

Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx

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Summary

1. Although many reintroduction schemes for the Eurasian lynx *Lynx lynx* in Germany have been discussed, the implications of connectivity between suitable patches have not been assessed.

2. We introduce an individual-based, spatially explicit dispersal model to assess the probability of a dispersing animal reaching another suitable patch in the complex heterogeneous German landscape, with its dense transport system. The dispersal model was calibrated using telemetric data from the Swiss Jura and based on a map of potential lynx dispersal habitat.

3. Most suitable patches could be interconnected by movements of dispersing lynx within 10 years of reintroduction. However, when realistic levels of mortality risks on roads were applied, most patches become isolated except along the German–Czech border. Consequently, patch connectivity is limited not so much by the distribution of dispersal habitat but by the high mortality of dispersing lynx. Accordingly, rather than solely investing in habitat restoration, management efforts should try to reduce road mortality.

4. *Synthesis and applications.* Our approach illustrates how spatially explicit dispersal models can guide conservation efforts and reintroduction programmes even where data are scarce. Clear limits imposed by substantial road mortality will affect dispersing lynx as well as other large carnivores, unless offset by careful road-crossing management or by the careful selection of release points in reintroduction programmes.

Key-words: conservation, large carnivores, large-scale approach, *Lynx lynx*, movement, spatially explicit individual-based model, species reintroduction

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Introduction

In densely populated regions, many animal populations are small and isolated due to habitat loss and fragmentation. If these populations contain only a few individuals, the probability of local extinction is high. Dispersal is a key process in determining the survival of

such spatially structured populations (Lima & Zollner 1996; Schippers *et al.* 1996; Collingham & Huntley 2000; Thomas, Bagnette & Lewis 2000). Particularly in intensively used landscapes, it is important to maintain exchange between subpopulations to reduce the risk of extinction and the loss of genetic diversity. Moreover, information on movement rates is critical for predicting extinction thresholds (Fahrig 2001). In short, the chances of dispersal succeeding depend on the connectivity of the landscape, and are consequently decreased in intensively used landscapes by barriers to dispersal imposed by humans, such as roads and the destruction

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of suitable habitat (Kaczensky *et al.* 1996; Mace *et al.* 1996; Cleveenger & Waltho 2000; Trombulak & Frissell 2000; Cleveenger, Chruszcz & Gunson 2001; Gibeau *et al.* 2002; Kerley *et al.* 2002; Saunders *et al.* 2002).

Models can be used to describe dispersal and estimate connectivity. The most recent developments in spatially explicit population simulation models (SEPM) have demonstrated the usefulness of integrating demographic and dispersal data with detailed knowledge of the landscape geometry (Akçakaya & Sjören-Gulve 2000; Wiegand, Revilla & Knauer 2004). However, there is a general lack of empirical information on the behavioural responses of animals to landscape structure (Turner *et al.* 1995; Lima & Zollner 1996), which may hamper the application of SEPM. Consequently, the dispersal modules of SEPM are often based on *ad hoc* assumptions about interactions between individuals and landscape structure as well as about the relevant spatial and temporal scales on which they take place. As a result, the initial enthusiasm for the use of such models has been dampened by criticism regarding the immense data requirements of SEPM, particularly the problems associated with parameterizing the dispersal process (Doak & Mills 1994; Ruckelshaus, Hartway & Kareiva 1997; Beissinger & Westphal 1998).

The case of a large carnivore, the Eurasian lynx *Lynx lynx* L., in Germany exemplifies the fate of many endangered species in human-dominated landscapes. During the first half of the 20th century the lynx disappeared everywhere in central Europe west of the Slovakian Carpathians due to persecution, habitat destruction and fragmentation, but it is now recovering in several European countries (Breitenmoser *et al.* 2000). In Germany various locations have been considered for reintroduction (Schadt *et al.* 2002a,b). Meanwhile natural immigration has occurred in the Bavarian Forest due to a reintroduced population expanding in the Bohemian Forest, Czech Republic, and a new reintroduction programme is underway in the Harz Forest (Wölfel *et al.* 2001).

Before considering reintroduction it is important to assess the suitability of the landscape for breeding habitat, and the connectivity of the candidate patches of potentially suitable habitat to optimize the success of reintroduction. Individual exchange among patches is important for the long-term survival of a population in small habitat patches. The first step has already been

taken by assessing the suitability of the German landscape for lynx: suitable habitat is fragmented, with many patches too small to hold viable populations (Schadt *et al.* 2002a,b). The next important step is to address the issue of dispersal and connectivity using some form of SEPM.

With lynx in Germany still extremely scarce, an inevitable issue in any reintroduction programme, data scarcity presents a major problem for parameterizing a SEPM. No empirical data are available for Germany, but there is limited information from other field studies. To deal with the uncertainty arising from the lack of direct measurements of our model parameters, we used the pattern-orientated modelling approach (Grimm *et al.* 1996; Wiegand *et al.* 2003). In this approach, the information needed to parameterize a model need not be directly provided by field measurements but can be inferred by comparing model output with a variety of observed 'patterns', which in our case arise from telemetric field data.

In this study, we introduce a model to assess the probability of dispersing lynx reaching other patches in complex heterogeneous landscapes. The objectives of the study were to: (i) parameterize an SEPM for lynx, and thus (ii) assess the connectivity between patches that could be hotspots for interactions between lynx populations, (iii) investigate the influence of road mortality on connectivity and (iv) assess the possible success of the reintroduction initiatives in Germany.

Methods

STUDY AREAS AND TELEMETRIC DATA BASIS

We used the telemetric data from dispersing lynx collected between 1988 and 1991 in the Swiss Jura Mountains to calibrate our dispersal model (Breitenmoser *et al.* 1993) (Table 1). The landscape of this area is comparable to Germany regarding land use, fragmentation and inhabitants. We obtained 303 radio-locations of six dispersing individuals (five females, one male) separated by intervals of at least 1 day (interday level). Radio-locations of subadults that were accompanying their mother in the natal home range before separation or had later established a home range were not used. The accuracy of the telemetric locations was 1 km², so we defined this as our spatial grain (Fig. 1).

Table 1. Telemetry locations of dispersing Eurasian lynx from Switzerland used to derive the patterns for model calibration (modified after Breitenmoser *et al.* 1993)

Lynx	Total observation period (days)	Number of locations	Start of dispersal	Last location	Maximum distance from starting point (km)	Fate
M16	78	74	03-04-90	19-06-90	28	Dead
F17	44	23	10-04-90	23-05-90	51	Dead
F20	284	121	24-03-91	31-12-91	64	Still alive
F13	144	56	27-03-89	17-08-89	25	Dead
F12	29	20	30-03-88	19-05-88	76	Dead
F19	22	9	15-04-91	05-05-91	6	Collar failure

