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Scenarios assessing the viability of a lynx population in Germany.
Szenarien für eine lebensfähige Luchspopulation in Deutschland.

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Hinweise zum Lesen der Dissertation

Die vorliegende Arbeit spannt den Rahmen von der Auswertung im Feld erhobener Daten bis hin zu detaillierten Szenarien und Management-Vorschlägen für eine lebensfähige Luchspopulation in Deutschland. Die Methodik der vorgestellten Modellansätze - Habitatmodellierung, Entwurf und Kalibrierung eines Ausbreitungsmodells und Einbezug populationsdynamischer Aspekte in ein Simulationsmodell - ist jeweils über die Thematik "Luchs in Deutschland" hinaus relevant. Daher sind die einzelnen Hauptkapitel in englischer Sprache verfaßt, und jedes Kapitel stellt für sich eine Einheit dar. Kurze Wiederholungen der wichtigsten Ergebnisse aus den vorherigen Kapiteln sind daher unvermeidlich. In den jeweiligen Kapiteln wird einleitend genauer auf die Modellierungs-Methode und den Stand der Forschung eingegangen. Den drei Kapiteln vorangestellt ist eine Einführung in die generelle Fragestellung mit einem kurzen Abriß des Forschungsstandes. Der chronologische Aufbau der einzelnen Kapitel aufeinander wird hier in einem eigenen Unterkapitel erläutert. Die wichtigsten Ergebnisse werden am Ende nochmals zusammengefaßt und diskutiert.

Explanation of the structure of this dissertation

The dissertation aims to develop management proposals for a viable lynx population in Germany. Consequently, the material presented here covers a range of approaches and techniques, from the analysis of field data to detailed modelling scenarios. As the methods in the single chapters - habitat modelling, design and calibration of a dispersal model and inclusion of population-dynamical aspects into a simulation model - extend the scope of "lynx in Germany" and are generally important for conservation biology, they are composed in English language. Each of the chapters represents a thematic unit, in which the methods and the state of research are highlighted more explicitly. Short repetitions of the most important results of the previous chapters are therefore inevitable. For each chapter, a short German introduction and summary of the most important results are provided.

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KAPITEL I

Allgemeine Einleitung

Problemdarstellung

Einst besiedelte der Europäische Luchs (*Lynx lynx* L.) ganz Europa, wurde aber innerhalb der letzten drei Jahrhunderte in Mitteleuropa mit Ausnahme der Slowakei ausgerottet (Thor & Pegel 1992; Breitenmoser *et al.* 2000). Wiederansiedlungen des Luchses in Deutschland wurden innerhalb der letzten drei Jahrzehnte vehement und kontrovers diskutiert und auch durchgeführt (Stahl 1972; Himmer 1978; Wotschikowsky 1981; Plän 1988; Goßmann-Köllner & Eisfeld 1989; Wotschikowsky 1992; Singer 1996). Jüngstes Beispiel ist die Diskussion um die Ansiedlung des Luchses im Harz, die derzeit durchgeführt wird (Pohlmeyer 1997a; Pohlmeyer 1997b; Barth & Pohlmeyer 2000a; Barth & Pohlmeyer 2000b; Barth & Pohlmeyer 2000c; Wotschikowsky, Kaczensky & Knauer 2001).

Generell spielen bei diesen Streitgesprächen die Fragen eine große Rolle, ob für den Luchs überhaupt Lebensraum in ausreichendem Maße vorhanden wäre, ob die Lebensräume untereinander vernetzt wären und in welchem Maße und in welcher Art sie das sein müssen, und ob es Anschluß an bereits etablierte Populationen gäbe. Mittlerweile findet eine natürliche Wiederbesiedelung Ostbayerns von einer allerdings durch Aussetzung begründeten Population in Tschechien her statt (Kluth, Wotschikowsky & Schröder 1989; Kaczensky 1998). Wölfl (1996) und Scherzinger (zitiert in Červený & Bufka 1996) berichten von 10-15 Luchsen, die – ausgehend vom tschechischen Nationalpark Böhmerwald – auf bayerischer Seite eingewandert sind. Mittlerweile scheint sich der Luchs entlang des deutsch-tschechischen Grenzgebirges etabliert zu haben. Allerdings sind die Zahlen auf deutscher Seite rückläufig, die Ursache dafür ist jedoch nicht bekannt (Wölfl *et al.* 2001). Dies unterstreicht die Aktualität des Problems. Bisher stehen jedoch keine Methoden zur Verfügung, mit deren Hilfe die oben gestellten Fragen beantwortet werden können.

