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Abstract: 1. After an absence of almost 100 years, the Eurasian lynx *Lynx lynx* is slowly recovering in Germany along the German-Czech border. Additionally, many reintroduction schemes have been discussed, albeit controversially, for various locations. We present a habitat suitability model for lynx in Germany as a basis for further management and conservation efforts aimed at recolonization and population development.

2. We developed a statistical habitat model using logistic regression to quantify the factors that describe lynx home ranges in a fragmented landscape. As no data were available for lynx distribution in Germany, we used data from the Swiss Jura Mountains for model development and validated the habitat model with telemetry data from the Czech Republic and Slovenia. We derived several variables describing land use and fragmentation, also introducing variables that described the connectivity of forested and non-forested semi-natural areas on a larger scale than the map resolution.

3. We obtained a model with only one significant variable that described the connectivity of forested and non-forested semi-natural areas on a scale of about 80 km<sup>2</sup>. This result is biologically meaningful, reflecting the absence of intensive human land use on the scale of an average female lynx home range. Model testing at a cut-off level of  $P > 0.5$  correctly classified more than 80% of the Czech and Slovenian telemetry location data of resident lynx. Application of the model to Germany showed that the most suitable habitats for lynx were large-forested low mountain ranges and the large forests in east Germany.

4. Our approach illustrates how information on habitat fragmentation on a large scale can be linked with local data to the potential benefit of lynx conservation in central Europe. Spatially explicit models like ours can form the basis for further assessing the population viability of species of conservation concern in suitable patches.

# Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx

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## Summary

1. After an absence of almost 100 years, the Eurasian lynx *Lynx lynx* is slowly recovering in Germany along the German–Czech border. Additionally, many reintroduction schemes have been discussed, albeit controversially, for various locations. We present a habitat suitability model for lynx in Germany as a basis for further management and conservation efforts aimed at recolonization and population development.
2. We developed a statistical habitat model using logistic regression to quantify the factors that describe lynx home ranges in a fragmented landscape. As no data were available for lynx distribution in Germany, we used data from the Swiss Jura Mountains for model development and validated the habitat model with telemetry data from the Czech Republic and Slovenia. We derived several variables describing land use and fragmentation, also introducing variables that described the connectivity of forested and non-forested semi-natural areas on a larger scale than the map resolution.
3. We obtained a model with only one significant variable that described the connectivity of forested and non-forested semi-natural areas on a scale of about 80 km<sup>2</sup>. This result is biologically meaningful, reflecting the absence of intensive human land use on the scale of an average female lynx home range. Model testing at a cut-off level of  $P > 0.5$  correctly classified more than 80% of the Czech and Slovenian telemetry location data of resident lynx. Application of the model to Germany showed that the most suitable habitats for lynx were large-forested low mountain ranges and the large forests in east Germany.
4. Our approach illustrates how information on habitat fragmentation on a large scale can be linked with local data to the potential benefit of lynx conservation in central Europe. Spatially explicit models like ours can form the basis for further assessing the population viability of species of conservation concern in suitable patches.

**Key-words:** GIS, large-scale approach, logistic regression, *Lynx lynx*, spatially explicit connectivity index, species reintroduction, statistical habitat model.

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## Introduction

Effective nature conservation and habitat restoration in human-dominated landscapes require an understanding of how species respond to habitat fragmentation. As anthropogenic activities such as agriculture or urban development become prevalent in a region, native habitats are reduced in area and exist ultimately as remnants in a highly altered matrix (Miller & Cale 2000). Large carnivores provide some of the clearest examples of the fate of species that have to cope with fragmented multi-use landscapes on a large scale. Central Europe was once covered by dense temperate deciduous forests. However, after more than 5000 years of intense human activities only 2% of the original prime forest remains. At the beginning of the 20th century, wolves *Canis lupus*, brown bears *Ursus arctos* and Eurasian lynx *Lynx lynx* were almost extinct. Since then, there has been slow recovery of wolves in Spain and Italy (Boitani 2000), and bears and Eurasian lynx in Scandinavia, the Carpathians and the Balkan Peninsula (Breitenmoser *et al.* 2000; Swenson *et al.* 2000).

The management and conservation of large carnivores is particularly difficult due to their large requirements for space. Intensive human land use is responsible for habitat fragmentation, which results in direct and indirect conflicts with those carnivores that compete with humans for the remaining semi-natural space and resources (Noss *et al.* 1996; Woodroffe & Ginsberg 1998; Revilla, Palomares & Delibes 2001). Many such species come into direct conflict with people because of their predatory habits. For example, the diet of lynx is basically formed of valuable game such as roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra*, but also includes sheep and red deer *Cervus elaphus* (Breitenmoser & Haller 1993; Jedrzejewski *et al.* 1993; Okarma *et al.* 1997; Jobin, Molinari & Breitenmoser 2000; Červený *et al.* 2002; Stahl *et al.* 2001). The patchy distribution of suitable habitat and construction of linear barriers such as highways can lead to higher mortality (Kaczensky *et al.* 1996; Mace *et al.* 1996; Cleverger, Chruszcz & Gunson 2001). Therefore, conservation strategies for large carnivores focus on the integration of the species into multi-use landscapes inevitably dominated by people (Schröder 1998; Linnell, Swenson & Andersen 2000; Linnell *et al.* 2001).

Basic questions about the management and conservation of large carnivores still remain unanswered, for example about minimum habitat requirements under the new landscape conditions, and about whether recovery is only a local-scale phenomenon or can be expected to a greater extent in areas with dense human populations. These complex large-scale issues require knowledge of the extent, spatial arrangement and connectivity of potentially suitable habitat. In densely populated central Europe, the case of the reinvading Eurasian lynx poses exactly these questions. Since 1970 several successful efforts have been made to reintroduce lynx in Switzerland, France, Slovenia and the Czech

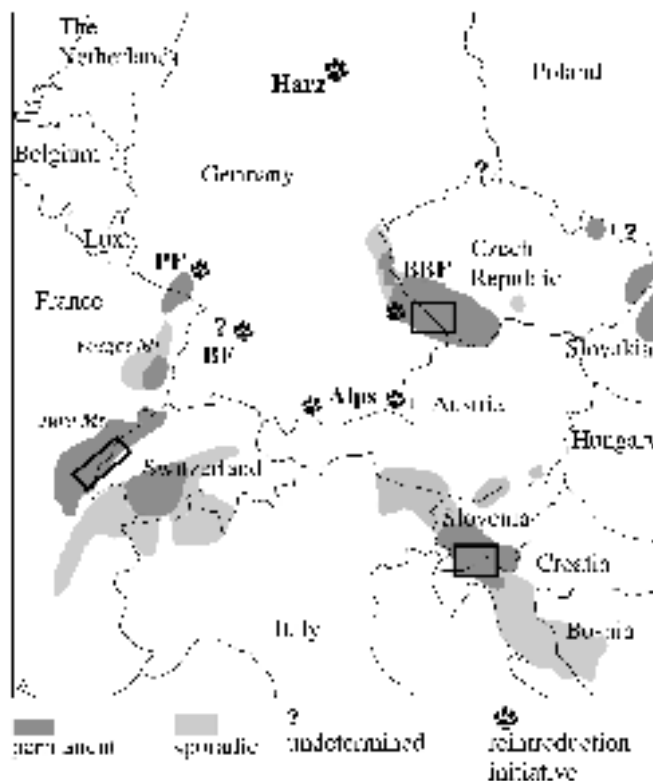
Republic (Herrenschmidt & Leger 1987; Breitenmoser *et al.* 1993; Červený, Koubek & Anděra 1996; Cop & Frković 1998). In Germany there has been much controversy over lynx reintroduction, but natural immigration has already occurred into the Bavarian Forest due to the expansion of a population reintroduced to the Czech Bohemian Forest (Červený & Bufka 1996) (Fig. 1).