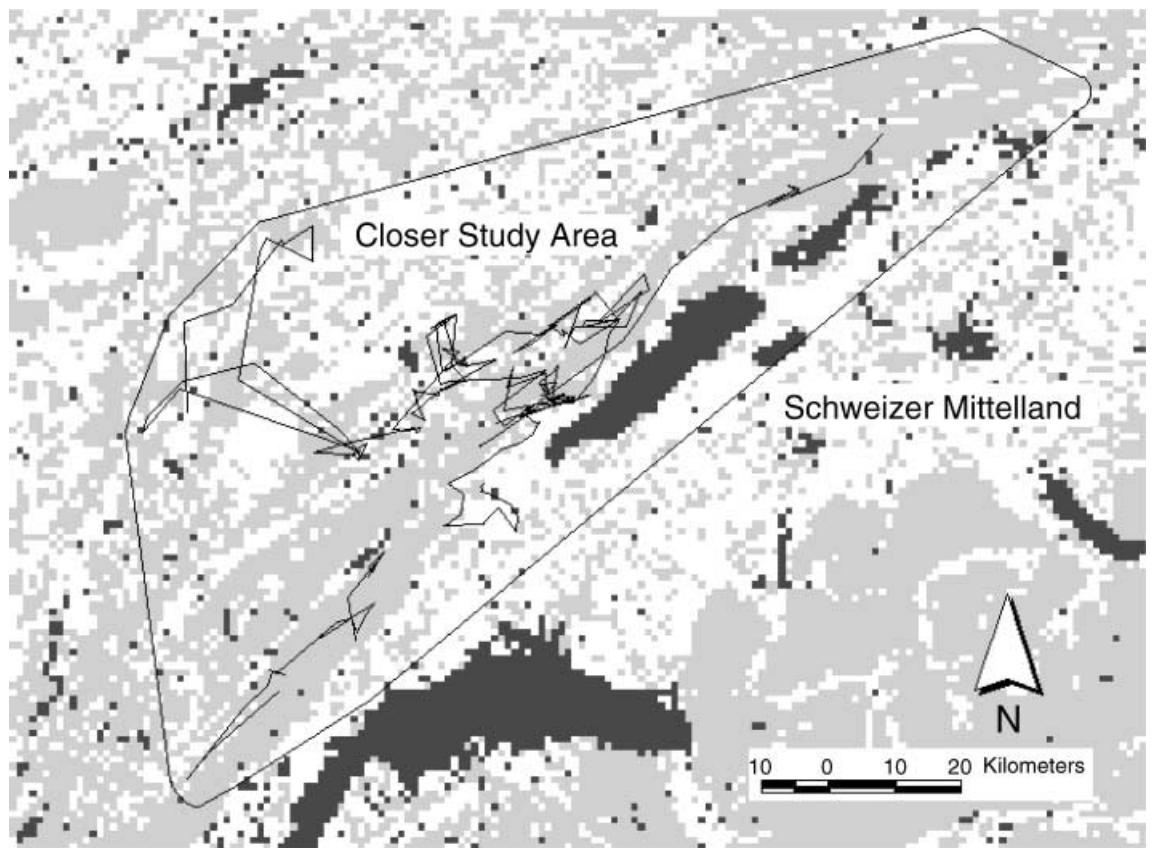


Fig. 1. Dispersal paths of the six dispersing subadult lynx in the Swiss Jura Mountains. Time laps between the locations are different and can be up to 20 days. Light-grey areas represent habitat suitable for dispersal and breeding populations, dark-grey areas are barriers (lakes and urban areas) and white areas represent matrix.

We then applied the calibrated dispersal model to the landscape of Germany, which has a patchy distribution of suitable lynx habitat. The human population density in Germany averages about 230 inhabitants km^{-2} , falling to about 100 in remote areas such as the low mountains of the Black Forest and the Bavarian Forest. Thirty per cent of the total area is forested and 2.5% is protected within national parks. Germany has a very dense road network consisting of 11 000 km of motorways and more than 50 000 km of highways and main roads. The average traffic flow lies between 35 000 and 55 000 cars per day on motorways, and between 2500 and 30 000 on highways and main roads.

THE HABITAT MAP

We used habitat suitability maps with a grid size of 1 km^2 for the area to which the model was applied (Germany) as well as for a closer study area (CSA), the area of model calibration. The CSA was the minimum convex polygon of all locations including residents within the Jura Mountains (Fig. 1). The habitat types of our maps could be summarized as breeding, dispersal, matrix and barrier habitat. Breeding habitat was determined by logistic regression as described in Schadt *et al.* (2002b) and was formed by cells with a probability cut-off level $P > 0.5$ based on a variable containing extensively used areas (forest and other

non-forested semi-natural land-use types) on a scale of about 100 km^2 . To define dispersal habitat, matrix and barrier, we assessed differences in the original seven habitat classes, (i) urban areas, (ii) forested areas, (iii) pastures, (iv) agriculture, (v) non-forested semi-natural land-use types, (vi) wetland and (vii) water bodies, in the CSA between the telemetric locations and the randomly distributed points with a log-likelihood ratio test. Only 48.2% of the random points were distributed in forest and other semi-natural non-forested land, compared with 85.5% of the telemetric locations. Considering only habitat classes with lynx observations revealed a departure from homogeneity between the four categories agriculture, pasture, forest and other semi-natural land cover ($G = 227$, $P < 0.01$, d.f. = 3). We thus defined any forested area and breeding habitat as preferred dispersal habitat (see Schmidt 1998; Palomares *et al.* 2000).

Urban areas, wetlands and lakes contained no lynx observations and were defined as barriers. The remaining areas, such as pastures and agricultural areas, were summarized as matrix, which is normally avoided by dispersing lynx and only used occasionally for passage. To simulate the effect of road mortality on connectivity, we created a second map with linear elements such as highways and main roads (two lanes), motorways (≥ 4 high-speed lanes) and large rivers (> 100 m wide).

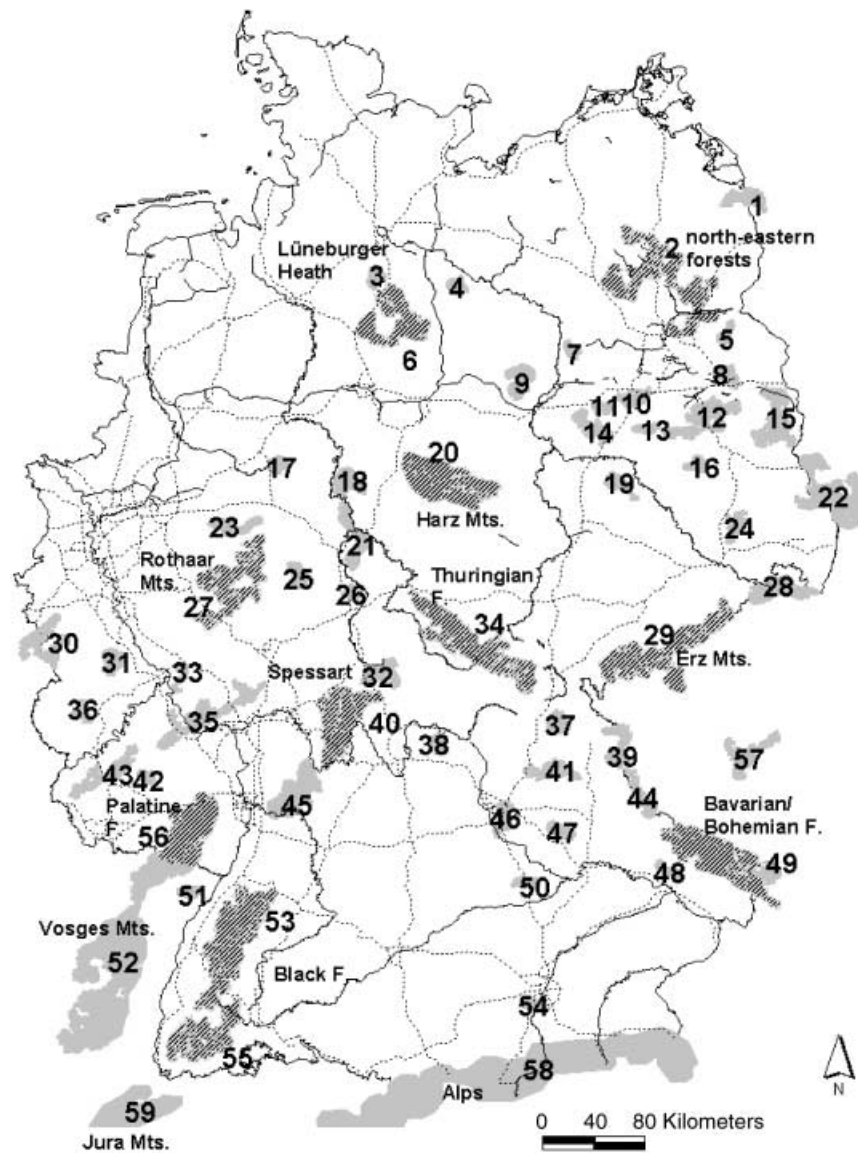


Fig. 2. Source and target patches for measuring the connectivity of the German landscape. Each patch is numbered. Hatched are source patches > 1000 km², grey are target patches > 100 km² (female home range size). Dotted lines are motorways, black lines are main rivers. Connectivity between the patches for the different scenarios is given in Appendix S1 in Supplementary material.

