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RULE-BASED ASSESSMENT OF SUITABLE HABITAT AND PATCH CONNECTIVITY FOR THE EURASIAN LYNX

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Abstract. Conservation biologists often must make management decisions based on little empirical information. In Germany, biologists are concerned that the recovery and reintroduction of Eurasian lynx (*Lynx lynx*) may fail because the remaining suitable habitat may be insufficient to sustain a viable population. However, no comprehensive study addressing this concern has been made that not only considers distribution of suitable habitat, but also connectivity to other populations. The aims of this study were (1) to quantify the amount and location of potentially suitable lynx habitat in Germany, (2) to estimate the connectivity between patches of suitable habitat, and (3) to evaluate lynx conservation programs. Habitat preferences of lynx were described in a rule-based model based on the availability of forest cover (defined by patch size) and the spatial structure of the habitat. Rules were implemented in a geographic information system to predict locations of suitable habitat. Optimal connections among patches were modeled using a cost-path analysis based on habitat-specific probabilities of lynx crossing patches. Results indicated wide variation in the size of patches of suitable habitat, with 10 areas each sufficiently large to sustain >20 resident lynxes. Overall, a total of 380 lynxes could be sustained by the 10 areas. Uncertainty analyses of model parameters and assumptions revealed little variation in predicted habitat, primarily because results were constrained by the actual distribution of forest habitat. Our analyses suggest that lynx reintroduction programs should emphasize large, connected areas and consider broad-scale habitat connectivity in the landscape. Our approach also demonstrates how biologically plausible rules can be applied in conservation to identify areas in which success is most likely, even when few empirical data are available.

Key words: conservation; cost-path analysis; decision-making process; Eurasian lynx; geographic information system, GIS; large-scale approach; limited resources; Lynx lynx; *patch connectivity; predictive habitat model; rule-based model; species reintroduction.*

Introduction

Conservation biology is frequently called a "crisis discipline" because of the urgency of the issues that must be addressed with few data and little money (Soulé 1986, Doak and Mills 1994). The management and conservation of large carnivores are especially difficult due to their large spatial requirements and potential conflicts with human activities (Noss et al. 1996, Woodroffe and Ginsberg 1998). Large carnivores have been considered competitors for game and livestock, and were vigorously hunted. Active predator control, along with habitat loss and fragmentation, led to their extinction from most cultivated landscape throughout Central Europe (Breitenmoser 1998, Breitenmoser et al. 2000). However, changes in land use and in human attitudes towards large carnivores during the past several decades have promoted the slow recovery of wolves (*Canis lupus*; Blanco et al. 1992, Boitani 2000), brown bears (*Ursus arctos*; Servheen et al. 1998, Swenson et al. 2000), and the Eurasian lynx (*Lynx lynx*; Breitenmoser et al. 2000; see Plate 1) in several European countries. In this paper, we present a rule-based model for predicting suitable habitat for the Eurasian lynx based on current knowledge, and apply it to the landscape of Germany.

Carnivore recovery presents a challenge for wildlife managers and conservation biologists because a viable population must be established while other conflicts are minimized, preferably before they occur. Knowledge of the extent, spatial arrangement, and connectivity of suitable habitat is required for predicting colonization of unoccupied habitat. With such knowledge, costly reintroduction programs in areas expected to un-

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PLATE 1. Eurasian lynx (*Lynx lynx*) is the third largest predator in Europe (after the brown bear and the wolf). Body mass of adults ranges between 12 and 15 kg, with males being larger than females. Lynx prefer vast connected forest patches. Photograph by Antonio Sabater/Enfoque 10.

dergo natural repopulation can be avoided, and habitat islands that might serve as suitable stepping stones for dispersing animals can be identified. Habitat models based on presence/absence data have proven useful (Morrison et al. 1992, Boyce and McDonald 1999), but field data to develop more sophisticated models are usually lacking for species in areas where they have been extirpated.

Quantitative rule-based modeling may be useful for developing and assessing plans for carnivore recovery. Rule-based modeling has been used successfully for a variety of taxa to assess effects of climate change, land-use change, and habitat fragmentation (Hansen et al. 1993, 1995, Dale et al. 1994, Irwin 1994, Offermann et al. 1995, Knick and Dyer 1997, White et al. 1997, Van Appeldoorn et al. 1998, Pearson et al. 1999, Urban 2000). Descriptors of landscape patterns have been related to anthropogenic disturbance and biotic communities (e.g., Miller et al. 1997), and information systems have been developed to support decision making in conservation and land-use planning (e.g., Cooperrider et al. 1999, Theobald et al. 2000). In quantitative rule-based models, verbal rules are replaced by equations (Starfield 1990). For example, in habitat evaluation procedures (HEP; Brooks 1997), which are based on habitat suitability indices (HSI; USDI Fish and Wildlife Service 1980, 1981), an algorithm is used to predict habitat suitability based on a selection of habitat variables (Cooperrider 1986; for examples, see Brennan et al. 1986, Davis and DeLain 1986, Doering and Armijo 1986, Fry et al. 1986). These models have been criticized, however, for including somewhat arbitrary equations that are difficult to interpret and for not including variables related to landscape context (Van Horne and Wiens 1991). We suggest a modeling approach using understandable rules closely linked to the biological requirements of a species, the lynx, and that incorporate landscape structure as perceived by the species (Lima and Zollner 1996).

By the first half of the 20th century, the lynx was extirpated from all of Europe west of the Slovakian Carpathians (Breitenmoser et al. 2000). However, several lynx reintroductions have occurred since 1970, e.g., in Switzerland (Breitenmoser et al. 1993), France (Herrenschmidt and Leger 1987), and the Czech Republic (Červený et al. 1996). In Germany, locations such as the Black Forest (Goßmann-Köllner and Eisfeld 1989), Palatine Forest (Himmer 1978), Harz Mountains (Pohlmeyer 1997), Bavarian Forest, and the Alps (Kluth et al. 1989) have been proposed for lynx reintroduction, and one project has begun in the Harz (Barth and Pohlmeyer 2000). Lynx have also dispersed naturally to the Bavarian Forest from a reintroduced population in the Bohemian Forest, Czech Republic (Wölfl et al. 2001) (see Fig. 1). Ten to fifteen lynx were reported to occur in the Bavarian Forest as of 1996, with additional sightings reported along the German–Czech border (Červený and Bufka 1996, Wölfl et al. 2001). Lynx sightings have also been reported from the Black Forest and the Palatine Forest (Fig. 1); these may be immigrants from a reintroduced population in the Vosges Mountains, France (Herrenschmidt and Leger 1987).