Diese Fragen nach der Möglichkeit einer lebensfähigen Luchspopulation in Deutschland werden in der vorliegenden Dissertation bearbeitet, indem anhand verschiedener Szenarien die mögliche Populationsentwicklung des Luchses, d. h. die Dynamik der Population in Zeit und Raum, untersucht wird. Damit beschäftigt sich die Arbeit konzeptionell mit einer Problematik, die bisher in der europäischen Luchsforschung nicht berücksichtigt worden ist.

Für die oben gestellten Fragen spielen große räumliche und zeitliche Skalen eine Rolle, die den Rahmen von Felduntersuchungen und Experimenten sprengen, denn Aussagen

über die Lebensfähigkeit von Populationen können etliche Dekaden überschreiten. Für den Luchs, der ca. 16 Jahre alt werden kann, sind bei solchen Aussagen z. B. Zeiträume von 100 Jahren adäquat. Für solche Langzeitvorhersagen über die Lebensfähigkeit von Populationen, die immer mit einer Abschätzung von Risiken und Wahrscheinlichkeiten verbunden sind, bedient man sich in der Ökologie theoretischer Modelle. Einer der Vorzüge der Modellierung ist, Wissen verschiedenen Typs zusammenfassen und in einen logischen Zusammenhang bringen zu können. Durch systematische Variation der Regeln über biologische Prozesse und durch Betrachtung verschiedener Managementszenarien kann das Modell helfen, ein besseres Verständnis der Dynamik des betrachteten Systems zu erlangen und die Auswirkung verschiedener Managementmaßnahmen (z.B. Aussetzungen, Anlegen von Grünbrücken, Aufforstungen) abzuschätzen. Populationssimulationsmodelle besitzen somit hohe naturschutzfachliche Relevanz, da sie eine Grundlage für die sachliche Diskussion um Zuwanderung, Ausbreitung und Überlebenschancen von Arten darstellen können. Auch bei der Frage nach den Auswirkungen der Zerschneidung von Lebensräumen auf Tierpopulationen können solche Modelle eine gute Ausgangsbasis für Planungen bieten.

Seit langem wird für Wiedereinbürgerungen gefährdeter Tierarten bzw. den zoologischen Artenschutz mehr Grundlagenforschung gefordert. "Aufgrund der kritischen Wertung der bisherigen Erfahrungen bei Ansiedlungen von Tierarten in Mitteleuropa wird betont, daß künftige Vorhaben sich in stärkerem Maße als bisher (...) auf gezielte Suche nach geeigneten Aussetzungsplätzen konzentrieren müssen" (ANL 1982). Des weiteren wird als "wesentlicher Mangel" der "noch bruchstückhafte Kenntnisstand über Bestand und Entwicklung der Fauna" bezeichnet (ANL 1982). Einige dieser Lücken in der Grundlagenforschung könnten durch Populationssimulationsmodelle geschlossen werden.

Der Luchs bietet sich als Modellierbeispiel an, da zum einen genügend Datenmaterial über seine Biologie vorhanden ist, und zum anderen mit der Modellierung der Luchspopulation ein aktuelles und kontrovers diskutiertes Thema des Naturschutzes abgedeckt wird. Die hierbei vorgestellte Methodik ist auf andere Arten übertragbar. Die Ergebnisse der Arbeit können auch für andere Wildtierarten eine interessante Diskussionsgrundlage für weitere Überlegungen zu Wiedereinbürgerungen, zu Management-Strategien und gegebenenfalls zu optimalen Aussetzungsstandorten liefern.