Given this situation, a large-scale assessment of habitat suitability is a necessary prerequisite for the evaluation of current initiatives for lynx reintroduction and management actions. Although the suitability of some areas for lynx has been ardently and controversially discussed in Germany, no quantitative habitat model yet exists to support these discussions, particularly one that can describe to what extent the species is tolerant of large-scale fragmentation. Some studies have modelled spatial factors that determine the distribution of the Eurasian lynx, but restricted to local areas (Zimmermann & Breitenmoser 2001) or using algorithms that do not apply to fragmented areas (Corsi, Sinibaldi & Boitani 1998). Schadt *et al.* (in press) developed a rule-based habitat model for lynx in Germany, but this model has not been validated with any field data.

We aimed to develop a home range suitability model for the lynx in central Europe based on current understanding of its requirements. We wanted our model to quantify general predictors for lynx home ranges to contribute to the design of a Germany-wide conservation plan by (i) identifying the broad distribution of suitable patches; (ii) obtaining an estimate of possible lynx home ranges in Germany; and (iii) providing a basis for a spatially explicit population simulation model to assess recolonization success and population development.

## Methods

Habitat models using presence-absence data and logistic regression are useful in formalizing the relationship between environmental conditions and species' habitat requirements, and in quantifying the amount of potential habitat (Morrison, Marcot & Mannan 1992; Boyce & McDonald 1999); they have been widely applied for a variety of purposes and species (Buckland & Elston 1993; FitzGibbon 1993; Wilson *et al.* 1997; Mace *et al.* 1999; Mladenoff, Sickley & Wydeven 1999; Palma, Beja & Rodrigues 1999; Rodriguez & Andrén 1999; Bradbury *et al.* 2000; Gates & Donald 2000; Manel, Buckton & Ormerod 2000; Orrock *et al.* 2000; Suarez, Balbontin & Ferrer 2000). The principle of this method is to contrast used habitat units vs. unused units in order to determine habitat suitability with a set of explanatory variables (Hosmer & Lemeshow 1989; Tabachnick & Fidell 1996). The regression function can then be extrapolated and mapped over target areas, in our case Germany and its neighbouring forests. We generated a home range suitability model based on local radio-tracking data obtained from lynx in the French and Swiss Jura Mountains (local study area), a landscape similar in fragmentation and population



**Fig. 1.** Permanent lynx populations in central Europe, sporadic and undetermined lynx occurrence (modified after Breitenmoser *et al.* 2000) and reintroduction initiatives for lynx in Germany. The black rectangles show the places from where we obtained telemetry data for developing the habitat model. PF, Palatine Forest; BF, Black Forest; BBF, Bavarian/Bohemian Forest.

density to the German low mountain ranges. This model was then extrapolated to Germany (large-scale study area) and evaluated with independent radio-tracking data from the low mountain range along the German–Czech border and from the Dinaric Mountain Range of southern Slovenia.

To provide a range of comparable data for areas not inhabited by lynx, i.e. unused units or non-observations, we created random home ranges in the local study area that we assumed to be in the general region of probable lynx movement and that lynx were likely to have visited, but where they had not settled as permanent residents. We assumed the resident home range areas to represent more desirable habitat than the non-occupied area.

#### SPATIAL SCALES

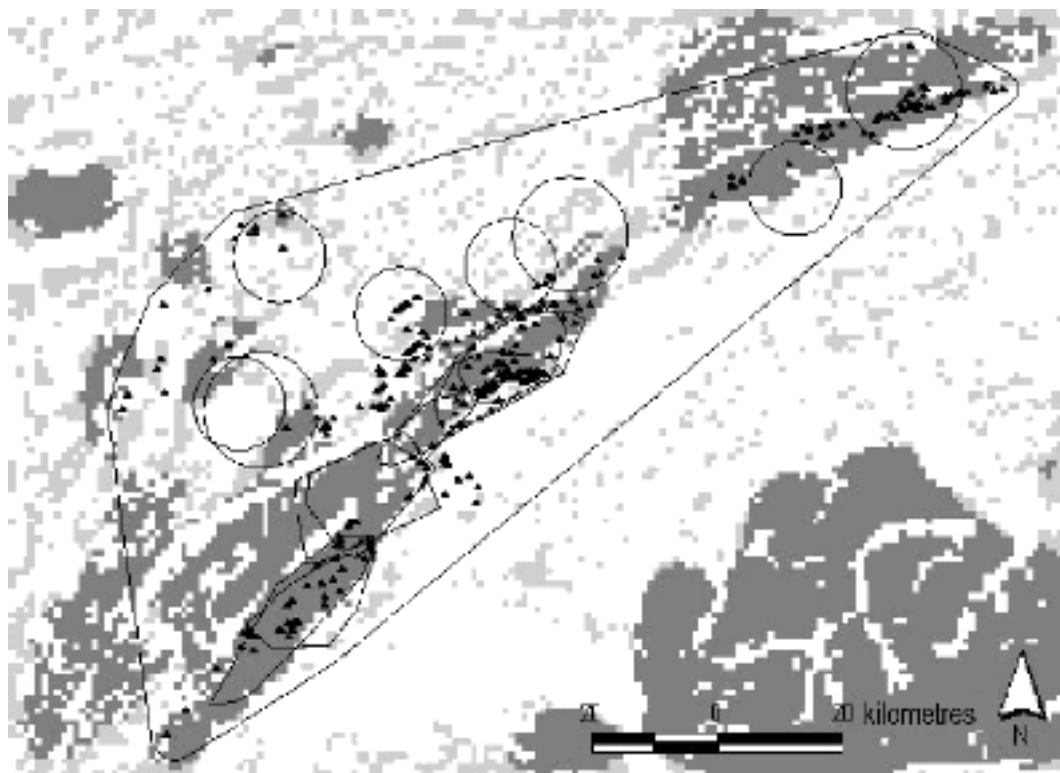
The basic units for our analysis were raster cells based on the total lynx home range area irrespective of the animal, to avoid pseudoreplication due to home range overlap. We did not use single lynx location data, although we also used the telemetry data to gain insight into preferred land-use types. As the accuracy of the telemetry location data was 1 km<sup>2</sup>, we defined this as the spatial grain or landscape resolution. In order to consider information that comprised forest fragmentation on a larger scale than our grid cell, we introduced two spatially explicit connectivity indices that described scale-dependent landscape properties to capture the individual's landscape perception over larger areas.

#### STUDY AREAS AND LYNX TELEMETRY DATA

##### *Local-scale data for model development*

Model development was based on lynx radio-collared and tracked in the Swiss Jura Mountains. The Jura Mountains are a secondary limestone chain between Switzerland and France with altitudes ranging between 372 and 1679 m a.s.l. The highlands are 53% covered by deciduous forest on the slopes, with coniferous forests on the ridges. Human population density reaches about 120 inhabitants km<sup>-2</sup>, and the area is intensively used for recreation. Cultivated areas are typically pastures used for grazing cattle (Breitenmoser & Baettig 1992; Breitenmoser *et al.* 1993).

We used 3402 radio-location data points published by Breitenmoser *et al.* (1993) from 13 individuals tracked from 1988 to 1991, of which four were resident females and three were resident males. The rest were dispersing subadults. One resident female had a home range shift during her observation period, and for analytical purposes we considered her home range as belonging to two different individuals (giving a total of five home ranges of female lynx). Following the methodology proposed by Breitenmoser *et al.* (1993), we removed outlier locations before estimating the home ranges of the resident lynx using minimum convex polygons (MCP). The average home range sizes were then 169 km<sup>2</sup> for females ( $n = 5$ ) and 263 km<sup>2</sup> for males ( $n = 3$ ). For our analysis we defined the 'closer



**Fig. 2.** Swiss Jura Mountain chain: home ranges of resident lynx (polygons), random home ranges (circles) and locations of dispersing lynx (triangles) in the closer study area (CSA). Light grey are grid cells that contain more than 66.6% of extensively used land-use types, such as forest or heathland (classified as *PExt* cells); dark grey are cells of the applied model with  $P > 0.5$  (see the results of the logistic regression).

study area' (CSA) as the MCP enclosing all locations, including residents and dispersers, to create a general region of probable lynx movement, with a buffer of 2.5 km, defined by the average daily distance moved (Fig. 2).