Broad-scale habitat assessment would help provide

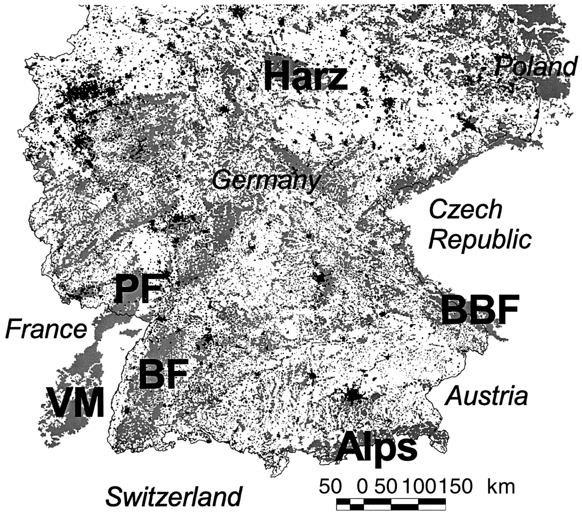

FIG. 1. Forests in Germany with adjacent forests in France, Poland, and the Czech Republic (in gray). Black = urban areas. Lynx reintroductions were planned for the Harz, Palatine Forest, the Black Forest, the Alps, and the Bavarian Forest. Lynx have been reintroduced to the Bohemian Forest, the Vosges Mountains, and the Harz. Abbreviations are: PF, Palatine Forest; BF, Black Forest; BBF, Bavarian/Bohemian Forest; and VM, Vosges Mountains.

information for the alternative proposals for lynx reintroduction in Germany. Predictive models of habitat for lynx have been created on a local scale (e.g., for the Black Forest in Germany [Goßmann-Köllner and Eisfeld 1989], and the Jura Mountains in Switzerland [Zimmermann and Breitenmoser 2002]), for different biomes (e.g., the Alps, see Corsi et al. [1998]), or on a broad scale, but without considering links to other suitable areas (Schadt et al. 2002). In this study, we developed a rule-based habitat model for lynx to synthesize current knowledge about a species and predict the distribution of its potential habitat. We then applied this model within a geographic information system (GIS) and addressed the following questions related to conservation planning for the Eurasian lynx in Germany: (1) What is the extent and arrangement of potentially suitable habitat for lynxes in Germany? (2) Are potential habitat patches connected to one another or to existing populations in the Bavarian and Bohemian Forests? (3) Are there barriers separating potential habitat locations? and (4) Which are the most suitable areas for applying lynx reintroduction programs?

METHODS

Study area and GIS mapping

Our study area comprised Germany and large adjacent areas covered by forest (see *Habitat requirements and dispersal of the lynx*) in neighboring countries: the Bohemian Forest in the Czech Republic, the forests along the German–Czech and German–Polish borders, as well as the Vosges Mountains in France (Fig. 1), totaling ~374 000 km². The German Alps were excluded from our analyses.

We used CORINE (COordination of INformation on the Environment) land cover classification as a database for our habitat and cost-path analyses. CORINE is a European project for uniform environmental data mapping. The maps were digitized from Landsat Thematic Mapper satellite data and geocoded with topographical maps on a scale of 1:100 000 (Deggau 1995). We reduced the original 64 categories of land cover to five: (1) urban areas, (2) agricultural areas and pastures, (3) forests (including tree plantations), (4) open areas with natural vegetation, and (5) bodies of water (lakes and rivers wider than 100 m). Road data were obtained from ArcDeutschland'500 (version 1.0 1993, ESRI, Redlands, California, USA), and by digitizing road maps on a scale of 1:200 000 for France, Poland, and the Czech Republic.

Habitat requirements and dispersal of the lynx

Model rules were based on current knowledge of the species' biology, especially in the Swiss Jura Mountains, with additional information derived from telemetry studies in Poland and the Swiss Alps. The Jura Mountains are a low mountain range comparable in elevation, land use, and population density to the low mountain ranges in Germany.

The distribution of the Eurasian lynx in Central Europe is closely linked to forest cover (Haller and Breitenmoser 1986, Breitenmoser and Baettig 1992). An average home range of the adult lynx in the Swiss Jura Mountains had at least 60% forest cover (F. Zimmermann, *personal communication*). The spatial structure and the degree of forest fragmentation are also important, as fragmented areas (forest interrupted by other land-use types) are only used for passage (Haller and Breitenmoser 1986). Although lynx did not stay permanently in forest areas <30 km² (Haller 1992), this minimum area (later defined as the core area) can be interrupted by open areas, but not by main highways or large urban areas (Haller 1992). A lynx home range can include narrow forest passages or even isolated forest patches (C. Breitenmoser and A. Jobin, *personal communication*), but they should be <1 km apart (Haller and Breitenmoser 1986). Roads, large rivers, or high mountain chains normally act as home range borders.

In the Swiss Jura Mountains the sizes of the intrasexually exclusively used home ranges average 168 ± 64 km² (±1 SD) for females ($n = 4$) and 264 ± 23 km² for males ($n = 3$), resulting in a density of 0.94 resident lynx per 100 km² (Breitenmoser et al. 1993). Similar figures are reported from the Swiss Alps and Poland (Jedrzejewski et al. 1996, Okarma et al. 1997, Schmidt et al. 1997, Breitenmoser et al. 2000).

The minimum space requirements of a viable lynx (or other feline) population are unknown. Thor and Pegel (1992) questioned experts and estimated the minimum viable population size to be at least 20 resident adult lynxes. The estimate of 20 territories for long-lived large vertebrates is also supported by Verboom et al. (2001). Assuming a density of 1 adult lynx per 100 km^2, 20 resident lynx would require $\sim$2000 km^2. Therefore, we estimate that a functionally connected patch of suitable habitat >2000 km^2 could sustain a viable lynx population.

The main prey of the Eurasian lynx are small wild ungulates, mainly roe deer (*Capreolus capreolus*), and chamois (*Rupricarpa rupricarpa*) or red deer (*Cervus elaphus*), where available (Breitenmoser and Haller 1987, Jedrzejewski et al. 1993, Okarma et al. 1997). In Switzerland, the ungulate density was estimated at $\sim$6–9 roe deer/km^2 and 1.2–1.9 chamois/km^2 in the Jura Mountains (Jobin et al. 2000). Comparable densities of prey species are reported from the Swiss Alps and Poland (Breitenmoser and Haller 1987, Jedrzejewska et al. 1994). Referring to the total area of Germany, including large unforested areas, the average take of roe deer is $3 \cdot km^{-2} \cdot yr^{-1}$, with an increasing trend (Deutscher Jagdverband 1999). The actual roe deer densities in good roe deer habitat, which contains a certain amount of forest, are thus higher. It seems reasonable to assume for our model that the densities of wild ungulates are well above the minimum requirements for the lynx in Germany and are not a limiting factor.

Although both sexes of the lynx normally disperse in their second year, long distance movements or home range shifts may also occur in adults (Breitenmoser et al. 1993). The average distance of dispersing subadults in the Swiss Jura Mountains was 43 km (n = 11), measured from the center of the maternal home range to the center of the range occupied by the animal, and the maximum distance covered was 98 km (Zimmermann 1998). In Poland the dispersal distances of juvenile lynx were in the same magnitude, ranging from 5 to 129 km (Schmidt 1998).