Modelle in der ökologischen Forschung

Modelle der Populationsdynamik des Eurasischen Luchses

Es gibt zahlreiche Publikationen zu Verbreitung und Ausbreitung, Demographie, Nahrungsökologie, Sozialverhalten und bevorzugtem Lebensraum des Eurasischen Luchses,

die vor allem aus Felduntersuchungen in der Schweiz stammen, teilweise aber auch aus Deutschland, Tschechien, Frankreich, Slowenien, Österreich, Polen, Skandinavien und Rußland (Pulliainen 1981; Gossow & Honsig-Erlenburg 1986; Haller & Breitenmoser 1986; Zachariae, Elstrodt & Hucht-Ciorga 1986; Herrenschmidt & Leger 1987; Kvam *et al.* 1989; Bieniek & Wolsan 1992; Breitenmoser & Baettig 1992; Haller 1992; Okarma 1992; Breitenmoser & Haller 1993; Breitenmoser *et al.* 1993; Jedrzejewski *et al.* 1993; Pulliainen, Lindgren & Tunkkari 1995; Vandel & Wecker 1995; Benda 1996; Červený, Koubek & Anděra 1996; Jedrzejewski *et al.* 1996; Okarma *et al.* 1997; Schmidt, Jedrzejewski & Okarma 1997; Sunde & Kvam 1997; Breitenmoser 1998; Cop & Frković 1998; Hucht-Ciorga 1998; Jobin 1998; Schmidt 1998; Stahl & Vandel 1998; Staniša 1998; Zimmermann 1998; Breitenmoser *et al.* 2000; Wölfl *et al.* 2001; Linnell *et al.* 2001a). An prediktiven Habitatmodellen, die die Größe von geeignetem zukünftigen Lebensraum abschätzen können, gibt es allerdings nur sehr kleinräumige Ansätze aus dem Schwarzwald (Goßmann-Köllner & Eisfeld 1989) und dem Land Salzburg (Slotta-Bachmayr 1998) und einen großräumigen Ansatz für ganz Deutschland (Schadt *et al.* in Druck). Mit diesen Modellen kann jedoch die zukünftige Populationsentwicklung nur schwer abgeschätzt werden, weil ihnen die zeitliche und populationsdynamische Dimension fehlt. In Deutschland fehlt neben einem datenbasierten Habitatmodell als Grundlage ein zeitlich-räumliches Modell, das den möglichen Verlauf der Ausbreitung und die Vernetzung von bestehenden und geplanten Luchspopulationen zeigt und verschiedene Möglichkeiten der Einwanderung bzw. Wiederansiedlung untersuchen und somit abwägen kann, ob und wie das Ziel einer lebensfähigen Luchspopulation in Deutschland erreicht werden kann.

Einem Modell, das oben genannte Forderungen erfüllen kann, sind zwei Komponenten immanent: Eine statische, nämlich die Auswahl geeigneter Habitate mit Geographischen Informationssystemen (GIS) als Grundlage für die Populationssimulation, und eine dynamische, eben die Simulation der Populationsentwicklung, die in Verbindung mit jener statischen die Simulation der Raumaufteilung (Territorienbesetzung), Demographie (Reproduktion und Mortalität) und der Abwanderung (Dispersal) von Individuen bzw. der Population erlaubt. Für beide Modell-Komponenten ist die Zahl bisheriger Ansätze in der europäischen Großsäugerforschung insgesamt gering (Wiegand 1998). Im folgenden sollen beide Modell-Komponenten vorgestellt werden.

Die statische Komponente: Habitatmodellierung

Grundsätzlich gibt es zwei Arten prediktiver Modelle, mit denen die Eignung eines Gebietes als Habitat für eine spezielle Tierart vorausgesagt werden kann, nämlich empirische bzw. statistische Habitatmodelle, die auf Feldstudien zur tatsächlichen Verbreitung der Art beruhen, und nichtquantitative Expertenmodelle. Bei empirischen Habitatanalysen wird beispielsweise eine multivariate Regression an verschiedenen Parametern (z. B. Wald-Feld-Verteilung, Straßendichte etc.) von Beobachtungs- und Nicht-Beobachtungsstandorten durchgeführt (Manley, McDonald & Thomas 1993; Mladenoff *et al.*

1995; Meyer, Irwin & S. 1998; Mladenoff, Sickley & Wydeven 1999; Woolf *et al.* 2002), und diese Ergebnisse können dann zur Vorhersage der Habitateignung der Art dienen. Sie gelten aber nur für das Gebiet, aus dem die Daten stammen (Morrison, Marcot & Mannan 1992). Auf statistische Habitatmodelle wird in Kapitel II näher eingegangen.