We defined source patches as the major patches of special management interest (> 1000 km²) and target patches as every suitable area > 100 km², which corresponds with the average home range size of a female lynx (Breitenmoser *et al.* 1993). Altogether, we obtained 59 patches, of which 11 were source patches (Schadt *et al.* 2002b) (Fig. 2).

MODEL DEVELOPMENT AND CALIBRATION

We developed behavioural rules on lynx dispersal that operated on an intraday time scale. The rules were based on general knowledge of dispersal and on movement analyses of the Iberian lynx *Lynx pardinus* (Revilla *et al.*, in press) and were implemented in a spatially explicit individual-based dispersal model (SEDM). Note that the Iberian lynx data were used not for model parameterization but to develop the dispersal rules.

The analysis of telemetric data for model calibration and the model application were based on the same habitat map as Schadt *et al.* (2002b). We analysed the telemetric data to obtain ‘patterns’ that could be directly compared with the model output. The patterns (see Movement patterns and parameter assessment) were properties of the dispersal path on the interday level, i.e. time laps separated by 1 day, and the seasonal level, i.e. the time span over which the lynx dispersed in the field.

The model was first implemented for the Swiss Jura Mountains for model calibration. During the model calibration we followed the protocol of data collection in the field as closely as possible. We exactly simulated the time span of each of the six dispersing lynx in the Jura Mountains on the habitat suitability map as observed in the field (Table 1), and each simulated lynx was released in the same location where they started

Table 2. Parameter ranges of the dispersal model, results of the calibration and parameters used for application to Germany. Results of the model calibration are given as the mean (\pm SD) of the best ($n = 1625$) parameter sets

Parameter	Symbol	Model calibration		Model application
		Range explored	Result	Parameter values used
Exponent of power function	x	1, 3-11, 5-22, ... , 20	11 (\pm 5)	100 parameter sets
Maximum number of intraday movement steps	s_{\max}	10, 20, 30, ... , 70	45 (\pm 17)	100 parameter sets
Probability of stepping into matrix	P_{matrix}	0, 0-01, 0-02, ... , 0-11	0-03 (\pm 0-02)	100 parameter sets
Probability of keeping the previous direction	P_c	0, 0-1, 0-2, ... , 1	0-53 (\pm 0-30)	100 parameter sets
Maximum residence in matrix cells	P_{maxmat}	Measured in the model	5 (\pm 4)	9, 40
Mortality probability on highways/rivers per crossing	M_{highway}	0, 0-15, 0-50, 0-75		0, 0-15
Mortality probability on main roads per crossing	M_{road}	0, 0-0005, 0-001, 0-002		0, 0-002
Baseline mortality probability per day	M_{base}	0, 0-0003, 0-0007, 0-001		0, 0-0007

dispersal after maternal separation. Thus, during model calibration we left out confounding demographic factors such as mortality. We analysed the simulated data in exactly the same way as the field data and compared simulated and observed patterns. The model rules operated on the intraday scale, where the response of the animal to the landscape configuration took place, and the patterns operated on the interday scale. Thus, we inferred parameters from the low scale (intraday) by matching patterns on the higher interday scale (Wiegand *et al.* 2003).

The parameter space of the model was systematically explored by covering the total possible parameter range (see below; Table 2). For each model parameterization we performed 100 replicate simulations to obtain a stabilized standard deviation ($< 1\%$ variability). We determined the best model parameterizations and model processes by systematically comparing the patterns extracted from the field data with the predicted patterns from the simulated data. A model parameterization was accepted when all the derived patterns (see below) were satisfied simultaneously (Wiegand *et al.* 2003, Wiegand, Revilla & Knauer 2004).

We used the linear regression of all parameterizations to find out how sensitive the model predictions were to the parameters. To assess the sensitivity of the model predictions to the remaining parameter uncertainty, we used linear regression of the accepted parameterizations (Wiegand *et al.* 2004). We scaled the dependent (pattern) and independent (parameters) variables to values between 0 and 1 and used the resulting regression coefficients β_i as indicators describing the sensitivity of the model output to the parameters. A coefficient $|\beta_i| = 1$ indicates strong sensitivity while parameters with small values $|\beta_i| \ll 1$ have little impact on the model prediction.

DISPERSAL MODEL RULES AND PARAMETER RANGES

Intraday number of steps

Lynx move one grid cell per step or stay in the cell, and each day we assigned a dispersing lynx a certain number

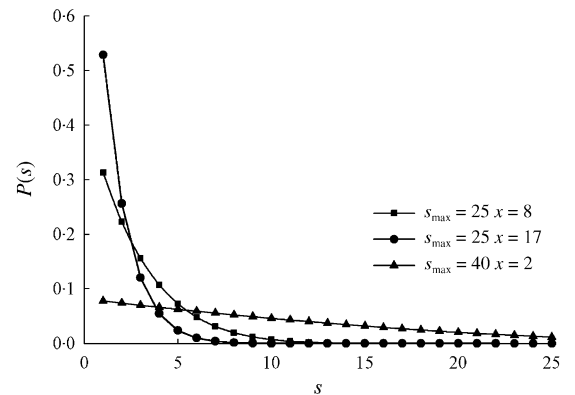


Fig. 3. Intraday step distribution for different parameter values, s_{\max} (maximum number of intraday steps) and x (exponent of equation 1, as described in the text).

of movement steps, s , based on a probability $P(s)$ (Fig. 3) using the power function:

$$P(s) = \phi \left(1 - \left(\frac{s-1}{s_{\max}-1} \right)^x \right) \quad \text{eqn 1}$$

with an exponent, x . Parameter s_{\max} gives the maximum number of steps that a dispersing lynx could cover during 1 day, and a normalization factor ϕ scaling $P(s)$ between 0 and 1, where:

$$\phi = \frac{1}{\sum_{s=1}^{s_{\max}} \left(1 - \left(\frac{s-1}{s_{\max}-1} \right)^x \right)}$$

The parameter range for s_{\max} was assessed by evaluating literature on lynx. In Poland the total distance travelled by Eurasian lynx during the period of activity (intraday) was on average 2.6–4.5 times longer than distances between locations taken once daily, which led to possible maximum distances between 26 and 46 km per activity period (Jedrzejewski *et al.* 2002). Similar figures apply to the Iberian lynx, for which the total maximum distance was 38.7 km within the period of activity (Revilla *et al.*, in press). From our telemetric data analysis in the Jura Mountains we therefore could

expect values between 30 and 55 km, as the daily maximum distance was 12 km ($n = 198$). We explored the parameter range for s_{\max} between 10 and 70 km. The exponent x of the power function was varied over a broad range to ensure large variability in step distribution (Table 2). Low exponent values yield linear distributions, whereas high exponent values raise the probability of a small number of movement steps (Fig. 3). The probability of moving to any of the eight adjacent cells or staying in the cell was determined by a certain searching strategy per step.