#### Local-scale data for model validation

**German–Czech data.** The forest cover of the low mountain chain along the German–Czech border (highest elevation at 1457 m) ranges from more than 90% in the inner parts (Šumava Mountains on the Czech side and Inner Bavarian Forest on the German side) to below 50% in the outer regions (e.g. Šumava Foothills, Outer Bavarian Forest and Fichtelgebirge). Population density ranges from 20 to 100 inhabitants  $\text{km}^{-2}$  (Červený & Bufka 1996; Wölfel *et al.* 2001) (Fig. 1). From the Šumava National Park we used the data of 714 radiolocations from five lynx observed between 1997 and 1999 (Bufka *et al.* 2000), one of them being a resident female having most of the centre of her home range in the Bavarian Forest on the German side. Two others were resident males and two were dispersing subadults.

**Slovenian data.** We used 677 telemetry locations from two resident females and three resident males over the period 1994–96 (Staniša 1998). The lynx were descendants of six lynx reintroduced in the region in 1973 (Cop & Frković 1998). The study area is part of the Dinaric

Mountain Range, stretching from Slovenia in the north to Albania in the south (Fig. 1). Elevations range from 300 to 1200 m, forest cover averages 90%, and the dominating forest community is *Abieti–Fagetum dinaricum*. Human population density is low, averaging 22 inhabitants  $\text{km}^{-2}$ , and the main human activities of the region are forestry, timber extraction and hunting with small amounts of recreation.

#### Large-scale study area for model application

Germany comprises an area of about 358 000  $\text{km}^2$  with an average population density of 230 inhabitants  $\text{km}^{-2}$ , which drops to about 100 inhabitants  $\text{km}^{-2}$  in places such as the low mountain ranges (e.g. Black Forest, Palatine Forest and Thuringian Forest). Urbanization accounts for 5% of the total area, and 30% of the total area is forested. The forests are clustered in areas formerly unsuitable for human activity in the low mountain ranges and in areas with poor soils in the north-east. Of the total area 2.5% is protected by National Park status. Germany has a very dense traffic network consisting of 11 000 km of highways and more than 50 000 km of interstate or main roads. We included neighbouring forest areas in Poland, the Czech Republic, France and Belgium in our large-scale study area. We excluded the Alps as the habitat requirements of lynx in alpine biomes differ from those in low mountain ranges where we obtained our data.

## GIS DATA BASE AND PREPARATION

*Data base*

We used 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. Information on roads was digitized from 1 : 250 000-scale road maps. Roads included highways, transeuropean roads and main roads. Other paved roads, unpaved roads, unimproved forest roads and trails were not considered. All data were georeferenced on a Transverse Mercator projection (spheroid Bessel, x-shift 3 500 000).

*Map preparation*

We created a raster map of 1-km mesh size and clipped it with the land use and road maps of the CSA in Switzerland. Each lynx home range was intersected with the raster map, and descriptive environmental variables were extracted for each cell. We created five non-used home ranges for females and three for males of the average size observed in the CSA. The position of these non-used home ranges was randomly assigned within the CSA, but without considering the area of lynx home ranges and big lakes (Bieler See and Neuenburger See) to help ensure that non-resident home range areas were likely to have been visited by lynx. Point distances were 7334 (9150) m from the edge, to avoid lying outside the CSA, and 14 668 (18 300) m between points, to avoid home range overlap in the same sexes for females (males). These points were then buffered with a radius of 7334 m (= area of 169 km<sup>2</sup>) for females and 9150 m (= area of 263 km<sup>2</sup>) for males. The random home ranges of the different sexes overlapped in two cases (Fig. 2).

LYNX BIOLOGY AND PREDICTIVE  
ENVIRONMENTAL VARIABLES

To improve the biological interpretability of the final model, we avoided choosing many potential landscape predictors that a priori were not directly linked to the biology of the species, and orthogonalizing them into independent axes with data aggregation techniques (e.g. with principal component or factor analysis; Tabachnick & Fidell 1996).

The Eurasian lynx is present in large continuous forest areas, although the forests can be interrupted by other land-use types such as pastures or agriculture. Intensive land use is tolerated as long as there is enough connected forest for retreat (Haller & Breitenmoser 1986; Breitenmoser & Baettig 1992; Haller 1992;

Breitenmoser *et al.* 1993; Schmidt, Jedrzejewski & Okarma 1997). Human activity may strongly affect the presence of large carnivores by direct elimination or by individual avoidance of areas used by humans (Mladenoff *et al.* 1995; Woodroffe & Ginsberg 1998; Revilla, Palomares & Delibes 2001; Palomares *et al.* 2001). Availability of prey may also be important. Unfortunately, uniform data on prey density do not exist, so we were not able to include this information in our model.

*Local-scale variables*

Initially we compiled a number of potential predictor variables to describe fragmentation of large forest areas and intensive human land use (Table 1). We included variables related to the presence of forest within each grid cell, such as the percentage of forest, *PFor*, the number of forest patches, *NPFor*, and the perimeter of forest patches, *PeriFor*. We included other land uses such as the percentages of arable land, *PAgr*, pastures, *PPast*, and other non-forested semi-natural areas, *PNat* (Table 1). We also included the total number of patches of any land use, *NPTot*, and the percentage of extensive human land use, *PExt*. The latter was defined as the combined percentage of forest areas, *PFor*, and other non-forested semi-natural land cover, *PNat*, when the percentage of both land uses per cell was  $\geq 66.6\%$  (Table 1). This ensured that we also included margin cells of extensively used areas. Human variables included the percentage of urban areas, *PUrb*, and the number of urban polygons per cell, *NPURb* (Table 1). We also compiled the total length of transeuropean and major roads, *R50*, per cell.

*Large-scale variables*

We introduced two spatial indices,  $R_A$  and  $R_C$ , that describe the connectivity or fragmentation of extensively used areas on larger scales than map resolution (Fig. 3). We defined the index  $R_A(x, y, r)$  as the proportion of extensively used cells, *PExt*, in the circular neighbourhood within radius  $r$  around a given extensively used cell  $(x, y)$ .  $R_A(x, y, r) = 1$  indicates that all cells in the neighbourhood  $r$  of  $(x, y)$  are extensively used cells, i.e. the suitable habitat in the neighbourhood  $r$  of  $(x, y)$  is non-fragmented, while  $R_A(x, y, r) < 1$  indicates that only a few cells in the neighbourhood  $r$  of  $(x, y)$  are extensively used. Alternatively, we may assume that the average cover of extensive land uses in the neighbourhood of a given cell determines habitat suitability. Therefore we define the second index  $R_C(x, y, r)$  as the proportion of extensive land-use types in the circular neighbourhood with radius  $r$  around a given cell  $(x, y)$ . Note that  $R_C$  may not be zero for cells with low cover of extensively used areas. If such cells, e.g. villages, are surrounded by larger forest areas,  $R_C$  assigns them a high index value. This assumption is reasonable because MCP representations of lynx home ranges

**Table 1.** Means of the land-use variables per cell in the random home ranges (HR) ( $n = 8$ ) and the home ranges of the resident lynx ( $n = 8$ ). \*\*Indicates differences of the Kruskal–Wallis tests at a significance level of  $P < 0.01$ , and \* at a significance level of  $P < 0.05$ ,  $n = 16$ , d.f. = 1. Retained variables (RV) for the logistic regression are marked with an  $x$