Quantitative information on the habitat selection of dispersing lynx is scarce. The directions and routes of lynx dispersal and emigration are apparently linked to the distribution and availability of forest and forest corridors. Open farmland is rarely used (Schmidt 1998). Telemetry data from dispersing lynxes in the Swiss Jura Mountains showed that 75% of all locations were in forest, only 25% in open areas (11% natural open areas, 11% pastures, and 3% agriculture areas), and none in urban areas (U. Breitenmoser, *unpublished data*). Therefore, we defined any forest as dispersal habitat, open areas as avoided matrix (hereafter referred to as ''matrix''), and urban areas as barriers.

Modeling strategy

We combined two types of GIS models: first, a rule-based habitat model to determine the location and size of suitable lynx habitat, and second, a patch connectivity model to find the best connections between these patches. Patches of suitable habitat were identified using a set of rules that describe lynx habitat preferences in relation to the shape and structure of different habitat types derived from a GIS database. To find and evaluate possible connections, we located paths between habitat patches using a method based on cost values for each habitat type (cost-path analysis), an approach similar to the assignment of permeability values to land-use types used by Boone and Hunter (1996) for grizzly bears. The results of both models were then used to evaluate overall habitat suitability.

The habitat model

Habitat preference information was summarized into the following rules:

Rule 1: Fragmentation of patches.—Fragmented forest areas were considered connected and suitable for home ranges if forest patches were separated by $\leq$1 km.

Rule 2: Barriers.—Main rivers, highways, and urban areas act as home range borders.

Rule 3: Minimum patch size.—A patch of suitable habitat should allow females and males to establish a home range. Because home ranges of males and females overlap, minimum patch size was determined by the spatial needs of a male ($\sim$200 km^2).

Rule 4: Core areas.—A home range should include at least one nonfragmented forest patch $\geq$30 km^2 not crossed by main roads (core area). To avoid very narrow forest strips from being included in a core area, the minimum width of a core area was considered 1 km. Also, to avoid home ranges from including inaccessible areas, forest patches >20 km from a core area were excluded.

Rule 5: Minimum forest cover.—A home range should comprise at least 60% forest cover.

For application of the rule set to the land cover map, Arc/Info 7.1.1 and ArcView 3.0b, including the extension Spatial Analyst, were used. To obtain a map of nonfragmented forest patches (rule 1), the vector data on land use (resolution of 100 m) were transformed to a raster map with a grain of 1 km^2, as this is the distance that the lynx can perceive as connected (Haller and Breitenmoser 1986) (Fig. 2A). Then, cells containing at least 25% forest cover (forest cells) and having at least three neighboring forest cells were selected for the ''forest neighbor map'' (Fig. 2B). This neighborhood analysis ensured that all forest patches within a forest cell, as well as between neighboring forest cells, were <1 km apart (rule 1). The forest cell map was overlaid with the barrier map, and nonfragmented forest patches (nfFP) $\geq$200 km^2 (rules 2, 3) were selected (Fig. 2C).

Core areas with a width >1 km (rule 4) were obtained similarly, only using a grain size of 0.11 km^2 (1/9 of 1 km^2 to later ensure with a neighborhood analysis that the forest core area is at least 1 km wide), and selecting all forest cells with eight neighboring forest cells. We buffered these remaining inner cells with 333 m to re-include their neighboring forest cells. This map was

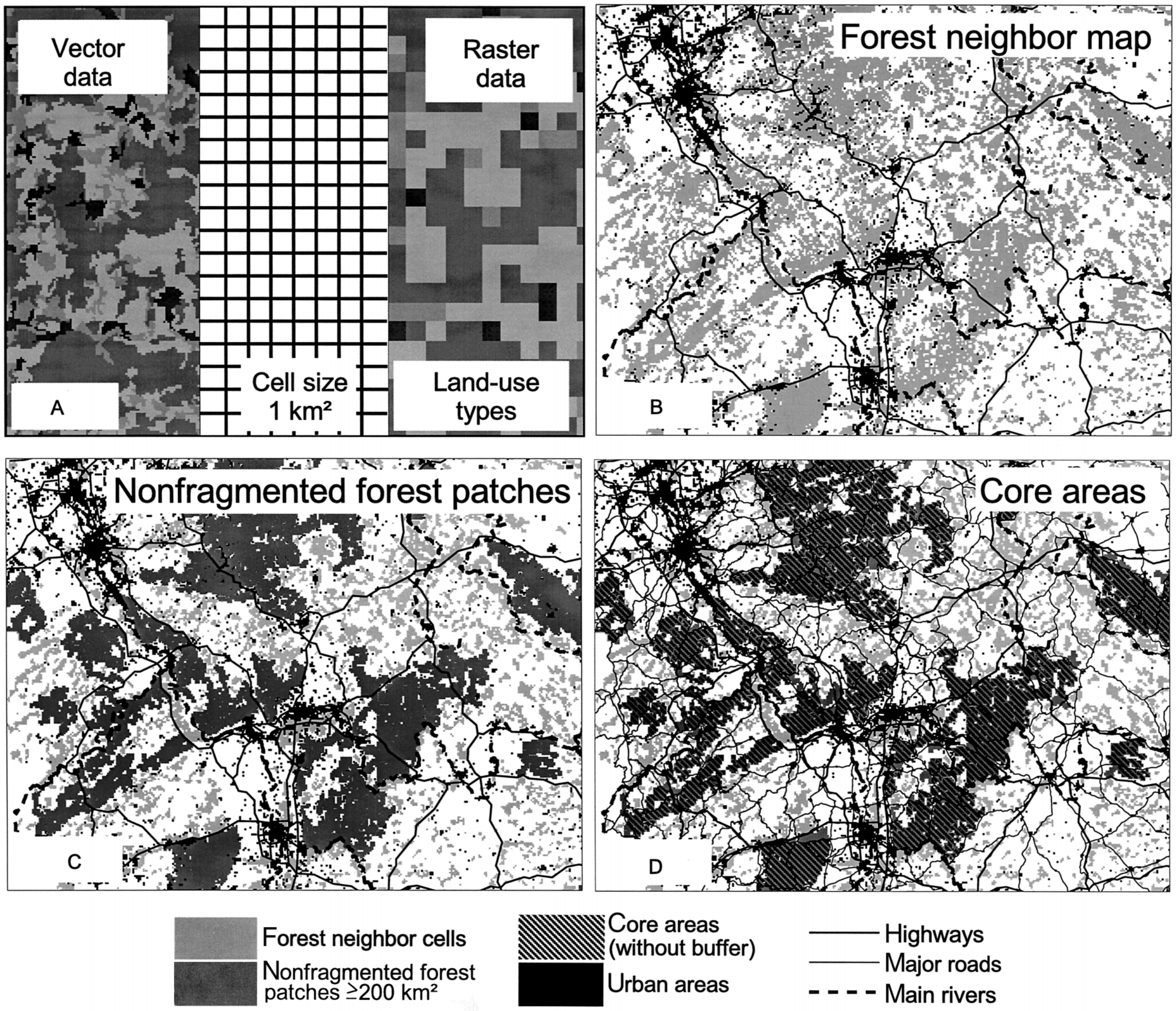

FIG. 2. Application of the rules for distinguishing suitable habitat patches to a GIS: (A) transforming the original land-cover map to a raster map with a cell size of 1 km^2, (B) neighborhood analysis to find nonfragmented forest cells, (C) selection of nonfragmented forest patches not crossed by barriers and large enough for a male home range (>200 km^2), and (D) map of nonfragmented core areas.