Correlated habitat-dependent walk

We assumed that dispersal direction depends upon local habitat quality as perceived by individual lynx. Consequently, the next cell on our map was chosen with a certain preference for dispersal habitat. The number of matrix cells, n_{mat} , was counted within the neighbourhood of three by three cells around the origin. The probability of leaving dispersal habitat, P_{leave} , was then dependant on the number of matrix cells around the cell of origin multiplied by a parameter, P_{matrix} , ranging from total avoidance of matrix ($P_{\text{matrix}} = 0$) to randomly choosing any surrounding cell [$P_{\text{matrix}} = 1/(9 - n_{\text{barr}})$], where n_{barr} is the number of barrier cells:

$$P_{\text{leave}} = n_{\text{mat}} \times P_{\text{matrix}} \quad \text{eqn 2}$$

We added a correlation factor, P_c , for keeping the previous direction within a day, which is backed up by analyses of the Iberian lynx (Revilla *et al.*, in press). P_c gives a probability between 0 and 1 of the next cell being in the same direction of movement; otherwise the next cell is chosen randomly. Note that the case $P_c = 0$ yields a random direction. The hierarchy was preference of dispersal habitat before correlation in the direction of movement. The first direction each day was chosen randomly.

During simulation runs, to adjust the model we measured the total number of consecutive steps that the animal moved in matrix habitat, P_{maxmat} . If a lynx was surrounded by matrix habitat, the probability of finding dispersal habitat again was very low because the searching type depended on the number of surrounding matrix cells. The measure P_{maxmat} can therefore be seen as a memory to return to dispersal habitat after an excursion to matrix, as observed for the Iberian lynx (E. Revilla, unpublished data). For model application to Germany we included the rule that a lynx returns to the location where it left the dispersal habitat when it reaches the threshold value of P_{maxmat} (= 9 cells; see below). To assess the sensitivity of this parameter and its implication for the connectivity of patches in Germany, we set the value of the parameter to an unrealistically high value of 40 matrix cells and compared the outcome with the results of our connectivity values gained by the adjusted value for P_{maxmat} with linear regression.

MOVEMENT PATTERNS AND PARAMETER ASSESSMENT

Based on our habitat suitability map, we defined four patterns that describe different properties of the observed dispersal path on a seasonal and a daily time scale. To decide whether our simulations matched a given pattern, we used statistical criteria along with published and unpublished data to define threshold values above which the pattern was satisfied.

Pattern 1: habitat use

Dispersing subadult individuals used dispersal habitat to a degree of 85.5% ($n = 303$) in the Jura Mountains. Randomization of the telemetric locations (10 000 samplings with replacement; Manly 1997) resulted in a distribution ranging from 78% to 92% (mean 84.34, SD 2.11) habitat use. As we know that matrix is only used for passage by dispersing lynx, we excluded the residual 5% in the lower tail and designated the pattern as satisfied when the mean of the simulated pattern was above 81%.

Pattern 2: average maximum distance

The maximum distance reached from the starting point of dispersal within the observation period was 76 km for the dispersing lynx in the Jura Mountains. The average maximum distance was 41.7 km (± 26.5 km SD, $n = 6$; Table 1; see Schmidt 1998; Zimmermann 1998). Owing to the high standard deviation in this pattern due to the different number of dispersal days of the subadults, we defined the pattern as replicated when the observed value of 41.7 km was inside the envelope (mean \pm SD) of the simulation.

Pattern 3: study area

We determined that a simulated lynx crossing the Schweizer Mittelland, the densely populated, rather flat, area between the Jura Mountains and the Alps (Fig. 1), did not satisfy the pattern study area. Since the beginning of the lynx project in the Jura Mountains, no lynx has ever been observed to cross this plain (U. Breitenmoser, unpublished data).

Pattern 4: step distribution

At the interday level, the distance moved was the Euclidean distance between two locations on consecutive days. Dispersing lynx moved on average 1.6 km (SD 2 km, range 0–11.5 km, $n = 198$). The distribution of distances at 1-km intervals follows the power function $P(d) = 0.70d^{-1.97}$ ($r^2 = 0.93$, $n = 198$), where $P(d)$ is the probability and d the net daily distance. We calculated the root of the mean squared deviation, ψ (equation 3), between simulated and observed distributions:

$$\psi = \sqrt{\frac{1}{12} \sum_{i=1}^{12} (\text{data}(i) - \text{sim}(i))^2} \quad \text{eqn 3}$$

where *data* and *sim* are the frequencies of the net daily distance distribution class (1–12 km) divided by the total number of observations. Randomization of the observed distribution (10 000 samplings with replacement) resulted in a distribution of the squared error, ψ , ranging from 0.012 to 0.046 (mean 0.029, SD 0.005). We defined the pattern as satisfied when the squared error, ψ , was below 0.037 excluding the residual 5% in the upper tail.

LINKING DEMOGRAPHICS TO THE LANDSCAPE

The application of the dispersal model to Germany to assess the connectivity of the suitable patches requires demographic parameters, i.e. different mortality risks per movement step (when crossing a linear barrier on our map) or day (baseline time-dependent mortality occurring stochastically). We estimated different mortality parameters for each of the two road types and rivers, and the per-day mortality probability, with a second pattern-oriented model calibration. To this end, we varied the mortality parameters across a broad range until we obtained results reflecting values reported in the literature (see below).

MODEL ANALYSIS

To consider the parameter uncertainty remaining after calibrating the dispersal model, we applied 100 randomly chosen parameterizations out of the accepted parameter combinations. In each source patch 100 lynx were released and allowed to disperse for 1, 3 and 10 years or until death in accordance with the model rules under different mortality scenarios. Because of the stochastic nature of the model, each lynx had a different pathway leading to arrival at various target patches.

Arrivals and mortality were registered. The connectivity between source and target patch was defined as the fraction of animals from the source patch that arrived at a certain target patch. Lynx were deleted at the border of Germany in scenarios with barrier mortality, because we did not have digital maps of the road systems of the adjacent countries. We avoided inferences on the connectivity of patches via corridors outside Germany.

To categorize the connectivity of the patches, we took the average connectivity plus one standard deviation as an optimistic assessment of the 100 simulation runs per parameter set. Connectivity was classified as: (i) very low connectivity, ranging between 1% and 5%; (ii) low connectivity, between 6% and 15%; (iii) medium connectivity, between 16% and 30%; (iv) high connectivity, between 31% and 50%, and (v) very high connectivity, with more than 50% probability of reaching another given patch.

We used non-linear regression to test for relationships between connectivity, distance between patches and the minimum number of linear barriers that had to be crossed, as connectivity is expected to be related to distance (Hanski 1994; Moilanen & Hanski 1998; Turchin 1998; Vos *et al.* 2001).

DISPERSAL SCENARIOS FOR GERMANY

Scenario 1: no mortality

This was our reference or baseline scenario. Neglecting dispersal mortality may highlight possible corridors between patches the effectiveness of which may depend on dispersal time and the configuration of the landscape.