Variable	Biological interpretation		Random HR $\pm$ SD	Lynx HR $\pm$ SD	RV	
<i>PUrb</i> (% of urban areas)	Intensive human land use	**	3.3 $\pm$ 2.3	0.7 $\pm$ 0.3		
<i>PAgr</i> (% of agriculture)	Intensive human land use		5.5 $\pm$ 8.8	10.2 $\pm$ 5.4		
<i>PPast</i> (% of pasture)	Intensive human land use	*	39.5 $\pm$ 20.8	11.2 $\pm$ 5		
<i>PFor</i> (% of forest)	Extensive human land use	*	40.9 $\pm$ 8.6	52.9 $\pm$ 2.5	$x$	
<i>PNat</i> (% of natural areas)	Extensive human land use	**	8.9 $\pm$ 4.1	24 $\pm$ 6.9	$x$	
<i>NPTot</i> (total no. of polygons)	Fragmentation		2.5 $\pm$ 0.4	2.5 $\pm$ 0.2	$x$	
<i>NPFor</i> (no. of forest polygons)	Extensive human land use	*	0.9 $\pm$ 0.1	1.1 $\pm$ 0.1	$x$	
<i>NP Urb</i> (no. of urban polygons)	Intensive human land use	**	0.1 $\pm$ 0.1	0 $\pm$ 0	$x$	
<i>PeriFor</i> (perimeter of forest)	Forest fragmentation	*	2614.5 $\pm$ 420.7	3220.5 $\pm$ 209.5		
<i>R50</i> (density of major roads in km/km <sup>2</sup> )	Intensive human land use		0.6 $\pm$ 0.3	0.3 $\pm$ 0.2	$x$	
$R_A$	Radius 1 km	Forest fragmentation	**	0.26 $\pm$ 0.17	0.66 $\pm$ 0.1	$x$
	Radius 3 km	Forest fragmentation	**	0.22 $\pm$ 0.16	0.58 $\pm$ 0.1	$x$
	Radius 5 km	Forest fragmentation	**	0.2 $\pm$ 0.15	0.53 $\pm$ 0.1	$x$
	Radius 7 km	Forest fragmentation	**	0.19 $\pm$ 0.14	0.47 $\pm$ 0.1	$x$
$R_C$	Radius 1 km	Forest fragmentation	**	1.13 $\pm$ 0.26	1.7 $\pm$ 0.13	$x$
	Radius 3 km	Forest fragmentation	**	1.11 $\pm$ 0.23	1.62 $\pm$ 0.12	$x$
	Radius 5 km	Forest fragmentation	**	1.11 $\pm$ 0.19	1.51 $\pm$ 0.12	$x$
	Radius 7 km	Forest fragmentation	**	1.11 $\pm$ 0.16	1.43 $\pm$ 0.13	$x$

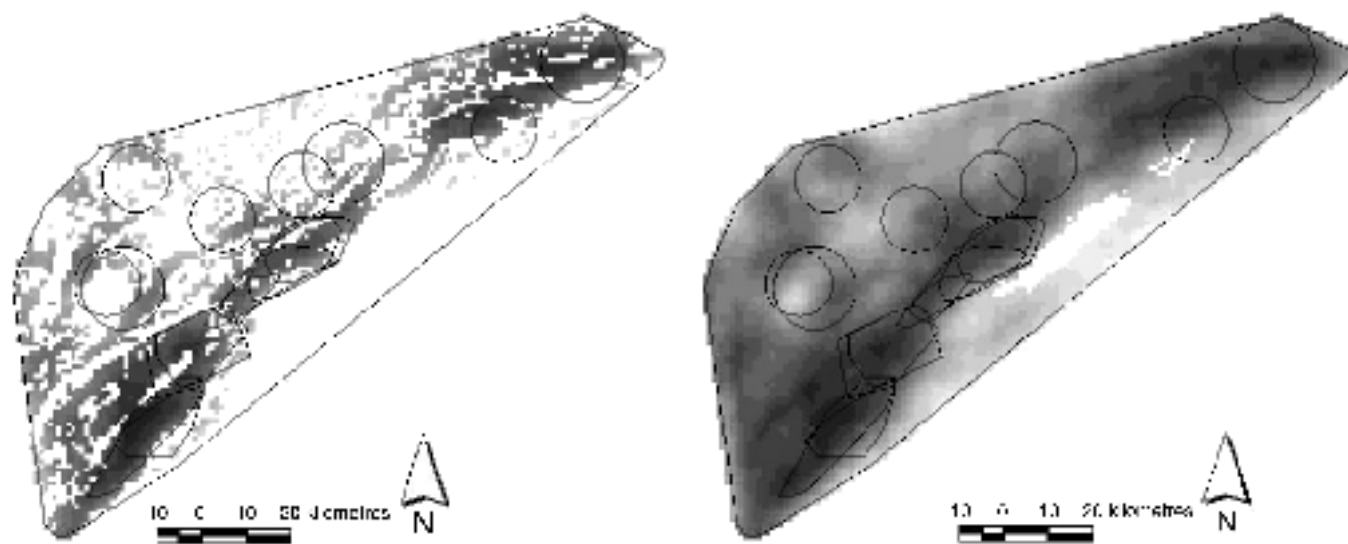
may include villages. We calculated both indices for radius  $r = 1, 3, 5$  and 7 km.

#### STATISTICAL ANALYSES AND MODEL DESIGN

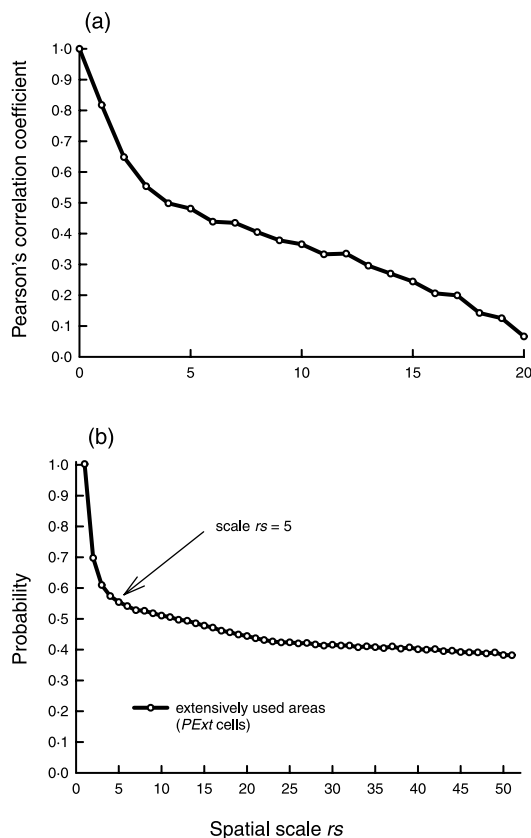
First, we used descriptive univariate analyses to test our data before entering them into the logistic model, as the ecological relevance of an explanatory variable is an important aspect of model evaluation (Noon 1986). Lynx home ranges created with the MCP method are conceptual approximations and may contain variables that do not make sense from the perspective of lynx biology. Variables that are not plausible can be excluded before being entered into the logistic regression. However, we did not want to exclude variables

that may influence lynx presence or absence, such as agriculture, beforehand, as this would constitute data dredging (Burnham & Anderson 1998). We therefore compared frequencies of telemetry data on the land-use classes with the same frequency of random points distributed in the CSA with a frequency test. Additionally we compared rank differences of the variables of the eight home ranges to the eight random home ranges with a non-parametric Kruskal–Wallis test.

As we divided the total home range area and also the random home ranges into raster cells of 1 km<sup>2</sup> (Fig. 3), we expected a high spatial autocorrelation in our dependent variable, i.e. a high probability that a cell contains the same information as its neighbouring cell (Lennon 1999). Therefore we could not include the data



**Fig. 3.** Example of the indices  $R_A$  (left) and  $R_C$  (right) with radii of 5 km each.  $R_A$  only uses the predefined cells with extensively used areas and calculates the percentage of more cells of that type around,  $R_C$  uses all cells and calculates the mean part of cells with extensively used areas around. Also shown is the closer study area (CSA). The colours from white to black indicate increasing values of the indices. Cells outside the CSA were not considered. For orientation the home ranges (polygons) of the resident lynx and the random home ranges (circles) are also shown.