then overlaid with a map of the main roads. Forest patches ≥30 km^2 were selected, producing a map of connected core area patches (CCP map; Fig. 2D). To ensure that the area of a potential home range was close enough to a core area, we buffered the core area with 20 km, and produced a map of buffered core area patches (BCP map). We combined the nfFP map and the BCP map to obtain a map of habitat patch borders (HPB map). Finally, we checked the patches for having at least 60% of forest cover (rule 5).

To obtain the number of adult resident lynx that could live in a given habitat patch, we divided each suitable habitat patch on the HPB map by the average female and male home range sizes. To test the effect of parameter changes on our results in respect of the model rules, assumptions, and parameters, we performed an uncertainty analysis (Turner et al. 1994, Liu and Ashton 1998), and tested four different scenarios (A–D) for the nfFP map (Table 1). Sensitivity was assumed to be high when the deviation from our model results exceeded 20%.

The patch connectivity model

The connectivity model comprised two steps. First, we determined the ''best'' connection between two patches of suitable habitat based on the habitat selection of dispersing lynx, and second, we evaluated the quality of such potential connections regarding length, habitat types, and barriers.

Cost-path analysis was used for finding the best connection by assigning a cost value for each habitat type in accordance with the habitat selection of dispersing lynx, then summing the costs for all cells belonging to a given path. Consequently, the absolute cost value of a path contains information on the length and suitability of the area crossed, and can be used to find the ''best''

TABLE 1. Uncertainty analysis with alternative scenarios for the maps with connected forest patches (nfFP map, 4 scenarios).

Parameter	Alternative nfFP maps: scenarios A	B	C	D	Standard parameter set
Grid cell size	1 km	1 km	2 km	3 km	1 km
No. neighboring cells	≥1	4	≥1	≥1	≥3

Notes: The nfFP map is the outcome of rules 1, 2, and 3. We did not vary rules 2 and 3, because there was a general agreement on the role of barriers and the approximate size of a male home range, and rule 4 appeared to be redundant (i.e., application of rule 4 did not change the patches of suitable habitat that resulted from rules 1–3).

connection between two patches (i.e., the connection or path with the lowest cost). We specified that an optimal path should be short, leading mainly through forest, and avoiding barriers such as bodies of water and urban areas. We cannot expect a dispersing lynx to find the optimal connection between two patches as indicated by the cost-path analysis. However, we assume that the cost-path analysis delivers a relative measure for comparing the connectivity between different patches, e.g., two patches that are connected by a low-cost optimal path will also be connected by many alternative low-cost suboptimal paths that dispersing lynxes may find.

As the cost-path analysis selects the best path according to its absolute cost, we defined the value for the habitat type with the lowest costs (forest = 1) and the highest costs (urban area and body of water = 1000) arbitrarily, and adjusted the value for open areas. The assessment of a cost value for matrix in relation to dispersal habitat is difficult. To translate the lynx's strong avoidance of matrix (see *Dispersal of lynx*) into a reasonable cost value, we assigned all open areas (e.g., heath, agricultural land, wetlands) a value of 20. To find out how sensitive the resulting connections were to the cost value of matrix, we varied this value over a wide range (i.e., 4, 7, 10, 30, 100, and 500). For the GIS implementation of the cost-path analysis we used a raster map with a grain of 1 km^2 that contained the cost values for the dominant land-use type within each cell.

Human-induced sources of mortality (e.g., roads) were considered in evaluating connections among habitat patches; however, roads are difficult to assess, and lynx may not actively avoid them. Therefore, we used ''negative risk points'' associated with each habitat type and each crossing event of a highway and large river. Given the lack of quantitative information on the risk of mortality, we based the number of negative points for a given habitat type and for crossing highways on qualitative and anecdotal information. We added one point for each km path length, 5 additional points for a matrix km used, 20 additional points for a larger river crossed, and 50 additional points for a highway crossed.

We categorized the connections by their total number of negative points into five categories of 50 points (Table 2) based on the data on dispersal distances of lynx in the Swiss Jura Mountains; e.g., the mean dispersal distance was 43 km, indicating that the lynx may reach a patch 50 km away through a forest path (=50 points). The maximum distance moved was 98 km, indicating that the lynx may be able to reach a patch 100 km away via a forest path (=100 points). A register with >100 points would be due mostly to the use of matrix or highway crossings with a high risk of mortality, which ought to make the successful use of such connections unlikely.

A connected patch network linked by good quality connections (category 1, Table 2) was referred to as a ''spatially heterogeneous population'' (Hanski and Gilpin 1991, Wells and Richmond 1995) or ''nucleus,'' and its total size was subclassified into areas too small for permanent lynx presence (<2000 km^2) and those big enough for a large population (>2000 km^2).

RESULTS

Patches of suitable habitat

The successive application of rules 1–5 revealed the patches of suitable habitat (Fig. 3). Interestingly, rule 4, which demands a 30-km^2 core area of forest patches not cut by main roads within a patch of suitable habitat, was already satisfied by rules 1–3, which was not clear at the beginning. Altogether, we detected 58 patches of suitable habitat (large enough for an overlapping male and female territory) in Germany, including patches that extended over the German border into the neighboring countries, with a total area ≈54 260 km^2.

The patches of suitable habitat were located in the low mountain ranges of south and central Germany, and in the large forests in the north and east of Germany (Fig. 3). On average they contained 75% forest and 2% urbanized areas. However, only ~50% of the 58 suitable patches were >500 km^2, and many were isolated (Fig. 3). We found 10 nuclei, with a total area ≈38 400 km^2, large enough to host ~230 resident female and 150 resident male lynxes in Germany and the immediately adjacent suitable areas of the Czech Republic and France (Fig. 3, Table 3). However, if we only consider the five nuclei of high suitability (Thuringian For-

TABLE 2. Classification of connections in their ability to provide exchange of individuals between suitable habitat patches and in their assumed risk of mortality.