Scenario 2: baseline mortality

Imposing baseline mortality, M_{base} , enabled us to distinguish the influence of roads and linear barriers on the connectivity of patches in Germany from other human influences such as poaching. We used values for daily mortality rates reflecting annual mortality rates of about 0.2, as given in the literature for dispersing animals (Tables 2 and 3). For example, in the protected population of Poland the annual mortality rate of subadult and adult lynx was on average 0.37 (Jedrzejewski *et al.* 1996). Poaching was the main factor, accounting for 71% of the total annual mortality rate (Jedrzejewski *et al.* 1996). Hence, the baseline mortality rate in this population was about 0.12. The annual baseline mortality rate of Iberian lynx dispersers was estimated to be about 0.22 without poaching and road deaths (Ferrerás *et al.* 2001).

Scenario 3: baseline and barrier mortality

Traffic accidents are the main cause of mortality of subadult lynx. Of 17 subadult lynx found dead in

Table 3. Parameter combinations used for the dispersal scenarios in Germany and their resulting annual mortality rates

Parameter			Results	Composed of		
M_{base}	M_{highway}	M_{road}	Total annual mortality rate (SD)	Baseline death	Death crossing motorways/rivers	Death crossing main roads
	0	0	0	0	0	0
0.0007	0	0	0.20 (0.01)	1 (0)	0	0
0.0007	0.15	0.002	0.51 (0.05)	0.31 (0.04)	0.40 (0.04)	0.29 (0.05)

Switzerland between 1988 and 1997, about 45% had died in traffic accidents, 25% had been killed by poachers, another 25% had died of diseases or natural accidents, and 5% were found dead of unknown causes (Schmidt-Posthaus *et al.* 2002). In a fragmented urban area north-west of Los Angeles, California, vehicular collision was the reason for at least 50% of the total mortality of bobcats and coyotes (Tigas, Van Vuren & Sauvajot 2002).

Total annual subadult mortality was estimated to be about 0.44 in the Jura Mountains and 0.56–0.6 in the Swiss Alps (Breitenmoser-Würsten *et al.* 2001). The total mortality rate for Iberian subadult lynx was estimated to be about 0.55 year⁻¹ (Gaona, Ferreras & Delibes 1998; Ferreras *et al.* 2001). Similar figures are reported for non-resident wolves *Canis lupus* in north-central Minnesota (0.48) and Alaska (0.62; Waser 1996). Hence, we set total annual mortality probabilities for subadults to 0.5, i.e. we kept the same parameter value of the baseline mortality, M_{base} , and added different mortality probabilities for crossing motorways, M_{motorway} , and main roads, M_{road} (Tables 2 and 3).

Results

MODEL CALIBRATION AND SENSITIVITY ANALYSIS

Only 17.6% of all model parameterizations ($n = 9240$) tallied with the data on lynx movement in Switzerland, i.e. satisfied all four patterns simultaneously (Table 2). Sensitivity analysis of the normalized dependent and independent variables of all parameterizations showed that all regression functions were highly significant ($P < 0.001$; Table 4). High r^2_{adj} values ($r^2_{\text{adj}} > 0.7$) for most patterns indicated that the linear regression models yielded good approximations. The most sensitive model parameter was the probability of stepping into matrix (P_{matrix}), followed by the maximum number of steps, s_{max} , and the exponent x of the equation for the number of intraday dispersal steps.

In the accepted parameter sets, the fit of the regression function was only high for the patterns habitat use

and average maximum distance. P_{matrix} was the decisive parameter for explaining the pattern habitat use, whereas the patterns step distribution and study area strongly depended on the maximum number of intraday steps, s_{max} , and the exponent of the equation, x , which were correlated ($r = 0.67$). This led to step distributions with very high probabilities of moving a few steps and rare events of large numbers of steps during the period of activity. This could reflect the behaviour of lynx remaining close to the carcass of their prey for up to a week and therefore moving only short distances before travelling a long way within a single night (Breitenmoser *et al.* 2000).

Within the accepted parameterizations the measure of residence in matrix cells P_{maxmat} was restricted to 5 cells (SD ± 4 ; Table 2), which is supported by analyses of Iberian lynx: the intraday maximum movement distance across a matrix was 9.5 km (Revilla *et al.*, in press). However, to assess the sensitivity of the model predictions to the parameter P_{maxmat} we ran simulations with an unrealistically high value of $P_{\text{maxmat}} = 40$ matrix cells. Connectivity values for scenarios 1 and 3 with a 10-year run and $P_{\text{maxmat}} = 40$ were closely related to a run with $P_{\text{maxmat}} = 9$ (Table 5, equations 4 and 5). Of course, with $P_{\text{maxmat}} = 40$ there were additional connections to other patches but their connectivity was very low ($< 3\%$). The difference in the connectivity values for the different maximum residence in the matrix was on average no higher than 1.4% (e.g. for scenario 1; Table 5). Thus, restricting P_{maxmat} to a value of 9 cells did not have any decisive effect on the model results.

THE SCENARIOS

Scenario 1: no mortality

Within a time span of 1 year, lynx reached connected source patches only indirectly via target patches that acted as stepping stones. The only connected source patches (good connectivity, iv) were the Northern and Southern Black Forest (53–55). These patches were only 3 km apart (Fig. 2 and see Appendix S1 in Supplementary material).

Table 4. Sensitivity analysis of model predictions based on all model parameterizations ($n = 9240$) and on the best parameter set ($n = 1625$). If not marked in the table, the P -value for the parameter coefficients is $P < 0.001$. Bold are high coefficient values $|\beta_i| > 0.7$

Pattern	n	Mean \pm SD	Range	r^2_{adj} (d.f. = 4)	P	Parameter coefficient β_i				
						Intercept	x , exponent of equation 1	s_{max} , maximum no. of intraday steps	P_c , autocorrelation probability	P_{matrix} , probability of stepping into matrix
Habitat use	9240	90.3 \pm 7.5	69.06–100	0.95	< 0.001	1	0.08	-0.08	-0.01	-0.75
Step distribution	9240	0.03 \pm 0.02	0.009–0.095	0.14	< 0.001	0.35	-0.2	-0.01 ($P = 0.16$)	0.04	0.03
Average maximum distance	9240	39.9 \pm 8.5	13.15–83.77	0.90	< 0.001	0.18	-0.43	0.41	0.26	0.15
Study area	9240	4.9 \pm 3.4	0–10	0.75	< 0.001	0.06	-0.44	0.46	0.22	0.61
Habitat use	1626	96.1 \pm 3.9	81.43–100	0.97	< 0.001	1	0.04	-0.04	-0.02	-0.9
Step distribution	1626	0.02 \pm 0.006	0.009–0.037	0.63	< 0.001	0.15	-0.88	0.86	0.30	0.14
Average maximum distance	1626	36.7 \pm 6.3	15.6–59.7	0.77	< 0.001	0.41	-0.55	0.65	0.46	0.23
Study area	1626	2.5 \pm 0.6	1–3	0.29	< 0.001	0.13	-0.76	0.86	0.60	0.65

Table 5. Results of the sensitivity analysis of the maximum residence in matrix cells, P_{maxmat} , and relation of connectivity values to distance between patches, d_{net} . Sensitivity was assessed with a linear regression function relating the two connectivity values $C_{P_{\text{maxmat}}, \text{scenario}}$ (equations 4 and 5). Connectivity $C_{\text{scenario}, \text{years}}$ is related with interpatch distance, d_{net} , following exponential decay functions (equations 6–8)

