of this knowledge at spatial and temporal scales which escape observation or experiments. This is especially important for PVA which operates usually at time horizons of 50 or 100 years and require risk assessment. Clearly, scale issues are fundamental to PVA. For example, not only minimum conditions from the ecological point of view are relevant but also the scale at which these conditions need to be analyzed to respond to the specific objectives of the PVA. Our objectives required a spatial scale of entire Germany and could thus not include details such as stand age of forests which may be important when analyzing habitat selection within the spatial scale of home ranges. Nevertheless, we selected the maximum spatial resolution sustained by our data (1 km²) which was also necessary to capture the essence of the response of dispersing lynx to landscape structure.

Processes at all other spatial scales relevant to our objective (e.g., selection of home ranges) were covered by rules which translated the minimum 1 km scale to the required scale.

4.1. Limitations of our model

We included into our model the most important known factors of lynx biology at a spatial resolution necessary to respond to our objectives. Those include landscape structure (which defined the locations where lynx may breed and canalized dispersal), mortality risk when crossing linear barriers such as highways, dispersal, social structure and demographics. We found clear and robust answers to our questions. However, as any model, we needed to make simplifying assumptions and have to discuss their potential impact on our results.

Empirical studies have shown that small populations in the wild can suffer increased risk in the long term because of inbreeding (Saccheri et al., 1998; Sobel et al., 1999; Ebenhard, 2000; Keller and Waller, 2002). The long-term survival of a population is influenced by genetic variation, which is a prerequisite for evolutionary adaptation to a changing environment, and the maintenance of population numbers and genetic variation should be a key aspect of plans for long-term population management (Lande and Barrowclough, 1987). Our model does not include the effects of inbreeding and genetic stochasticity, i.e., random genetic drift, and could underestimate the risk of extinction (although cf. Keane et al., 1994; Ballou, 1997). However, the founder effect could be greatly limited with a release number of 15–20 individuals since this number of effective founders can have a quite diverse genetic pool. It would be necessary to ascertain how many initial individuals or how many immigrants per generation are needed to avoid genetic bottlenecks or inbreeding depression. The genetic structure and variability of the two Swiss lynx populations reintroduced in the Alps and Jura Mountains are presently being studied, and the results should be included in further assessments of suitable areas for reintroduction.

Another potential mechanism known from general PVA models to influence viability are catastrophic events as an element of environmental stochasticity that can sharply reduce population size in a short time. Then again, severe environmental changes such as a sudden reduction of the main prey (roe deer) or breeding habitat, or a severe disease, are unlikely for lynx, and there is no historical information on their occurrence for this species. Nevertheless, there is evidence of lynx losses due to infections with mange in the Swiss Alps. Though it seems improbable that mange will occur as an epidemic in lynx, it may have an impact on the population (Ryser-Degiorgis et al., 2002). The impacts of occasional deaths due to disease have been taken into account as 'baseline mortality' in the model.

One of the major uncertainties in the model is that we did not consider the behavioural flexibility of lynx. They could probably learn to use underpasses or green-bridges, and this would reduce the mortality risk. In this case, the model results would underestimate patch connectivity. Additionally, lynx react to many small-scale features in the landscape during dispersal, such as ribbons of vegetation along rivers (Zimmermann, 2004), and this information is lost on the 1 km^2 scale of our habitat model. But this has been balanced in the dispersal model by a certain probability to step into matrix, which accounts for the presence of small scale factors that attract lynx into the matrix.

4.2. The future of a lynx population in Germany

According to the model results, a population in the Harz Forest (20) under the current landscape situation would only be viable if the mortality rates of the resident animals could be kept very low. As known from other populations in Spain or Poland, such a mortality scenario is rather unrealistic. In areas of suitable habitat outside national parks where road mortality and poaching still occur, the mortality rate may be as high as 0.3 (Ferreras et al., 2001). Even in the protected area in Poland, poaching makes up 71% of the population's total mortality rate of 0.37, while in Switzerland road kills and poaching account for 70% of mortality (Zimmermann, 1998; Schmidt-Posthaus et al., 2002). Whether these human-induced mortality factors can be neglected in Germany is thus highly unlikely. Consequently, under the expected mortality scenarios the probability of a lynx reintroduction into the Harz Forest succeeding is only about 0.5 for a time window of 50 years (Fig. 2(b)).