Stehen in dem zu untersuchenden Gebiet keine ausreichenden Verbreitungsdaten zur Verfügung, wird das Habitatmodell mit Hilfe von Literaturangaben, Freilanddaten aus vergleichbaren Gebieten oder über Expertenbefragung quantifziert. Solche Expertenmodelle können mathematisch oder deskriptiv sein. Expertenmodelle wurden bereits für eine Reihe von Arten verwendet, um die Auswirkungen des Klimawandels, von Landnutzungsänderungen und Habitatfragmentierung abzuschätzen (Hansen *et al.* 1993; Dale *et al.* 1994; Irwin 1994; Hansen *et al.* 1995; Offermann *et al.* 1995; Knick & Dyer 1997; White *et al.* 1997; van Appeldoorn *et al.* 1998; Pearson, Drake & Turner 1999; Urban 2000). Landschaftsvariablen werden mit anthropogener Störung und Eigenschaften von Lebensgemeinschaften in Verbindung gebracht (vgl. Miller, Brooks & Croonquist 1997), und Informationssysteme wurden entwickelt, um die Entscheidungsfindung in Naturschutz und Landschaftsplanung zu vereinfachen (vgl. Cooperrider *et al.* 1999).

Die meisten Habitatmodelle, wie der gängige HEP-Ansatz (Habitat Evaluation Procedures, vgl. US Fish and Wildlife Service 1980 and 1981; Brooks 1997), zählen zu den mathematischen Expertenmodellen. Ähnlich wie bei den Regressionsmodellen wird die Habitateignung durch eine Gleichung mit ausgewählten Habitatvariablen beschrieben, die jedoch nicht durch Felddaten bestimmt wurden, sondern auf Expertenschätzungen beruhen. Diese Modelle wurden jedoch unter anderem dafür kritisiert, daß die Algorithmen eher willkürlich erscheinen und schwer zu interpretieren sind. Außerdem sind Variablen mit Bezug zur Landschaft bisher nicht integriert worden (Van Horne & Wiens 1991).

Im Gegensatz dazu liegen deskriptiven Modellen einfache verbale, "ökologische" Regeln zugrunde, die die Habitatnutzung von Wildtierarten aus der Sicht der Individuen verständlich und nachvollziehbar beschreiben (Starfield 1990). Diese Regeln können dann auf einer digitalen Kartengrundlage mit Hilfe eines GIS ausgewertet werden, um geeignete von ungeeigneten Flächen zu unterscheiden (vgl. Schadt *et al.* in Druck). In Habitatmodellen wird zwar der Landschaftsbezug berücksichtigt und über die durchschnittliche Populationsdichte die mögliche Anzahl an Individuen in geeignetem Habitat errechnet, populationsdynamische Aspekte werden dabei jedoch vernachlässigt (Lutze, Wieland & Schultz 1998).

Die dynamische Komponente: Populationssimulation

Nicht-räumliche Populationssimulationen

Angesichts zunehmender Zerstörung von Lebensraum vieler gefährdeter Arten insbesondere durch Habitatfragmentierung gewinnen Populationsgefährdungsanalysen ("population viability analyses", PVA) im praktischen Naturschutz vielfach an Bedeutung (Doak & Mills 1994; Starfield 1997; Beissinger & Westphal 1998); sie sind mit einer Vielzahl von Modelltypen bearbeitet worden (Boyce 1992). Die Palette dieser Modelltypen reicht von analytischen Modellen (vgl. Wissel 1989; Lande 1993) über nichtstochastische bzw. stochastische Matrixmodelle (Shaffer 1983; Caswell 1989) bis zu individuenbasierten Modellen (DeAngelis & Rose 1992; Judson 1994). Die ersten beiden Modelltypen haben den Nachteil, daß sie entweder biologische Informationen nur minimal berücksichtigen können oder nur an große Populationszahlen angepaßt sind. Bei individuenbasierten Modellen kann man Informationen über die Biologie der Arten ohne Umweg über mathematische Gleichungen in Regeln formulieren und in das Modell einbringen, was die Kommunikation zwischen Modellierern und Anwendern erleichtert und zur allgemeinen Verständlichkeit des Modells beiträgt. Zudem erlaubt der individuenbasierte Ansatz den Vergleich realer Raum-Zeit-Strukturen mit Simulationsergebnissen, d. h. zu jedem Zeitpunkt in der Simulation kann genau bestimmt werden, in welchem Zustand (Altersstruktur, Anzahl der Individuen,...) sich die Population befindet. Ein weiterer Vorteil ist, daß die zugrundeliegende Einheit des Modells einem Individuum entspricht, was besonders für die Simulation gefährdeter bzw. einwandernder Arten geeignet ist, da es sich dabei meist um wenige Individuen handelt. Ein solcher individuenbasierter Ansatz liegt der vorliegenden Dissertation zugrunde.