Connections	Category 1	Category 2	Category 3	Category 4	Category 5
Suitability	high suitability	intermediate suitability	low suitability	suitability questionable	unsuitable, no connection
Negative points	0–50	51–100	101–150	151–200	>201
Description	short connection (13 km) leading mainly through forest (76%), with short distances (1.8 km) through matrix	short connections (24 km), but with a possible highway crossing (0.7), with short distances (3.6 km) through matrix	longer connection (46 km) with longer distances through matrix (7.3 km) and possible highway crossing (0.8)	long connection (58 km) with very long distance through matrix (13 km) and possible highway crossing (0.9)	very long (130 km) with very long distance through matrix (35 km), several highway crossings (2.1), and possible river crossing (0.3)
Expected exchange of individuals	regular	irregular, but rather likely	irregular, but rather rare	rare event	none
Expected risk of mortality	low	intermediate	high	high	very high

Notes: The categorization of the connections into five classes was based on their length, the habitat types used, and the number of highways and rivers necessary to cross. The description and evaluation of the different categories (average length, distance through open areas, and highway crossings; in parentheses) are results from the analysis of 57 connections (see Table 4).

est, German–Czech border, Bavarian Forest, and the northeastern forests I and II), we obtain a population size of 111 resident females and 71 resident male lynxes.

Connection analyses

We analyzed 57 connections between patches of suitable habitat. On average, 78 $\pm$ 16% ($\pm$1 SD) of the connections were covered by forest, and the longest distance across nonforested areas was 2.1 $\pm$ 1.7 km. Connections between categories 1 and 2 only differed significantly in the number of highways crossed, and connections of categories 2 and 3 differed only in total length. Connections of categories 3 and 4 differed in distance through open habitat, while connections of categories 4 and 5 differed in total length, highway crossings, and distance through open habitat (Table 4). The mean length of connection categories 1–4 was <50 km, and is within the range of dispersal distances observed in the Swiss Jura Mountains. Thus, we assume that connections of category 1 may enable the regular exchange of individuals and can guarantee connectivity between patches of suitable habitat, while connections of categories 2–4, which are crossed by a highway or have longer distances through the matrix, may constitute a barrier that prevents the regular exchange of individuals, and are less suitable. However, category 5 connections (mean length 130 km) were far above the observed dispersal range, suggesting that they were unlikely to enable the exchange of individuals (Table 2).

Potential connection between nuclei

If we assumed that suitable connections (categories 1 and 2) permit the exchange of individuals, several patches of suitable habitat could be connected (Fig. 3). However, most of the suitable connections interconnect small patches or lead from a large patch of suitable habitat to a small satellite patch (e.g., from the Black Forest or the northeastern forests). The 10 nuclei were mostly isolated (i.e., no suitable connection exists); only the Thuringian Forest and the nuclei German–Czech border and the Bavarian Forest were linked by category 2 connections (Fig. 3). Thus, the Thuringian Forest plays a key role within the network of possible nuclei because it is also spatially close (connections of category 3) to another nucleus (Spessart-Rhön), suggesting a possible recolonization of the latter nucleus through a source population in the Thuringian Forest. The northeastern forests may be connected to vast forests in Poland. In contrast, the Harz Mountains and the Black Forest appear quite isolated (Fig. 3).

Uncertainty analyses

A change in the parameter values did not exceed the threshold of 20% deviation of habitat area in the different scenarios (Table 5). In general, the total number of suitable patches changed little (from 56 to 59 patches), but the distribution of the patch sizes varied (Table 5). Scenarios A and B had the same grid size as our parameter set, but in scenario A we allowed each forest cell, irrespective of the number of neighboring cells, to form the forest neighbor map. This led to an enlargement of existing suitable patches, because all the cells on the margins of the suitable patches could now be included, resulting in a shift of patches into the >2000 km² category. Furthermore, more fragmented forest patches containing long, narrow areas could be included in this scenario, leading to a higher number of forest patches, and, in the end, to a greater area of