The results show that viable populations would also be possible in the other major patches such as the Thuringian Forest (34), the Black Forest (53, 55) and Palatine Forest (56), but only assuming low mortality for resident and dispersing lynx. A linkage in the form of the colonization of other source patches is not given for the source patch Harz (20). An exception is the Bavarian Bohemian Forest (49) that is connected along the German–Czech border with the Erz Mountains (29), a result that is also supported by field data (Wölfl et al., 2001). The Thuringian Forest (34) could also be linked with the patches along the German–Czech border (29, 28, 39, 44, 49) and with the Rhön (40).

New motorway construction, as planned and being carried out between the Harz Forest (20) and the Thuringian Forest (34) as well as between the Erz Mountains (29) and the Bavarian Forest (49), will additionally worsen colonization success in new patches. Even short motorway sections can play a significant role as barriers. In Slovenia, a stretch of motorway 30 km

long accounted for 31% of the total mortality of brown bears *U. arctos* in the area (Kaczensky et al., 1996). The fact that lynx are 'bad colonizers' is apparent from the Swiss Alps, where lynx had to be translocated from the Western to the Eastern population in the Alps. Barriers were not only constituted by high and snow-capped mountain rifts, but especially by urbanized valleys, which additionally contain motorways or waterways. It can therefore be concluded that in Germany lynx will probably remain restricted to the release patch. But there is also positive news in a postulation of the Federal Nature Conservation Agency for protecting the movement corridors between the source patches, including measures to minimize animal–vehicle collisions (Reck et al., 2004).

Movement in fragmented landscapes was included to a certain degree by using data from the Swiss Jura Mountains, although there were too few data to determine whether lynx actively avoid motorways or if instead fences prevent them from crossing. If the latter applies, movement could be guided, and green-bridges or underpasses would reduce the mortality risk of dispersers. Experience of the effectiveness of wildlife passages mainly stems from other species (Kaczensky et al., 1996; Rodríguez et al., 1996, 1997; Clevenger and Waltho, 2000; Gloyne and Clevenger, 2001; Clevenger et al., 2001). This implies testing methods to reduce traffic collisions, including measures to increase the attractiveness of existing bridges and underpasses for wildlife.

At any rate, it is questionable whether a lynx population will have a bright future in Germany if we conclude that in certain areas they will be restricted to their release patches. Of course, survival may be possible in the individual patches for some time, but releases in isolated patches do not contribute to an overall connected population. Wildlife conservation means more than simply releasing a species in a given area. We must consider the development of the population as well as linkage to other existing populations. In this sense, we strongly recommend using PVA before launching reintroductions to assess the most suitable areas.

4.3. Recommendations for reintroductions

The results show that about 10 females are needed to successfully establish a minimum viable population if mortality is kept low. We also showed that the success of a reintroduction can be influenced by the number of lynx released. This tallies with findings on critical population sizes for other large carnivores (e.g. Saether et al., 1998). If demographic parameters such as the birth rate are uncertain, it would be better to release more animals to 'be on the safe side'. This could also reduce the risk of inbreeding. In addition, more females than males can be released. However, high mortality among residents cannot be compensated for by releasing a large number of

animals. Monitoring programs should be launched that exceed the life span of the animals to assess reintroduction success (IUCN/SSC, 1995).

This study shows that simulation models are useful tools for establishing the comparative effectiveness of reintroduction plans designed to increase the viability of the species (Van Appeldoorn et al., 1998). We recommend PVA and the assessment of land change scenarios (Dale et al., 1994; White et al., 1997; Pearson et al., 1999; Urban, 2000; Serneels and Lambin, 2001; Morris et al., 2002) before a species is released, so that efforts can be focused on the most promising and fruitful areas, as well as releasing an appropriate number of animals that is most likely to lead to a successful reintroduction.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biocon.2005.02.015.

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