**Fig. 4.** (a) Spatial correlation coefficient. The Pearson correlation coefficient between two variables  $v_i$  and  $m_i$  taken over all cells  $i$  of the closer study area, where  $v_i$  is the value of the variable 'extensively used areas' in a given cell  $i$ , and  $m_i$  the mean value of this variable within a ring of radius  $r$  and width 2 around cell  $i$ . (b) Probability of finding an undisturbed cell at distance  $rs$  away from an arbitrary extensively used cell within the closer study area.

of all cells into the regression analyses as this would lead to pseudoreplication and to an overparameterized model adjusted too closely to the training data set. Thus, in such a model the spatially autocorrelated explanatory variables are detected as 'significant' much more frequently (Fielding & Haworth 1995; Carroll & Pearson 2000). To calculate spatial autocorrelation of spatial lag  $rs$ , we used Pearson's correlation coefficient for the percentage of the most important independent variable in the home range area, *PExt* (Table 1 and Fig. 4a), and calculated the probability of finding an extensively used cell at distance  $rs$  away from an arbitrary extensively used cell (Fig. 4b). To reduce the amount of cells in the logistic regression, we considered only those cells having a distance between them showing a lower correlation.

We avoided strong multicollinearity between the explanatory variables by choosing the variable that correlated most strongly with the dependent variable for the logistic regression. We considered two independent variables to be strongly correlated when  $r > 0.75$ , determined by the correlation matrix of the predictors (Spearman-Rho, two-tailed).

Variables were entered into a multiple logistic regression (logit link and a binomial error distribution using

procedure GENMOD; SAS Institute Inc., Cary, NC). Full models were not overdispersed (overdispersion parameter for all the full models considered  $< 1.27$ ,  $P > 0.08$ ; Table 2), hence indicating a good agreement between data and the selected link and error distribution (McCullagh & Nelder 1989). Therefore we did not further consider overdispersion in the estimation of parameters. Graphical inspection of the residuals did not show any trend or systematic departure from model assumptions. After the evaluation of the full models we followed a 'step-up' approach to find the minimal adequate model that best explained the dependent variable without incorporating unnecessary variables (Wilson *et al.* 1997; Bradbury *et al.* 2000). Initially, models were fitted in which the effects of the variables were tested one at a time. From these initial models we selected the one with the lowest Akaike information criterion (AIC) (Burnham & Anderson 1998), to which we added, one at a time, the rest of the variables, resulting in a series of two-variable models (Wilson *et al.* 1997). The process was finished when addition of new variables did not reduce the AIC. The minimal adequate model was considered to be the one with the lowest AIC and, in the case of similar AIC values, the one with the smaller number of predictors. The result is a model with the following formula:

$$\text{logit}(P) = \beta_0 + \beta_1 \times V_1 + \beta_2 \times V_2 + \dots + \beta_n \times V_n \quad \text{eqn 1}$$

where  $P$  is the probability of a cell belonging to a lynx home range and  $\beta_0$  is the intercept. The  $\beta$ s are the coefficients assigned to each of the independent variables during regression. The  $V$ s represent the various independent variables. Probability values can be calculated based on equation 1, where  $e$  is the natural exponent:

$$P = e^{\text{logit}(P)} / 1 + e^{\text{logit}(P)} \quad \text{eqn 2}$$

We chose the model with the best classification of correctly predicted lynx home range cells (sensitivity) for methodical reasons: absences cannot be considered as being as certain as presences (Schröder & Richter 2000) because the reintroduced population involved is still expanding (Stahl *et al.* 2001).

We also used receiver operating characteristic (ROC; Fielding & Bell 1997; Guisan & Zimmermann 2000; Pearce & Ferrier 2000; Schröder & Richter 2000; Osborne, Alonso & Bryant 2001) as a threshold or cut-off independent measure of model accuracy. An ROC was obtained by plotting the true positive proportion of correctly predicted occurrences (sensitivity) on the  $y$ -axis against the false positive proportion of correctly predicted absences (specificity) on the  $x$ -axis. The area under the ROC curve (AUC) was used to test for greater significance than the area under a random model, with  $\text{AUC}_{\text{crit}} = 0.5$ , i.e. the chance performance of a model lies on the positive diagonal of the ROC plot. Values between 0.7 and 0.9 indicate a reasonable discrimination ability appropriate for many uses, for



**Table 2.** Results of the logistic regressions for the variables described in the text. Each model varied the index  $R_A$  or  $R_C$  and its radii. Each logistic regression resulted in a model with only one significant variable, as listed below. Sensitivity and specificity refer to the percentage of correctly classified occurrences and non-occurrences, respectively (both at  $P = 0.5$ ). \*Indicates the final model we chose for assessing suitable lynx home range habitat in Germany.  $\beta_0$  refers to the intercept

Model	Model information					Model parameters					
	<i>n</i>	deviance	AIC	d.f.	Sensitivity	Specificity	Variable	$\beta \pm SE$	Wald $\chi^2$	d.f.	<i>P</i>
m1	62	74.5	78.5	60	74.3	48.1	$R_A1$	$2.43 \pm 0.81$	8.93	1	0.0028
							$\beta_0$	$-1.26 \pm 0.59$	4.63	1	0.0314
m2	62	69.8	73.8	60	85.7	51.9	$R_A3$	$3.60 \pm 1.06$	11.5	1	0.0007
							$\beta_0$	$-1.77 \pm 0.68$	6.71	1	0.0096
m3*	62	66.7	70.7	60	91.4	55.6	$R_A5$	$4.55 \pm 1.28$	12.65	1	0.0004
							$\beta_0$	$-2.13 \pm 0.77$	7.75	1	0.0054
m4	62	64.0	68.0	60	88.6	59.3	$R_A7$	$5.59 \pm 1.55$	13.10	1	0.0003
							$\beta_0$	$-2.48 \pm 0.86$	8.43	1	0.0037
m5	86	104.2	108.2	84	74.4	65.1	$R_C1$	$1.02 \pm 0.28$	13.35	1	0.0003
							$\beta_0$	$-1.05 \pm 0.37$	7.76	1	0.0053
m6	86	103.4	107.4	84	76.7	62.8	$R_C3$	$1.16 \pm 0.31$	13.93	1	0.0002
							$\beta_0$	$-1.09 \pm 0.38$	8.14	1	0.0043
m7	86	101.4	105.4	84	76.7	60.5	$R_C5$	$1.32 \pm 0.34$	15.42	1	0.0001
							$\beta_0$	$-1.17 \pm 0.39$	9.01	1	0.0027
m8	86	100.7	104.7	84	76.7	62.8	$R_C7$	$1.43 \pm 0.36$	15.90	1	0.0001
							$\beta_0$	$-1.20 \pm 1.39$	9.31	1	0.0023

example a value of AUC = 0.8 means that, in 80% of all cases for a randomly chosen area with presence, a greater presence probability is being calculated than for a randomly chosen area with non-presence (Fielding & Haworth 1995; Pearce & Ferrier 2000).

To apply the model to our large-scale study area we selected the cut-off level for a given probability *P* of our model ex posteriori by comparing the evolution of presence-absence prognosis. We chose a cut-off value in between the optimum cut-off value,  $P_{opt}$  (maximum of proportion of correct classifications), and the occurrence probability value,  $P_{fair}$  (least error of the model), where false presence predictions and false absence predictions have the same probability of occurring (Schröder & Richter 2000).

The predictive power of the model with the thus found cut-off value *P* was then validated with a set of telemetry data from the German-Czech border and Slovenia. For this we created home ranges with the same method of outlier removal as used for the Swiss data (Breitenmoser *et al.* 1993). For assessing the average number of lynx that could live in the patches of our large-scale study area, we used the core area size plus one standard deviation (non-overlapping part of the home range) of female lynx (99 km<sup>2</sup>) and the average core area size of male lynx (185 km<sup>2</sup>; Breitenmoser *et al.* 1993) to assess the possible number of lynx in Germany, and divided the suitable patches in Germany by these areas.

## Results

### UNIVARIATE DESCRIPTION OF LOCAL DATA

Lynx radio-locations were not randomly distributed, showing a clear tendency for avoidance of intensively

used land-use types (arable land and pastures) and a preference for forest ( $\chi^2 = 2740$ , d.f. = 7,  $P < 0.01$ ), with almost 80% of the locations of resident lynx in forest. Differences in the use of semi-natural non-forested areas were minimal.