Räumlich-explizite Populationssimulations-Modelle (RPSM)

Die ersten Modelle, die die Bedeutung räumlicher Strukturen (z.B. die Verteilung von Habitat und Nicht-Habitat) auf die Populationsdynamik untersucht haben, berücksichtigen den Raum nur indirekt über Individuenaustauschraten zwischen Populationen. Aus den sogenannten Patchmodellen (vgl. Wiens 1997) entwickelte sich die Metapopulationstheorie (Levins 1970; Hanski 1991; Hanski & Gilpin 1991), später folgte die Source-Sink-Theorie (Pulliam 1988), die beide Schlußfolgerungen für den praktischen Naturschutz nahelegten, z. B. in der Anlage von Biotopverbundsystemen und Korridoren. Auch den Populationsmodellen der mit dem Europäischen Luchs vergleichbaren Arten, z. B. dem Puma in den USA (Beier 1993) und dem Pardelluchs in Spanien (Gaona, Ferreras & Delibes 1998) fehlt die räumliche Komponente, die aber im konkreten Fall wichtig wäre, um beispielsweise Ausbreitungsengpässe und Barrieren herausfiltern zu können, die durch die Landschaft bedingt sind. Die gegenwärtige Forschung konzentriert sich nicht zuletzt deshalb zum einen auf die Weiterentwicklung der ursprünglichen Metapopulationstheorie ("incidence function", Hanski 1994), zum anderen auf die Entwicklung räumlich-expliziter Populationsmodelle (Dunning *et al.*

1995; Pulliam & Dunning 1995), deren Impulse von konkreten Schutzbemühungen für gefährdete Arten ausgingen.

Räumlich-explizite Populationsmodelle verbinden eine Populationssimulation mit einer Landkarte, die die räumliche Verteilung von für Populationen relevanten Objekten im Raum beschreibt. Die Auswirkungen einer sich ändernden Landschaft auf die Populationsdynamik können dann im Modell untersucht werden (Dunning *et al.* 1995; Holt *et al.* 1995; Turner *et al.* 1995). Ein weiterer wichtiger Punkt ist, daß in RPS-Modellen die Wanderungen der Individuen der Population zwischen bestimmten Habitaten modelliert werden können. Anschließend kann quantitativ beschrieben werden, wie dies die Populationsdynamik beeinflußt (Dunning *et al.* 1995). Durch die Abhängigkeit der Individuen vom geographischen Raummuster, die sich mit vorgegebenen Präferenzen in bestimmten Habitattypen aufhalten und fortbewegen, können RPS-Modelle beispielsweise auch zur Erkennung wichtiger Wanderkorridore beitragen, die sich aus dem Fortbewegungsmuster ergeben.

Die Methode der individuenbasierten, räumlich-expliziten Modellierung ist am besten geeignet, um die Frage nach der Lebensfähigkeit einer Luchspopulation in Deutschland zu beantworten. In den USA wurden RPS-Modelle beispielsweise für Vögel entwickelt (Pulliam, Dunning & Liu 1992; McKelvey, Noon & Lamberson 1993; Lamberson *et al.* 1994; Liu, Dunning & Pulliam 1995; Letcher *et al.* 1998; Walters, Crowder & Priddy 2002), also für eine in wichtigen Merkmalen sehr stark vom Fall des Luchses abweichenden Tiergruppe. Daneben gibt es nur ein Beispiel für ein großräumiges RPS-Modell, nämlich die Simulation der Bärenausbreitung in den Alpen (Wiegand 1998), wobei Demographie, Raumaufteilung und Ausbreitungsverhalten ebenfalls nicht direkt auf den Luchs übertragen werden können.

Fragestellungen, Methodik und Aufbau der Arbeit

Die Dissertation legt zur Beantwortung der Frage nach der Lebensfähigkeit einer Luchspopulation die Methode der individuenbasierten, räumlich-expliziten Modellierung zugrunde, welche die Synthese zweier Modelltypen herstellt und eine Habitateignungskarte mit der Simulation der Ausbreitung und Populationsdynamik verbindet.