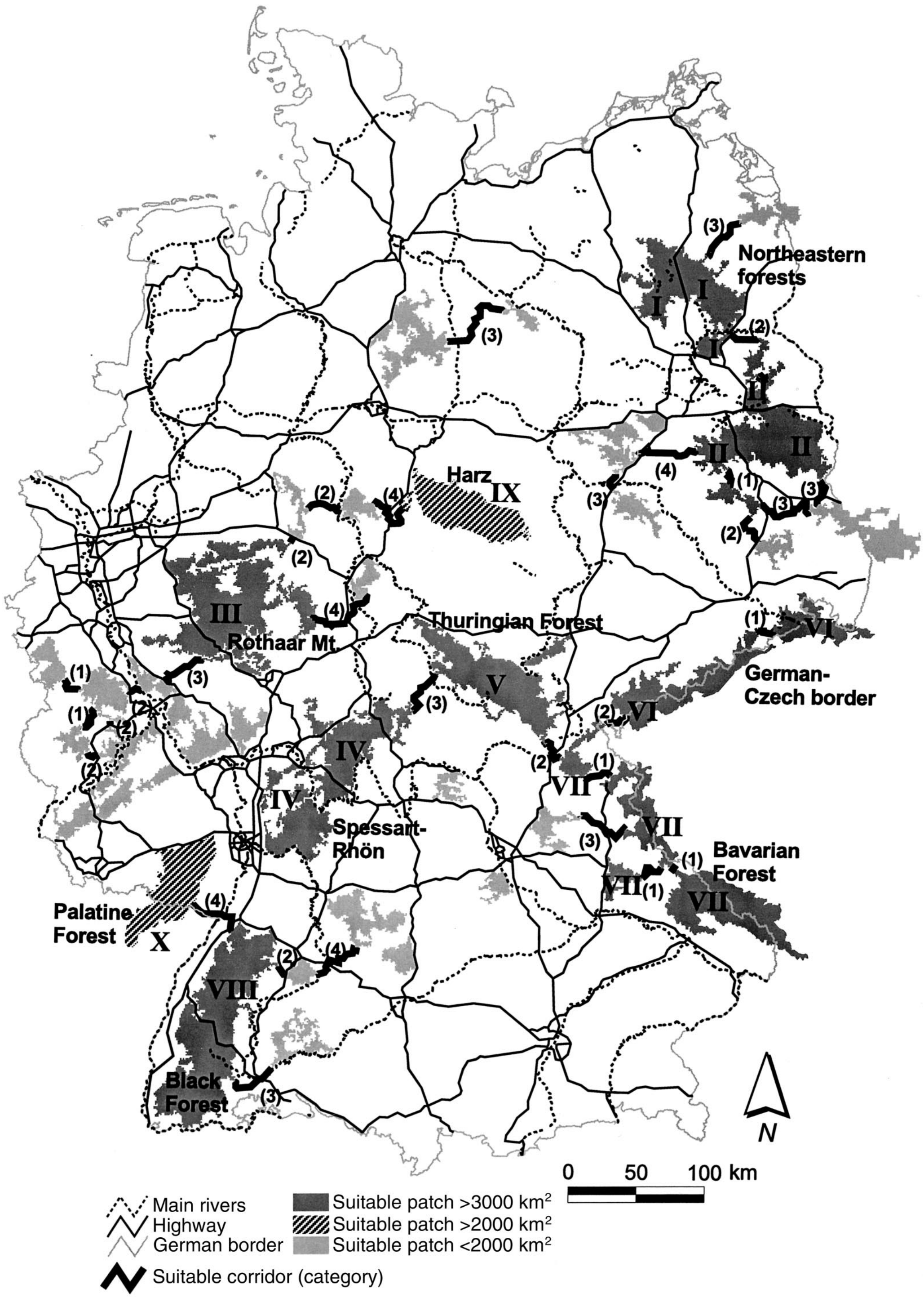

FIG. 3. Results of the habitat model. The map shows the HPB map with the resulting patches of suitable habitat. The functionally connected patches (nuclei) are numbered, and the shading indicates their size: <2000 km^2 (light gray), >2000 and <3000 km^2 (hatched), >3000 km^2 (dark gray). The connections between the patches from category 1 (high suitability) up to category 4 (low suitability) are shown as bold black lines, and their category is marked with a number in parentheses. Note that not every connection of category 1 is shown, as sometimes the connection was too short to be pictured. Highways are shown as solid black lines, and rivers as black dotted lines. The nuclei are: (I and II) Northeastern forests, (III) Rothaar Mountains, (IV) Spessart-Rhön, (V) Thuringian Forest, (VI) German–Czech border, (VII) Bavarian Forest, (VIII) Black Forest, (IX) Harz, and (X) Palatine Forest.

TABLE 3. Description of the different nuclei over 2000 km².

Nucleus	Total size (km²)	Total size core areas (km²)	No. female home ranges	No. male home ranges	Forest cover (%)	Fragmentation index (km²)
High suitability						
Northeastern forests I	3193	1426	19	12	64	14.5
Northeastern forests II	4177	1769	25	16	76	15.4
Thuringian Forest	3419	1801	20	13	78	16
German–Czech border	3132	1555	19	12	88	22
Bavarian Forest	4659	2280	28	18	81	17.3
Suitable						
Spessart-Rhön	4314	2235	26	16	79	16.5
Black Forest	5623	3116	33	21	77	13
Palatine Forest and Northern Vosges Mt.	2236	1871	13	8	93	29
Low suitability						
Rothaar Mountains	5373	1982	32	20	70	5.3
Harz	2286	1604	14	9	83	25
Total	38 412	19 639	229	145	…	…
Mean	…	…	…	…	79	17.4

Notes: Total size gives the joined area of forest patches with interspersed matrix. To calculate the potential number of female/male territories, we divided the total size of the nucleus by the mean territory size reported from the Swiss Jura Mountains (168 km² for female and 264 km² for male). Forest cover is the percentage of forest cover of the total patch. The fragmentation index is the average size of nonfragmented forest patches (nfFP map, rule 1) and is calculated by dividing the total forest area of a suitable patch by the number of single forest polygons within that suitable patch. The three suitability classifications were based on size, functional connectivity to other nuclei or to existing lynx populations, and fragmentation.

suitable patches. Scenario B is more restrictive, and only allows forest cells with at least four neighboring cells to form the forest neighbor map. The reduced amount of suitable habitat was due to the edge effects that occur here. Scenarios C and D have different grid sizes, therefore we obtained a shift from the <2000 km² category to the >2000 km² category because a cell comprised a greater area. On the other hand, the total area was reduced. As the grid cell size was enlarged, more different land-use types fell within the cell raster, while fewer cells reached the threshold of 25% necessary to be converted into a forest cell.

Of the 57 connections analyzed, 39 were classified under categories 1–4. In order to see how sensitively these 39 connections reacted to parameter changes, we varied the cost-values for matrix from the original 20 (standard connection) to values of 4, 7, 10, 30, 100, and 500. Of course, the lower we set the cost-value for matrix, the more we obtained a straight-line connection between the patches. Therefore, with an unrealistically low matrix value of 4, we obtained different best connections between patches in many cases. However, the connections of the cost values for matrix of 7 and 10 did not result in any new paths. Here, in some cases, we obtained slight variations of the standard paths, which we did not consider to be new connections because they did not downgrade the connection category (Fig. 4C). When altering the matrix value to 30, we obtained slight variations in the standard connection (Fig. 4C), and two new routes (Fig. 4A and B). In the

TABLE 4. Comparison between connections in different categories.

		Path composition (km)			Crossings		
Category	n	Total length**	Longest nonforest distance**	Distance through open areas**	Forest (%)	Highway**	River
1	12	13.4 ± 13	0.89 ± 0.99	1.8 ± 1.7	76.2 ± 29	0.0 ± 0.0[a]	0.1 ± 0.3
2	10	23.6 ± 8.3[aa]	1.39 ± 1.29	3.6 ± 3.0	85.4 ± 10.7	0.7 ± 0.5[a]	0.1 ± 0.3
3	9	45.7 ± 16.3[aa]	1.71 ± 1.65	7.3 ± 5.0[aa]	82.6 ± 11.9	0.8 ± 0.4	0.1 ± 0.3
4	8	58.1 ± 9.7[bb]	2.35 ± 0.85	13 ± 2.6[aabb]	77.4 ± 5.7	0.9 ± 0.4[bb]	0.1 ± 0.4
5	18	130 ± 87.6[bb]	3.46 ± 1.84	35 ± 28.7[bb]	74.6 ± 8.1	2.1 ± 1.5[bb]	0.3 ± 0.6
1–2	22	18 ± 12[aa]	1.12 ± 1.14[a]	2.6 ± 2.5[aa]	80.4 ± 22.6	0.3 ± 0.5[aa]	0.1 ± 0.3
3–4	17	51.6 ± 14.6[aa]	2.01 ± 1.37[a]	9.8 ± 4.8[aa]	80.1 ± 9.6	0.8 ± 0.4[aa]	0.1 ± 0.3
1–5	57	63.5 ± 68.8	2.1 ± 1.7	14.9 ± 21.2	78.5 ± 15.7	1.0 ± 1.2	0.2 ± 0.4

Notes: Shown are the mean ± 1 SD. Significant differences between means of neighboring categories were assessed through a Mann-Whitney U test and are indicated with the same superscript letters within a column (single letters [e.g., ''a''] indicate $P < 0.05$; double letters [e.g., ''aa''] indicate $P < 0.01$). Overall comparison of the means of the categories 1 to 5 were assessed with a Kruskal-Wallis test (**$P < 0.01$).

TABLE 5. Uncertainty analysis of the habitat model with alternative scenarios (see Table 1) for the maps with nonfragmented forest patches (nfFP map).