Lynx home ranges had significantly fewer urbanized areas, *PUrb* and *NPUrb*, and significantly more areas with semi-natural non-forested land cover, *PNat*, than random home ranges (Table 1). Lynx home ranges tended to have more forest cover, *PFor*, more forest polygons, *NPFor*, and a greater perimeter of forest, *PeriFor*. As we might expect from lynx biology, combined variables had significantly higher index values,  $R_A$  and  $R_C$ , within lynx home ranges. On the other hand, compared with the random home ranges, we found twice the percentage of arable land, *PAgr*, in lynx home ranges and only a quarter of the percentage of pastures, *PPast*. These variables reflect both the specific landscape structure of the Jura Mountains and the MCP method for creating home ranges, and are not related to the known habitat preferences of lynx. Therefore they were excluded from the logistic regression.

### SPATIAL AUTOCORRELATION

The most important independent variable, extensively used areas, *PExt*, was highly autocorrelated at small spatial scales (Table 1 and Fig. 4a,b). Thus, to obtain a set of data that were spatially independent we removed neighbouring cells, retaining one of 25 cells (i.e.  $r_s = 5$ ) and hence obtaining a sample size of  $n = 62$  ( $R_A$  indices) and  $n = 86$  ( $R_C$  indices). For  $r_s = 5$  the spatial correlation coefficient of *PExt* was  $c = 0.5$  (Fig. 4a), and the probability of finding an extensively used cell in distance  $r_s = 5$  from an arbitrary *PExt* cell in the closer study site was 54% (Fig. 4b).

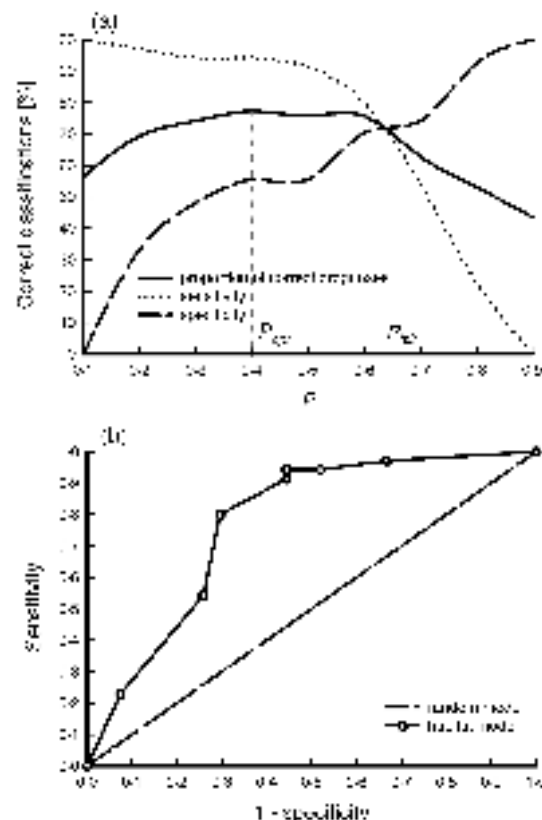
## CORRELATION ANALYSIS

*NP<sub>Urb</sub>* and *P<sub>Urb</sub>*, and *PeriFor* and *P<sub>for</sub>*, were highly correlated, and therefore contained very similar information. The variables with the greatest explanatory effect in respect to the response variable, *NP<sub>Urb</sub>* and *P<sub>For</sub>*, were retained. The indices for  $R_A$  and  $R_C$  of variable *PE<sub>Ext</sub>* were also highly inter- and intracorrelated within the different radii. As the indices  $R_A$  and  $R_C$  represent the connectivity of the same variable at different scales, we calculated eight different models for both  $R_A$  and  $R_C$ , each with the four different radii and the rest of the predictors. With this we avoided the danger of undertaking the kind of a priori screening that can lead to deleting the superior explanatory variable (MacNally 2000).

## LOGISTIC MODELS

For the logistic regression using the  $R_A$  index, we only used *PE<sub>Ext</sub>* cells, which explains the reduced amount of cells ( $n = 62$ ) in comparison with the models with the  $R_C$  indices ( $n = 86$ ). In all cases, the minimal adequate model chosen contained only one variable related to the fragmentation of forest and natural areas at different scales, with a higher probability that a cell belonged to a lynx home range with decreasing fragmentation, which means an increasing  $R_A$  or  $R_C$  value. The model with the highest sensitivity included  $R_{A5}$  as a predictor (model 3 in Table 2). A circle with a radius of 5 km represents an area of about 80 km<sup>2</sup>, which is approximately the size of the core area of a female lynx's home range ( $72 \pm 27$  km<sup>2</sup>; Breitenmoser *et al.* 1993). Note that this does not reflect a forest patch of this size, but a continuous configuration of forest and other semi-natural land cover types of at least 50% in a circle around any cell.

For further application of the chosen model we used the classification prognoses of the model (Fig. 5). The optimum cut-off value would be  $P = 0.4$ , and the least error of the model was close to  $P = 0.6$ . We therefore chose for model transfer a cut-off value in between  $P_{opt}$  and  $P_{fair}$  of  $P = 0.5$ . The model ROC plot had an AUC of 0.77, indicating reasonable discrimination (Fig. 5).



**Fig. 5.** (a) Percentage of correct prognoses of the total model, sensitivity and specificity of the chosen model in dependence on  $P$ . (b) ROC plot for the chosen habitat model. AUC is 0.77. The chance performance of a model (e.g. a random model) is  $AUC = 0.5$ ; models that out-perform chance have greater AUC values. AUC is a convenient measure for overall fit.

## MODEL VALIDATION

Application to the area of the German–Czech border and Slovenia on average explained more than 80% of the cells within home ranges and of the telemetry locations above a cut-off level of  $P > 0.5$ , which is even higher than in the training data set (Table 3 and Figs 2 and 6). The model classification accuracy of independent data was therefore high.

**Table 3.** Comparison of the model results (model m3 in Table 2) for the Swiss, German–Czech and Slovenian data using cells within the home ranges (HR) and telemetry locations (locs; without considering the outliers) of resident lynx for  $P > 0.5$  (cf. Figs 1 and 6)

Area	Females (F)/males (M)	$n$ HR	% observed HR cells correctly classified (SD)	$n$ locs	% observed telemetry locations correctly classified (SD)
Swiss Jura Mountains	F	5	70.4 (7.2)	1898	78 (17.5)
	M	3	82.2 (15.1)	1059	88.1 (9.5)
	Total		75 (11)		82 (15)
German–Czech border	F	1	96.4	198	93.9
	M	2	83.3 (8.5)	198	74.8 (6.5)
	Total		88 (10)		81 (12)
Slovenia	F	2	80.6 (6)	382	95.2 (2.5)
	M	3	88.8 (2.1)	146	98.7 (2.2)
	Total		86 (6)		97 (3)

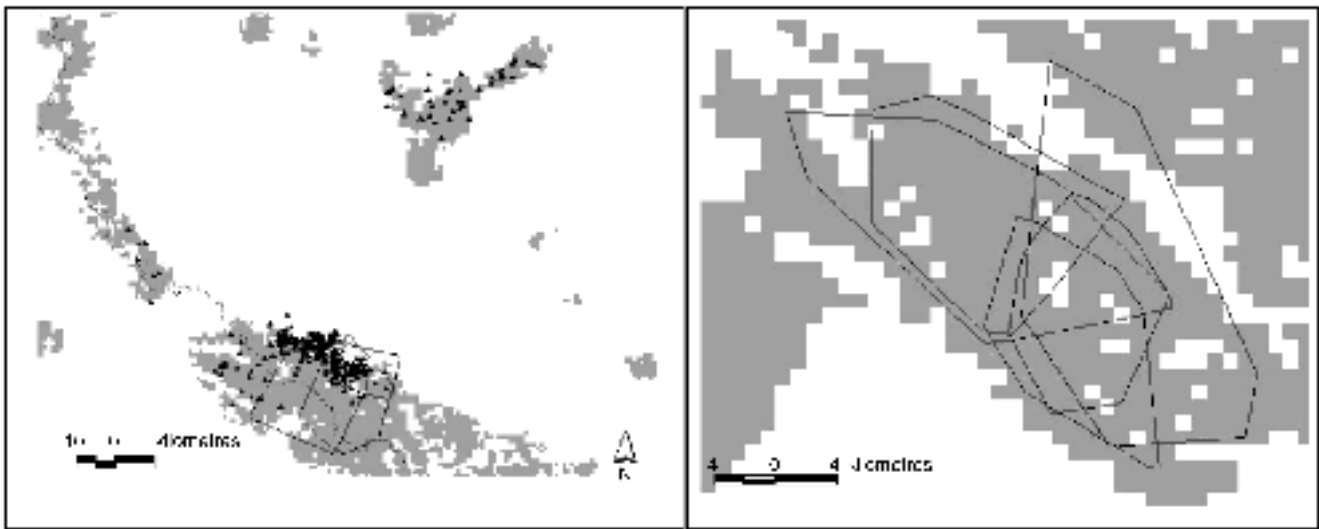


Fig. 6. Independent model validation with data from the German–Czech border (left) and Slovenia (right). Grey cells show suitable areas for lynx home ranges based on the applied model, polygons show the home ranges of resident lynx, and triangles show locations of dispersing animals in the Czech Republic.