Equation number	r_{adj}^2	P	d.f.	n	Equation
Sensitivity analysis of P_{maxmat}					
4	0.994	< 0.001	1	238	$C_{\text{mat40}, \text{scen1}} = 1.4 + 0.96 \times C_{\text{mat9}, \text{scen1}}$
5	0.995	< 0.001	1	56	$C_{\text{mat40}, \text{scen3}} = 1.0 + 0.94 \times C_{\text{mat9}, \text{scen3}}$
Relation of connectivity values $C_{\text{scenario}, \text{years}}$ to distance between patches d_{net}					
6	0.77	< 0.0001	1	134	$C_{\text{scen1}, 10} = 125 \times \exp(-0.03 \times d_{\text{net}})$
7	0.74	< 0.0001	1	134	$C_{\text{scen2}, 10} = 106 \times \exp(-0.04 \times d_{\text{net}})$
8	0.71	< 0.0001	1	134	$C_{\text{scen3}, 10} = 167 \times \exp(-0.08 \times d_{\text{net}})$

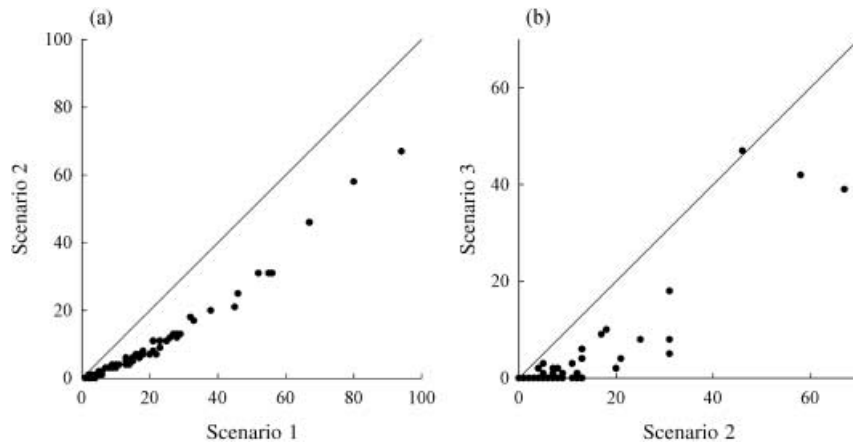


Fig. 4. Connectivity values of the scenarios plotted against each other. Adding only baseline mortality (scenario 2) decreases connectivity values almost linearly in comparison with scenario 1 without any mortality (a), but adding road mortality (scenario 3) makes connectivity between patches unpredictable (b).

Within a time span of 3 years, the source patches did not form an interconnected network but some source patches were connected to others, e.g. the Erz Mountains and the Bavarian Forest (29–49).

Within a time span of 10 years, we obtained 134 connections to other patches. As a result, the source patch system in Germany was interconnected on at least a 5% connectivity level, either directly or via target patches, and the main areas for potential lynx populations were linked together, e.g. the Erz Mountains (29), Bavarian Forest (49), Thuringian Forest (34), Rothaar Mountains (27) and Harz Mountains (20), Palatine Forest (56) and Black Forest (53, 55). The known connection of the Bavarian Forest with the patch in the Czech Republic (49–57) occurred in 13% of the cases (Bufka *et al.* 2000). All the source patches were interconnected below the 5% connectivity level, but these were the most sensitive connections that disappeared as soon as any mortality factors were introduced (see below). The time dependency of connectivity was shown in the time increment from 1 to 10 years.

Scenario 2: baseline mortality

Imposing a total annual baseline mortality probability of about 0.2 did not change the overall picture obtained from the simulation runs above (see Appendix S1 in

Supplementary material). After 10 years the connectivity between patches was the same, only the percentage of dispersers that reached another patch decreased (Fig. 4a). The connectivity from field data between the Bavarian Forest (49) and the Czech patch (57) had decreased from 13% to 9% in these 10 years and from 4% to 2% in 3 years.

Scenario 3: baseline and barrier mortality

Introducing barrier mortality dramatically reduced the connectivity values. Within a time span of 10 years only source patches separated by extremely small distances or without motorways between them were interconnected, such as the patches along the German–Czech border (49–29) (Fig. 2; see Appendix S1 in Supplementary material). Overall, the 3-year runs showed similar connectivity values to the 10-year runs, although the patches along the German–Czech border were not connected on a 3-year time scale. The low connectivity of the German landscape due to traffic mortality compared with the simulation results of the scenarios without road mortality illustrated the strong impact of roads on dispersal success. The effect of spatially dependent mortality on connectivity was not evident, and was different from time-dependent mortality, e.g. our baseline mortality (Fig. 4b).

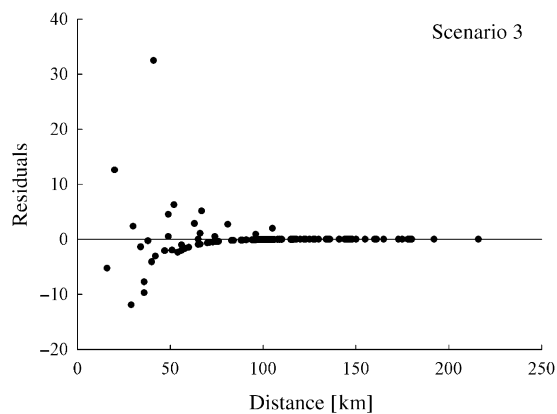


Fig. 5. Residuals of the exponential decay function (8) relating connectivity and distance, as described in the text. Residuals vary strongly for short distances, showing the importance of landscape structure (distribution of matrix and dispersal habitat) and roads on dispersal success.

CONNECTIVITY AND INTERPATCH DISTANCE

When relating Euclidean interpatch distance, d_{net} , with connectivity, distance alone was not a good predictor of connectivity, especially for close patches. Although r_{adj}^2 values were high for all regressions of the exponential decay functions ($r_{\text{adj}}^2 > 0.7$ for equations 6–8; Table 5), the high fit was mainly due to no connectivity at larger distances (connectivity = 0). The residuals showed extremely high variation for short distances (Fig. 5), i.e. no relation between distance and connectivity could be found over short distances. This was due to the strong influence of landscape configuration on the behaviour of dispersing lynx, i.e. the distribution of dispersal habitat. This finding is extremely important for the conservation of populations, where connectivity is often assessed only as a function of distance.

Discussion

THE MODELLING APPROACH

Our question concerning connected patches required the construction of a dispersal model and the quantification of several parameters. The data necessary for parameter quantification are often assumed to be insufficient, and criticism of SEDM has emphasized problems associated with parameterizing dispersal processes (Ruckelshaus, Hartway & Kareiva 1997; Beissinger & Westphal 1998). We tackled parameter estimation by calibrating the dispersal model with field data to understand the landscape- and individual-level processes before forecasting any effects of human activities (*sensu* Conroy *et al.* 1995). Next we considered human activity and varied parameter values for the different mortality sources over plausible ranges. For scenario 3 we used only model predictions of model runs that yielded overall mortality rates coincident with data from Poland and Spain. This two-step pattern-oriented

procedure enabled all model simulations used for predictions to tally with the current knowledge of lynx. As the problem of data scarcity will not be solved in the near future, we have to make the best out of the existing information for decision-making in conservation and management.

We only had data for one dispersing male. Because male mammals generally disperse further than females, we might underestimate the connectivity to various patches, thus producing conservative estimates of connectivity. However, this is acceptable given our objective of assessing the possible success of reintroduction initiatives in Germany.

One possible limitation of the model is that we had to base the intraday movement rules on information published on other populations and from analyses of the Iberian lynx. As a result, we may have overlooked some rules that are potentially important in Germany. However, even for a rather simple approach of a correlated habitat-dependent walk, about 18% of all model parameterizations produced a model behaviour that tallied with our data on the interday and the seasonal time scale (i.e. the four patterns), hence verifying the reliability of our dispersal model.