Scenario	Total size (km^2)	Number of nonfragmented forest patches <500 km^2	<2000 km^2	>2000 km^2	Total
A	56 871	28	22	9	59
B	45 840	29	21	6	56
C	53 830	28	19	11	58
D	51 910	31	15	11	57
Standard parameter set	54 260	30	21	7	58

first case (Fig. 4A), the new connection was in the same category as the standard connection (category 3, cf. Table 2). In the second case (Fig. 4B), the connection was downgraded from category 4 to category 5 (Table 2), and thus becoming unsuitable. A similar picture emerged for cost values of 100 and 500 for matrix. Here, we only obtained three new routes, in two cases downgrading a connection from category 4 to 5 (from nucleus III to a satellite patch, cf. Fig. 3), and from category 1 to 2 in unsuitable areas in western Germany. Another connection leading from the Bavarian Forest (nucleus VII, cf. Fig. 3) to a satellite patch took another direction, but remained classified as category 1.

DISCUSSION

Conservation biologists often have to make decisions with little information derived from detailed field studies. The urgency of many conservation issues makes it impossible to wait until such empirical data are obtained; instead, managers must make the best out of existing information (Walters 1986, Clevenger et al. 1997, Merrill et al. 1999). In our work we present a GIS as a problem-solving tool for large-scale analysis of landscape structure based upon the needs of a far-ranging species. We suggest that such an approach can be a useful initial approximation for obtaining maps of the distribution of suitable habitat and patch connectivity to facilitate actions in wildlife management and conservation when field data are limited, when there are no resources to collect new field data, and time is pressing. Our approach allowed a qualitative assessment of habitat suitability with respect to isolation, patch size, and the fragmentation of the patches.

The use of neighborhood rules provides a species'

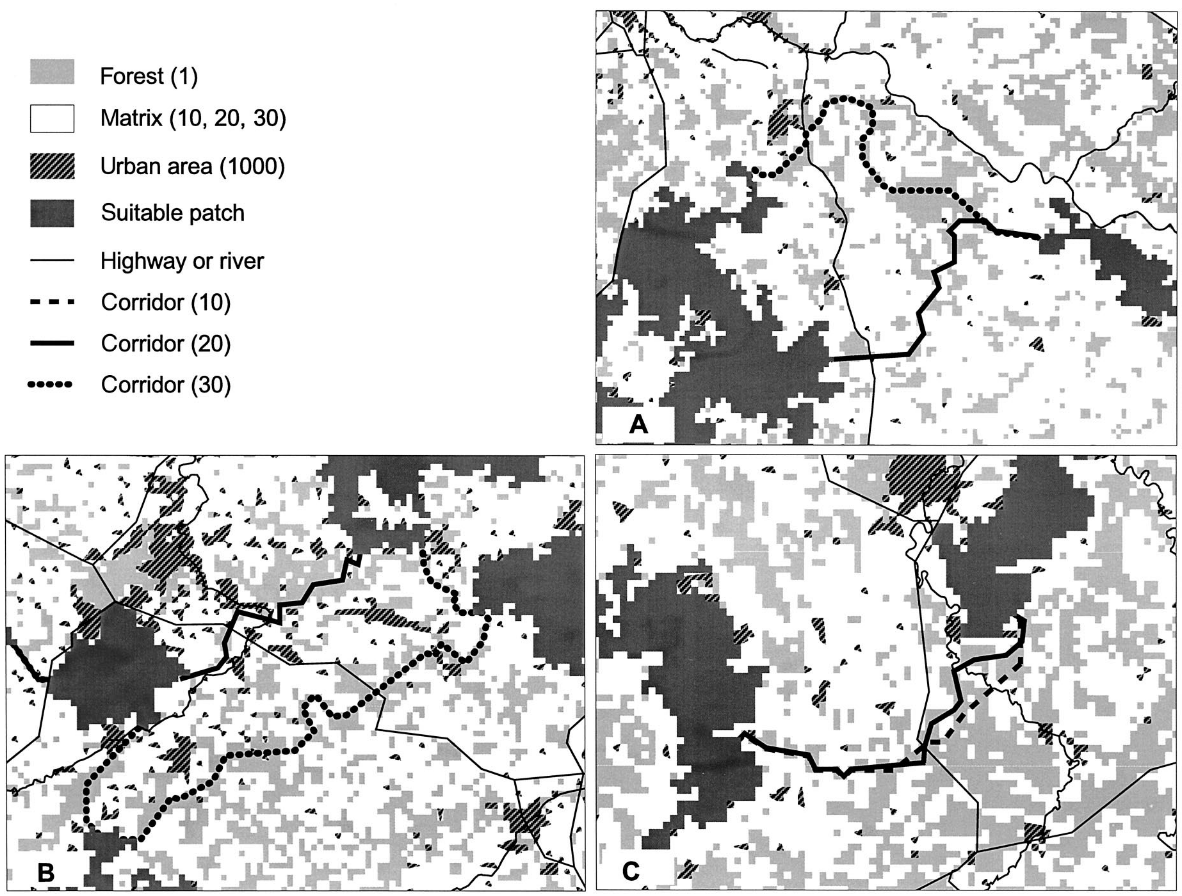

FIG. 4. Examples of suitable connections. Different routes are shown for different cost values of the matrix: 10, solid lines; 20 (standard parameter), dotted lines; 30, dashed lines.

perception of landscape structure (With 1997). With such an approach, the consequences of land-use change, new road construction, and fragmentation can also be addressed for other target species with different habitat requirements and dispersal capabilities. For example, Dale et al. (1994) did this for a variety of species in the tropics prone to extinction due to further forest fragmentation based on their area requirements and gap-crossing ability. Hansen et al. (1995) developed an approach to identify bird species at risk at present and under disturbance-management scenarios using habitat maps, species-habitat associations, and other natural history characteristics of species to quantify habitat suitability for each bird species. White et al. (1997) present an approach for estimating the potential risk to biodiversity from future landscape change associated with land development.

As the spatial requirements of a large carnivore population are vast and the available forest habitats in Central Europe are often fragmented landscape mosaics, large-scale cross-boundary approaches are necessary (Mladenoff et al. 1995, Corsi et al. 1999). Our modeling approach is not restricted to the lynx, but can be used as a general assessment of large connected landscapes in an organism-centered analysis, which is important for the effective development of conservation strategies (With 1997, Pearson et al. 1999).