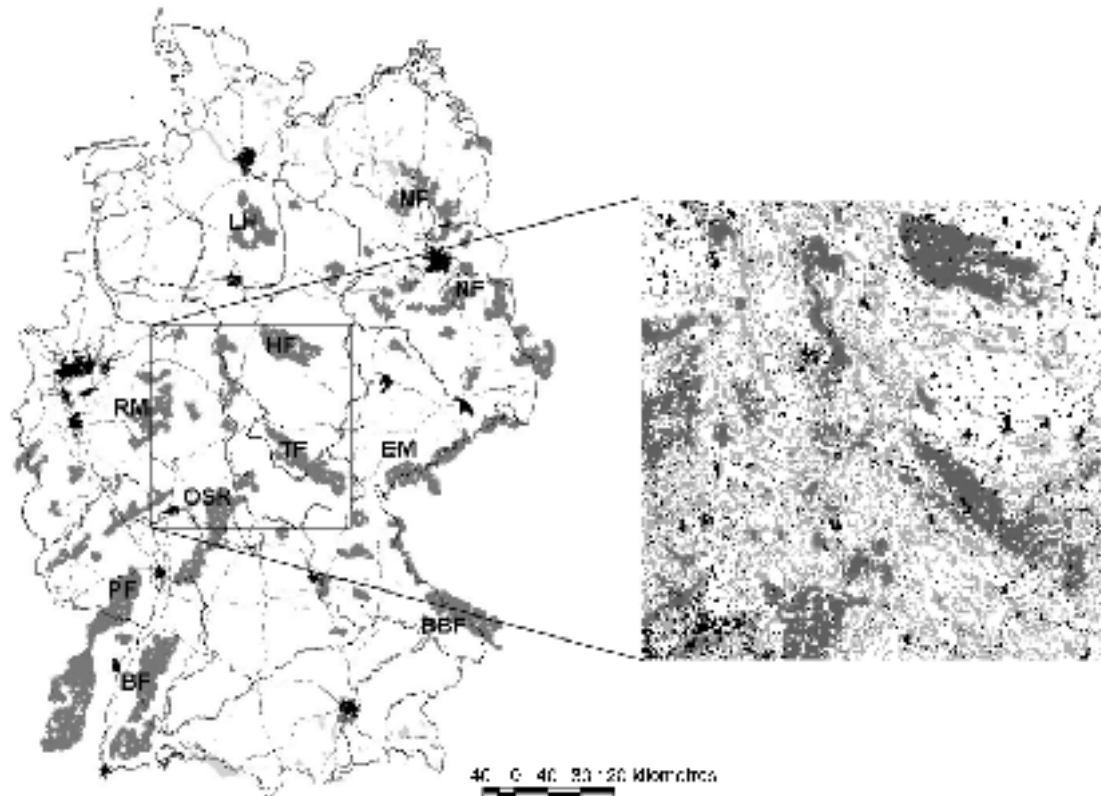
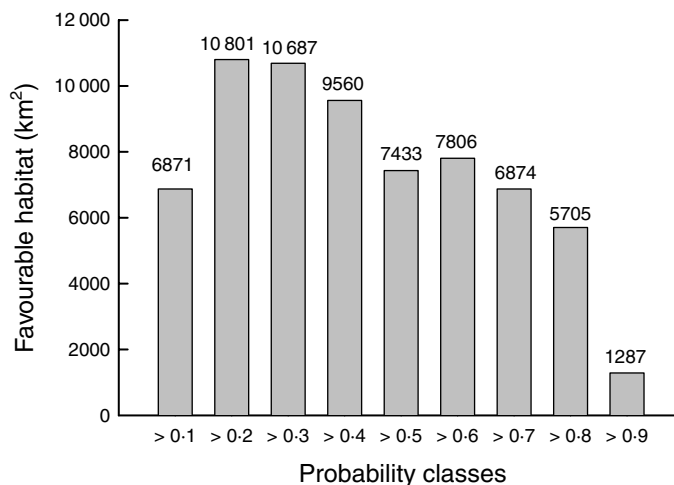


Fig. 7. Favourable lynx home range areas in Germany with an area  $\geq 99 \text{ km}^2$  and a  $P$ -level  $> 0.5$  based on the logistic model (dark grey). Water bodies (light grey), rivers (solid black line) and highways (dotted black line) show further influences that could minimize home range numbers by a fragmentation effect. Black polygons show the biggest urban areas. HF, Harz; NF, North-eastern Forest; TF, Thuringian Forest; BBF, Bohemian-Bavarian Forest; PF, Palatine Forest; BF, Black Forest; LH, Lüneburger Heath; OSR, Odenwald-Spessart-Rhön; RM, Rothaar Mountains; EM, Erz Mountains. The inset shows the preparation of the map for a simulation model. Black, barriers, e.g. urban areas and water bodies; white, matrix, e.g. agriculture and pasture; light grey, dispersal habitat, e.g. any natural vegetation type such as forest or heathland; dark grey, breeding habitat, e.g. suitable cells based on the results of the logistic model.

#### MODEL PREDICTION FOR THE LARGE-SCALE STUDY AREA

Suitable areas of habitat in the large-scale study area were mainly concentrated in the low mountain ranges

of Germany (PF, RM, BF, HF, OSR, TF, BBF, EM; Fig. 7), the forest of Lüneburger Heath (LH; Fig. 7) and the large forests in the north-east (NF; Fig. 7) and close to the Polish border. These big patches are surrounded by smaller suitable satellite patches.



**Fig. 8.** Favourable habitat area in Germany based on probability levels from the logistic regression model. Of a total area of 357 909 km<sup>2</sup>, 328 804 km<sup>2</sup> (92%) was unsuitable for lynx home ranges.

**Table 4.** Suitable patches in Germany (cf. Fig. 7) based on the logistic regression model, with patches bigger than 99 km<sup>2</sup> based on maximum core area sizes of female lynx in the Swiss Jura Mountains (Breitenmoser *et al.* 1993). Home range (HR) numbers correspond with core areas and are calculated by dividing the area by 99 km<sup>2</sup>

Suitable patch	Size (km <sup>2</sup> )	No. of female HR
Lüneburger Heath (LH)	1193	12
North-eastern Forest (NE)	5185	52
Odenwald-Spessart-Rhön (OSR)	2151	21
German-Czech border (Bavarian/Bohemian Forest, Erz Mountains) (BBF, EM)	4637	46
Thuringian Forest (TF)	1676	17
Black Forest (BF)	2974	30
Palatine Forest (with Vosges Mountains) (PF)	5232	52
Harz Forest (HF)	1566	16
Rothaar Mountains (RM)	1551	16

About 81% of Germany consists of unsuitable area for lynx, and these grid cells were not considered in the logistic regression because they contained less than 66% of extensively used areas. Of the remaining 67 024 km<sup>2</sup> a total of 29 105 km<sup>2</sup> (43%) reached a *P*-level above 0.5 (Fig. 8). Considering only those areas with *P* > 0.5 that are ≥ 100 km<sup>2</sup>, we obtained a total area of 32 266 km<sup>2</sup> for Germany and neighbouring forest areas in France, the Czech Republic and Poland, which is reduced to 24 119 km<sup>2</sup> for Germany only (Table 4 and Figs 6 and 8); at typical home range size, this leaves space for about 370 resident lynx in the suitable patches in Germany.