CONNECTED PATCHES AND MANAGEMENT CONCLUSIONS

The connectivity of patches has often been considered as purely a function of distance (cf. Ricketts 2001; Verboom *et al.* 2001). However, there is a need to include the behavioural ecology of the target species and the landscape structure when assessing connectivity. Our analyses show that connectivity is the outcome of multiple factors related to landscape configuration, e.g. distance and effective isolation through matrix habitat and roads. This could be crucial in conservation biology, especially for predicting the success of reintroduction schemes when local populations have to be linked (see Cramer & Portier 2001). Understanding the factors that determine variability in patch connectivity is a major challenge, not only for obtaining a thorough understanding of the ecology of populations in fragmented landscapes but also for improving our ability to conserve species (Ricketts 2001; Gibson *et al.* 2004).

For 10-year simulations that consider only baseline mortality (i.e. not road mortality), landscape structure had a very constraining impact on movement directionality in Germany. Matrix habitat isolates source patches (e.g. between patches 2–6) or hinders connectivity between them (e.g. between 40 and 56 or 2–29), although the direct distance between the point of release and arrival in a target patch is shorter than between other connected patches (Fig. 2).

The model results showed that patch connectivity is also time-dependent. This is an important result because many dispersal models do not explicitly consider time, merely specifying the maximum number of

steps an individual can make. This may sound trivial but has important consequences for management. Even when mortality was neglected, almost none of the source patches was directly connected within a time lap of 1 year. Only when running the simulations without mortality for at least 3 years did we obtain an interconnected patch system where source patches were linked either directly or indirectly via target patches. Target patches where dispersers can survive and settle play a crucial role for the connectivity of the source patches. This result also suggests that dispersal habitat may enhance connectivity between patches, and so investing in land restoration and reducing the fragmentation of connected forests resembling dispersal habitat is recommended (*sensu* Simberloff *et al.* 1992).

For lynx management in Germany it is important to understand that most patches were connected when the simulations were run for a long time without mortality. Even when considering baseline mortality of 0.2 year⁻¹, the patch system remained interconnected. Thus, it is not just the distribution of dispersal habitat that limits patch connectivity in Germany but also factors contributing to dispersal mortality, such as the dense road network. For a patchily distributed Iberian lynx population in Spain, management scenarios yielded a similar result (Ferrerias *et al.* 1992, 2001). In fact, when realistic mortality probabilities on roads were applied, the majority of the patches were isolated, apart from those along the German–Czech border. Road mortality was therefore a very sensitive parameter in our scenarios, and very expensive habitat restoration could be pointless if road mortality is not reduced (Mao, Suárez & Díez 2004). Currently, a nation-wide wildlife corridor concept is set up to include wildlife crossings into new road constructions to minimize mortality.

If the lynx population along the German–Czech border is to spread into other suitable patches in Germany, management should concentrate on improving a link with the Thuringian Forest, preferably releasing lynx there. Unfortunately, to date no such initiative has been proposed. In our model, a link to the Thuringian Forest is only possible when neglecting the effect of roads. This does not mean that there is no future for a lynx population elsewhere in Germany. For example, many of the source and target patches in the north-eastern forests are connected but the extent to which these patches have source–sink dynamics or a metapopulation structure and are viable without immigration can only be assessed with a population viability analysis (PVA; Boyce 1992).

Regarding the ‘natural’ colonization of a patch as a possible management option, it must be borne in mind that this requires the arrival of both females and males, and that long-range dispersal is influenced by the population dynamics on the natal patch. However, probing such issues would necessitate the integration of demographic data. Our model provides a useful template for developing the movement component of such a PVA.

PROPOSALS FOR FUTURE APPLICATIONS AND RESEARCH

Our model can be applied to a variety of assessments of the effects of land-use changes (including road construction) and management scenarios on landscape connectivity (White *et al.* 1997), on the use of corridors as enhancing links between patches (see reviews of Simberloff *et al.* 1992; Rosenberg, Noon & Meslow 1997; Beier & Noss 1998; Haddad, Rosenberg & Noon 2000) and also as a basis for analysing neutral landscape models and finding thresholds in fragmented landscapes (Gustafson & Gardner 1996; Keitt, Urban & Milne 1997; With 1997; King & With 2002). Given the result that the source patches in Germany are mostly isolated, a PVA for individual patches would be essential to assess the long-term viability in these isolated patches.

Clearly, the results from our dispersal model can only be used as qualitative hypotheses on connectivity because the model could not be validated due to a lack of independent data. We therefore recommend that field studies in the future analyse dispersal in order to gain more insight into dispersal behaviour in fragmented landscapes.

SYNTHESIS AND APPLICATIONS

Our study shows that individual-based dispersal models can be applied to management problems even if data are sparse. We provide a clear protocol for the analysis of field data and for model calibration. Our approach can be used for a variety of species with similar management problems. Our results show that species’ behaviour needs to be taken into account when measuring connectivity between patches, and that connectivity is not solely a function of distance between patches. These are very significant results for conservation. Our main biological result is that the individual patches in Germany are probably isolated, the main reason being not the distribution of habitat suitable for dispersal but the dense transport system, resulting in high mortality. This gives clear management directives for dealing with reintroductions of lynx in Germany.

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Supplementary material

The following material is available from
<http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE933/JPE933sm.htm>

Appendix S1. Connectivity values (%) for the different scenarios, as described in the text. For the numbers of the source and target patches see Fig. 2.