Benefits and shortcomings of our modeling approach

As in every modeling approach, uncertainty in data and assumptions of the model influence interpretation of the results. Uncertainty analyses showed that the model results were similar when the rules on forest shape and fragmentation across a biologically plausible range were altered. The identification and location of connections between suitable habitat patches also proved stable against changes of the standard parameter set. Only when using very low cost values for matrix did the connections change, but these values can be assumed to be below a biologically realistic range. We suspect that the low sensitivity of the model results to altered parameters is due to the strong constraining impact of landscape structure, i.e., the spatial arrangement of forests and barriers, such as highways or rivers. In medieval times, the mountain ranges were unsuitable for agriculture due to climatic conditions, poor soils, and steep slopes, and were mainly used for grazing livestock. Large uncut forest areas remain limited to these mountain ranges and the areas with poor soils in northeastern Germany. Thus, there are not many ''degrees of freedom'' for alternative outcomes. The limited variability in landscape connectivity when habitat is abundant is consistent with predictions from theory (With 1997). In random landscapes, and when using a conservative nearest-neighbor rule, habitat is connected when it occupies $\geq$59% of the landscape. Values of the threshold for habitat connectivity are even lower for mobile species, such as the lynx, which can cross gaps of unsuitable habitat. Such species would not perceive the landscape as fragmented until habitat occupied $<$30% of the landscape (Pearson et al. 1996, Fahrig 1997, With 1997). In the German forest clusters, the percentage of forest cover is $>$60%, which will therefore produce stable results even when neighborhood rules are changed. Hence, the extent of forest in the landscape and its spatial geometry predict the model outcome of suitable habitat areas and connectivity among patches.

A possible criticism of our habitat model is its inclusion of only one environmental variable, forest cover, and its fragmentation due to matrix (open areas) or barriers (urban areas, highways, and major rivers). This is a reasonable assumption because the Eurasian lynx is a forest species with large space requirements. Other quantitative large-scale habitat analyses of large carnivores have also shown that one key resource alone can sufficiently describe the favorable habitat (e.g., Mladenoff et al. 1995, Mladenoff and Sickley 1998, Palomares et al. 2000, Schadt et al. 2002).

Another problem could be basing the minimum viable population size on 20 resident lynxes. Of course, if these assumptions do not hold in the German landscape, for example, due to higher road mortality, a viable population requires more individuals. Thus, small nuclei such as the Harz will be unsuitable. However, our maps with possible numbers of lynxes can easily be accessed, and the suitability of the patches can be updated quickly when new data on minimum viable population sizes are available.

The use of corridors for the conservation of biological diversity in fragmented landscapes has been debated for over two decades and reviewed several times (Simberloff et al. 1992, Rosenberg et al. 1997, Beier and Noss 1998). A variety of case studies have been conducted (e.g., Demers et al. 1995, Haddad 1998, 2000, Brooker et al. 1999, Danielson and Hubbard 2000, Mech and Hallett 2001, Nicholls et al. 2001, Palomares 2001), along with the theoretical framework in neutral landscapes (e.g., Gustafson and Gardner 1996). It was not our goal to determine whether animals actually moved among patches along the corridors we identified, and we are aware that such an optimal path does not reflect the actual dispersal behavior of the lynx. Evaluating the proportion of lynxes reaching other patches entails a data-calibrated, spatially explicit dispersal model far beyond the scope of our study. We addressed the question: What are the chances that a lynx will reach another patch? If even the ''best'' route seems very unlikely to be passable, then it is highly improbable that the patches will be connected. However, with this approach, we consider the habitat selection of the species, the spatial structure of the habitat, and the influence of barriers on dispersal success. Thus, our model constitutes an advance over the usual approach that defines connectivity between patches only due to their distance, as criticized by Gaona et al.

(1998). We could also have used a spatial grain <1 km^2 to obtain a better representation of landscape features, such as riparian vegetation or elevation. But evidence for the inclusion of such detailed rules was sparse, and we decided to keep our model as simple as possible.

Another criticism could be that our model is a theoretical one that does not justify the selection of model rules on a statistical basis through analysis of field data, and that it thus may lack objectivity in the selection of crucial habitat factors (i.e., Dupre et al. 1996). But a second approach based on logistic regression of field data is highly coincident with our findings (Schadt et al. 2002). Irrespective of the availability of field data, overall habitat suitability, including assessment of connectivity among populations, must be addressed because of the controversial discussions on reintroductions in Germany. Extrapolations of current knowledge are of course always liable to misinterpretation. It is often forgotten that models do not represent the truth, but rather assumptions, which are the simplification of one's current best understanding of the system (Van Horne and Wiens 1991, Starfield 1997).

Management implications

Our analysis provides an initial approximation of the possible distribution, amount, and fragmentation of favorable lynx habitat in Germany. The model results suggest that conservation planning should focus on the three connected nuclei (the patches of suitable habitat along the Czech border, the Bavarian Forest, and the Thuringian Forest). The small population in the Bavarian forest could also be linked to the large population in the Slovakian Carpathians as it was in the 1950s and 1960s (Červený et al. 1996). For the Bavarian Forest, cross-border coordination and cooperation with the Czech Republic would be necessary. The same is true for the northeastern forests with Poland, and the Palatine Forest with France.

Apart from these patch networks, the other nuclei of reintroduction are rather isolated or suffer from high human impact (cf. Table 3). Possible reintroduction programs in the Black Forest, Harz Mountains, and Palatine Forest therefore do not seem to have a high potential for spreading the lynx into other suitable areas; moreover, the small populations have a higher risk of extinction. Thus, the current release of lynxes into the Harz might actually be counterproductive. Due to the highly polemic nature of the discussions about lynx reintroduction in Germany, the failure of a reintroduction scheme here could hinder future conservation actions in other areas.

Summarizing the results, we see large differences in the connectivity of the nuclei. If we consider lynx recovery in terms of limited financial resources, the most effective way seems obvious: The recovery of the lynx in the Thuringian Forest will have a much bigger effect than in the Harz Mountains. However, administrative responsibilities in Germany are restricted to the provincial level, and there is no legal reason or precedent to coordinate activities on a cross-province scale. The suitable habitat patches are situated in 12 different provinces, and at the moment, all recovery initiatives focus only on one single habitat patch, the Harz, in one province. Lynxes are presently being released here, but the government of Lower Saxony is not in contact with the neighboring government of Saxony-Anhalt, to which almost 50% of the Harz Mountains belong. Therefore, we strongly recommend a coordinated approach throughout Germany as a whole, since the spatial level of decisions should match the spatial level of concern.

Conclusions and guidelines for further research

Maps of wildlife habitat generated by GISs ought to increase our understanding of spatial processes and contribute to land-use planning by representing habitats from a species perspective (Knick and Dyer 1997). We based our model on how the species perceives the landscape, and the seemingly arbitrary nature of the values we had to set for the minimum width of core areas or the cost values for matrix shows how little research has been done in this field for the Eurasian lynx. A modeling approach such as our qualitative model can reveal gaps in knowledge, and concentrate further data gathering and analysis, especially in these fields.

Patch connectivity should be assessed with a more realistic approach in an individual-based, spatially explicit model. In particular, a population viability analysis (PVA; Boyce 1992) should be conducted to see whether, under realistic demographic parameters, the assessed minimum number of 20 resident lynxes holds for a viable population. The potential impacts of human activities, such as road construction and reforestation schemes, should then be projected under alternative management scenarios using simulation models to make conservation planning both clearer and better informed.

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