## Discussion

### GAINS AND SHORTCOMINGS

The use of models to predict the likely occurrence or distribution of conservation target species is an important first step in conservation planning and wildlife management (Pearson, Drake & Turner 1999). Effective and correct model assessment therefore has real significance to fundamental ecology as well as conservation biology (Manel, Williams & Ormerod 2001).

Here we developed a statistical habitat model to predict suitable areas for lynx in central Europe, based on our current understanding of its biology; a model that can be applied to similar kinds of landscapes, for example in Belgium, Scotland, the Netherlands and France. Although we have specifically addressed the situation of the Eurasian lynx in central Europe, we are confident that our approach may also be used for other species and purposes, where only local data exist but large-scale information on fragmentation or the influence of other land-use types is needed (Mladenoff *et al.* 1995; Osborne, Alonso & Bryant 2001). The future of large carnivores in central Europe will depend on our ability to protect and promote suitable areas and connecting corridors where they can be managed effectively (Corsi, Duprè & Boitani 1999; Palomares *et al.* 2000; Palomares 2001). It will also depend on the correct management of reintroduction schemes, and the prior detection of potential areas where conflicts with human economic activities and illegal hunting might occur.

A potential problem with our model is that it was built on data from an expanding population. It is unknown whether the unoccupied areas are really unsuitable or whether the population was not saturated

and would also spread into these areas when the best areas are occupied. Lynx are also present in the French part of the Jura Mountains (Stahl *et al.* 2001), but it is currently not known if the sightings or findings of lynx prey remains correspond to resident lynx or to floaters. For our model we cannot be absolutely sure whether our supposed absence data would be so in the future, but this only leads to an underestimate of the power of the independent variables (Boyce & McDonald 1999), i.e. an underestimate of suitable habitat in more fragmented areas. If home ranges now occupied an area with a high occurrence probability, this would rather confirm the validity of the model. For many threatened, rare and elusive species limited data only are available, and especially for rare and endangered species their whole range is never occupied. However, these are exactly those species for which management decisions are required (Palma, Beja & Rodrigues 1999). We recommend updating our models for lynx with new data as soon as they are available in order to determine which other habitat variables could be constraining lynx presence.

Care must be taken with logistic regression as a predictive tool. Many approaches with logistic regression include a variety of landscape variables that are available from maps rather than from biological requirements of the species (Odom *et al.* 2001). Therefore they cannot be applied elsewhere and may not produce new insights into the biology of the species. Our model constitutes an advance in that we analysed the species requirements and eliminated variables that were not plausible from lynx biology. We found a significantly high proportion of other non-wooded semi-natural land-cover types within lynx home ranges. A fragmented forest area interrupted by semi-natural non-wooded areas could also attract roe deer, which is the main prey of lynx. We can therefore assume that in the study area the absence of intense human land use is the decisive factor for establishing lynx home ranges. Distribution of forest alone was not important in this case, as we have a high distribution of forest cover over the entire study area.

Local landscape variables were not significantly different between lynx and random home ranges, but a variable comprising a regional scale (cf. Mladenoff *et al.* 1995; Massolo & Meriggi 1998; Carroll, Zielinski & Noss 1999). We can therefore assume that models like ours for the Eurasian lynx can be transferred to other areas without considering local structures such as forest composition or distribution of prey. Small-scale structures are presumably more important for intraterritory use and for dispersal than for predicting regional home range distribution.

An additional problem in the context of logistic regression is dealing with spatial autocorrelation of the dependent variable, which leads to overparameterized models that are not general habitat predictors for species presence (Lennon 1999). The selection of cells to avoid the effect of spatial autocorrelation could have led to the exclusion of cells with a high percentage of urban areas, so this variable was therefore not a signi-

ficant discriminator of lynx home ranges and random home ranges. This circumstance is reinforced by the fact that the MCP method for calculating lynx home ranges is a conceptual approximation. At the margins of the MCP many cells with land-use types that are not used by lynx can be included in the logistic regression. However, in the  $R_A$  models cells with less than 66% extensively used areas are excluded from the analysis beforehand. Furthermore, the reduction of spatial autocorrelation leads to general predictions of habitat suitability, which in our case was necessary for model application at very large spatial scales.

A crucial question in applied biology is to what extent information is transferable between geographical areas (Rodriguez & Andr en 1999). If the transferability of the model is not examined and verified, only local applications are possible (Morrison, Marcot & Mannan 1992; Fielding & Haworth 1995; Rodriguez & Andr en 1999). General validity requires new applications in space and time (Brooks 1997; Schr oder & Richter 2000; Manel, Williams & Ormerod 2001). In our case, model validation with independent data from other regions like the German–Czech border and Slovenia showed accuracy of more than 80%. Comparing our model results with data on population development along the German–Czech border from 1990 to 1995 ( erven y, Koubek & And era 1996) and with data from 1999 (W offl *et al.* 2001), there is a very high concordance with our model results. The high prediction accuracy is due to the fact that these areas are not very fragmented and consist almost only of forest.

#### IMPLICATIONS FOR MANAGEMENT AND FUTURE RESEARCH

Our analysis provides insight into the distribution, the amount and the fragmentation of favourable lynx habitat in central Europe and especially Germany. The patches of suitable habitat are located mainly in the low mountain ranges of south and central Germany and in the large forests in the north and east of Germany. However, the distribution of suitable areas is patchy and many of them seem isolated (L uneburger Heath, LH; Fig. 7) or fragmented by highways or rivers (Odenwald-Spessart-Rh on, OSR; Fig. 7), which make them seem unsuitable as focal areas for reintroduction. Isolated patches can cause populations to suffer from demographic and genetic effects when they are too small and lack immigration. Experts estimate that minimum numbers for viable populations are at least 50–100 individuals (Seidensticker 1986; Shaffer 1987; Allen, Pearlstine & Kitchens 2001). Assuming an overlap of one male per female, only the north-eastern forests (NF), the Palatine Forest with the Vosges Mountains (PF) and the German–Czech area (EM + BBF) can host up to 100 lynx, while the Black Forest (BF) could host up to 60 lynx, making these the most suitable target areas. However, local-scale factors, such as roads, could make these areas unsuitable, and

therefore we need to proceed with more detailed models at local scales before accepting an area as suitable for lynx reintroduction (Kaczensky *et al.* 1996; Mace *et al.* 1996; Trombulak & Frissell 2000).

Comparing the model results with a previous rule-based approach (Schadt *et al.*, in press), we found a high concordance in the distribution and also the number of female home ranges within suitable areas. For example, for the Black Forest, the Thuringian Forest, the Harz and the German–Czech border, we found almost the same number of female home ranges with deviations  $\pm 3$  home ranges when comparing the two modelling approaches. But the number of female home ranges is reduced by approximately one-third in the current model for the Rothaar Mountains and increased by approximately one-third for the north-eastern forests. One reason for this is the fragmentation of the Rothaar Mountains, which was not considered in the rule-based approach of Schadt *et al.* (in press). In addition, we had a high proportion of natural non-forested heathland in the north-eastern forest area, which increased the number of female home ranges not considered in the rule-based approach. This clearly shows how important it is to counter-test and evaluate qualitative and quantitative models before basing management schemes such as reintroductions on only one assessment.

Population viability analyses (Boyce 1992; Lindenmayer *et al.* 2001) should now be the next step in assessing whether the existing habitat patches in Germany are large enough to host populations of lynx and to what degree viability is influenced by local-scale factors (e.g. road mortality). Our example shows how models can provide a sound basis for a spatially explicit population simulation to answer questions on the viability of carnivore populations under ‘real’ conditions.

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