References

- Akcakaya, H.R. & Sjören-Gulve, P. (2000) Population viability analyses in conservation planning: an overview. *Ecological Bulletins*, **48**, 9–21.
- Beier, P. & Noss, R.F. (1998) Do habitat corridors provide connectivity? *Conservation Biology*, **12**, 1241–1252.
- Beissinger, S.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, **62**, 821–841.
- Boyce, M.S. (1992) Population viability analysis. *Annual Review of Ecology and Systematics*, **23**, 481–506.
- Breitenmoser, U., Breitenmoser-Würsten, C., Okarma, H., Kaphegyi, T., Kaphegyi-Wallmann, U. & Müller, U.M. (2000) *The Action Plan for the Conservation of the Eurasian Lynx (Lynx lynx) in Europe*. Bern Convention Meeting. Council of Europe, Bern, Switzerland.
- Breitenmoser, U., Kaczensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. (1993) Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. *Journal of Zoology (London)*, **231**, 449–464.
- Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Capt, S., Laass, S., Siegenthaler, A. & Breitenmoser, U. (2001) Untersuchungen zur Luchspopulation in den Nordwestalpen der Schweiz 1997–2000. *KORA Bericht*, **9**, 1–92.
- Bufka, L., Cerveny, J., Koubek, P. & Horn, P. (2000) Radio-telemetry research of the lynx (*Lynx lynx*) in Sumava: preliminary results. *Proceedings Predatori v Myslivosti 2000* (eds Czech Forestry Association), pp. 143–153. Hranice, Czech Republic.
- Clevenger, A.P. & Waltho, N. (2000) Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta Canada. *Conservation Biology*, **14**, 47–56.
- Clevenger, A.P., Chruszcz, B. & Gunson, K. (2001) Drainage culverts as habitat linkages and factors affecting passage by mammals. *Journal of Applied Ecology*, **38**, 1340–1349.
- Collingham, Y.C. & Huntley, B. (2000) Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications*, **10**, 131–144.
- Conroy, M.J., Cohen, Y., James, F.C., Matsinos, Y.G. & Maurer, B.A. (1995) Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications*, **5**, 17–19.
- Cramer, P.C. & Portier, K.M. (2001) Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. *Ecological Modelling*, **140**, 51–80.
- Doak, D.F. & Mills, L.S. (1994) A useful role for theory in conservation. *Ecology*, **75**, 615–626.
- Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65–74.
- Ferreras, P., Aldama, J.J., Beltran, J.F. & Delibes, M. (1992) Rates and causes of mortality in a fragmented population of Iberian lynx (*Felis pardina* Temminck, 1824). *Biological Conservation*, **61**, 197–202.
- Ferreras, P., Gaona, P., Palomares, F. & Delibes, M. (2001) Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx. *Animal Conservation*, **4**, 265–274.
- Gaona, P., Ferreras, P. & Delibes, M. (1998) Dynamics and viability of a metapopulation of the endangered Iberian Lynx (*Lynx pardinus*). *Ecological Monographs*, **68**, 349–370.
- Gibeau, M.L., Clevenger, A.P., Herrero, S. & Wierzchowski, J. (2002) Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation*, **103**, 227–236.
- Gibson, L.A., Wilson, B.A., Cahill, M. & Hill, J. (2004) Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *Journal of Applied Ecology*, **41**, 213–223.
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J. & Wissel, C. (1996) Pattern-oriented modelling in population ecology. *The Science of the Total Environment*, **183**, 151–166.
- Gustafson, E.J. & Gardner, R.H. (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, **77**, 94–107.
- Haddad, N.M., Rosenberg, D.K. & Noon, B.R. (2000) On experimentation and the study of corridors: response to Beier and Noss. *Conservation Biology*, **14**, 1543–1545.
- Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151–162.
- Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A.N. & Milkowski, L. (1996) Population dynamics (1869–1994), demography, and home ranges of the lynx in Białowież Primeval Forest (Poland and Belarus). *Ecography*, **19**, 122–138.
- Jedrzejewski, W., Schmidt, K., Okarma, H. & Kowalczyk, R. (2002) Movement pattern and home range use by the Eurasian lynx in Białowież Primeval Forest (Poland). *Annales Zoologici Fennici*, **39**, 29–41.
- Kaczensky, P., Knauer, F., Jonozovic, M., Huber, T. & Adamic, M. (1996) The Ljubljana–Postojna Highway: a deadly barrier for brown bears in Slovenia. *Journal of Wildlife Research*, **1**, 263–267.
- Keitt, T.H., Urban, D.L. & Milne, B.T. (1997) Detecting critical scales in fragmented landscapes. *Conservation Ecology*, **1**, 1–18.
- Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B. & Hornocker, M.G. (2002) Effects of roads and human disturbance on Amur tigers. *Conservation Biology*, **16**, 97–108.
- King, A.W. & With, K.A. (2002) Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling*, **147**, 23–39.
- Lima, S.L. & Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131–135.
- Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J. & Zuuring, H. (1996) Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology*, **33**, 1395–1404.
- Malo, J.E., Suárez, F. & Díez, A. (2004) Can we mitigate animal–vehicle accidents using predictive models? *Journal of Applied Ecology*, **41**, 701–710.
- Manly, B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London, UK.
- Moilanen, A. & Hanski, I. (1998) Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology*, **79**, 2503–2515.
- Palomares, F., Delibes, M., Ferreras, P., Fedriani, J.M., Calzada, J. & Revilla, E. (2000) Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. *Conservation Biology*, **14**, 809–818.
- Revilla, E., Wiegand, T., Palomares, F., Ferreras, P. & Delibes, M. (in press) Effects of matrix heterogeneity on animal dispersal:

- from individual behaviour to metapopulation-level parameters. *American Naturalist*.
- Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87–99.
- Rosenberg, D.K., Noon, B.R. & Meslow, E.C. (1997) Biological corridors: form, function and efficacy. *Bioscience*, **47**, 677–687.
- Ruckelshaus, M., Hartway, C. & Kareiva, P. (1997) Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology*, **11**, 1298–1306.
- Saunders, S.C., Mislivets, M.R., Chen, J. & Cleland, D.T. (2002) Effects of roads on landscape structure within nested ecological units of the Northern Great Lakes Region, USA. *Biological Conservation*, **103**, 209–225.
- Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T. & Trepl, L. (2002a) Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx in Germany. *Ecological Applications*, **12**, 1469–1483.
- Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., Koubek, P., Huber, T., Stanisa, C. & Trepl, L. (2002b) Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology*, **39**, 189–203.
- Schippers, P., Verboom, J., Knaapen, J.P. & Apeldoorn, R.C.V. (1996) Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography*, **19**, 97–106.
- Schmidt, K. (1998) Maternal behavior and juvenile dispersal in the Eurasian lynx. *Acta Theriologica*, **43**, 391–408.
- Schmidt-Posthaus, H., Breitenmoser-Würsten, C., Posthaus, H., Bacciarini, L. & Breitenmoser, U. (2002) Causes of mortality in reintroduced Eurasian lynx in Switzerland. *Journal of Wildlife Diseases*, **38**, 84–92.
- Simberloff, D., Farr, J.A., Cox, J. & Mehlmann, P.W. (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology*, **6**, 493–505.
- Thomas, C.D., Bagnette, M. & Lewis, O.T. (2000) Butterfly movement and conservation in patchy landscapes. *Behaviour and Conservation* (eds L.M. Gosling & W.J. Sutherland), pp. 85–104. Cambridge University Press, Cambridge, UK.
- Tigas, L.A., Van Vuren, D.H. & Sauvajot, R.M. (2002) Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation*, **108**, 299–306.
- Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.
- Turchin, P. (1998) *Quantitative Analysis of Movement*. Sinauer Associates, Sunderland, MA.
- Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J., Liu, J., Loeb, S. & McKelvey, K. (1995) Usefulness of spatially explicit population models in land management. *Ecological Applications*, **5**, 12–16.
- Verboom, J., Foppen, R., Chardon, P., Opdam, P. & Luttikhuisen, P. (2001) Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biological Conservation*, **100**, 89–101.
- Vos, C.C., Verboom, J., Opdam, P.F.M. & Ter Braak, C.J.F. (2001) Toward ecologically scaled landscape indices. *The American Naturalist*, **157**, 24–41.
- Waser, P.M. (1996) Patterns and consequences of dispersal in gregarious carnivores. *Carnivore Behaviour, Ecology and Evolution* (ed. J.L. Gittleman), pp. 267–295. Cornell University Press, Ithaca, NY.
- White, D., Minotti, P.G., Barczak, M.J., Sifneos, J.C., Freemark, K.E., Santelmann, M.V., Steinitz, C.F., Kiester, A.R. & Preston, E.M. (1997) Assessing risks to biodiversity from future landscape change. *Conservation Biology*, **11**, 349–360.
- Wiegand, T., Jeltsch, F., Hanski, I. & Grimm, V. (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos*, **100**, 209–222.
- Wiegand, T., Knauer, F., Kaczensky, P. & Naves, J. (2004) Expansion of brown bears (*Ursus arctos*) into the eastern Alps: a spatially explicit population model. *Biodiversity and Conservation*, **13**, 79–114.
- Wiegand, T., Revilla, E. & Knauer, F. (2004) Reducing uncertainty in spatially explicit population models. *Biodiversity and Conservation*, **13**, 53–78.
- With, K.A. (1997) The application of neutral landscape models in conservation biology. *Conservation Biology*, **11**, 1069–1080.
- Wölfel, M., Bufka, L., Cerveny, J., Koubek, P., Heurich, M., Habel, H., Huber, T. & Poost, W. (2001) Distribution and status of lynx in the border region between Czech Republic, Germany and Austria. *Acta Theriologica*, **46**, 181–194.
- Zimmermann, F. (1998) Dispersion et survie des Lynx (*Lynx lynx*) subadultes d'une population réintroduite dans la chaîne du Jura. *KORA Bericht*, **4**, 1–50.

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