Dazu ist in einem ersten Schritt die statistische Analyse der Habitatanforderungen und der Raumnutzung des Luchses notwendig (siehe Kapitel II). Diese Analyse, basierend auf einer logistischen Regression, stützt sich hauptsächlich auf die seit ca. 20 Jahren im Schweizer Jura gesammelten Telemetriedaten; Daten aus Slowenien und Tschechien werden für die Modell-Validierung hinzugezogen, da es für Deutschland noch keine Ergebnisse aus Felduntersuchungen gibt. Die Daten aus dem Schweizer Jura bieten sich besonders an, da dieser naturräumlich und siedlungsgeographisch gesehen den Verhältnissen im Untersuchungsgebiet Deutschland relativ gut entspricht. Die Ergebnisse werden mit einem Geographischen Informationssystem auf das Untersuchungs-

gebiet übertragen. Von Bedeutung ist, daß die Landschaftsanalyse des Schweizer Jura aus dem "Blickwinkel des Luchses" erfolgt; nur so läßt sich eine Analyse der Struktur der Landschaft vornehmen, die das räumliche Verhalten des Luchses erklärt. Wichtig ist für das später auf der Habitateignungskarte aufbauende Simulationsmodell vor allem, daß sich Habitatqualitäten abgestufter Nutzungsintensitäten (z.B. für Fortpflanzung und Abwanderung) bis hin zu Barrieren ergeben.

Die Frage, welche der geeigneten Lebensräume von abwandernden Luchsen erreicht werden können oder isoliert sind, wird in Kapitel III untersucht. Die Abwanderung von Individuen und damit die Ausbreitung der Population ist einer der Schlüsselprozesse in der Populationsdynamik allgemein. Allerdings sind Abwanderungsmodelle schwer zu parameterisieren, da oft geeignete Daten fehlen (Dunning *et al.* 1995). Daher wird auf die Abwanderungskomponente des Simulationsmodells besonderer Augenmerk gelegt. Hierzu werden von Felddaten aus dem Schweizer Jura über statistische Analysen Abwanderungsmuster generiert. Diese Muster dienen der Kalibrierung des Abwanderungsmodells, wobei die besten Parametersätze hergefiltert werden ("pattern-oriented modelling approach", Grimm *et al.* 1996; Wiegand, Revilla & Knauer 2002). Über die Methode der indirekten Parameterschätzung werden dann für die Extrapolation nach Deutschland Mortalitätswerte ermittelt. In einem ersten Simulationsmodell, das nur die Abwanderung berücksichtigt, wird so der Einfluß der Straßen und der Landschaftskonfiguration, also der räumlichen Verteilung der in Kapitel II ermittelten Habitattypen, auf die Verbindung zwischen den Lebensräumen abgeschätzt. Ein solches Teilmodell kann allerdings nicht vorhersagen, wie sich die Populationsentwicklung auf die Verbindung der Lebensräume auswirken wird, d.h. welchen Einfluß der kontinuierliche Nachschub an abwandernden Jungluchsen bzw. die kurzzeitige Besiedelung von "Trittsteinen" haben wird.

Diese Fragen werden in Kapitel IV behandelt; hier wird der gesamte Lebenszyklus des Luchses berücksichtigt, d.h. neben Abwanderung auch Territorienbelegung, Fortpflanzung, Alterung und Mortalität. Die demographischen Parameter der Simulationsszenarien, die wie bereits das Teilmodell der Abwanderung (Kapitel III) auf der Habitatkarte (Kapitel II) ablaufen, entstammen Freilanddaten hauptsächlich aus der Schweiz, Spanien und Polen. Mit Hilfe dieses Gesamtmodells ist es möglich, verschiedene Szenarien im Hinblick auf die Erhaltung einer lebensfähigen Luchspopulation im Untersuchungsgebiet zu testen.

Nicht untersucht werden in der vorliegenden Arbeit lokale Maßnahmen und Planungen, wie konkrete Trassenführungen von Straßen oder die beste Lage von Grünbrücken. Solche detailgetreuen Aussagen sind mit den vorliegenden Modellen nicht möglich und liegen auch nicht im Rahmen dessen, was diese Arbeit beantworten will. Auch die Frage, wozu es denn überhaupt Luchse wieder in Deutschland geben sollte, kann mit dem gewählten Ansatz nicht beantwortet werden, denn dies ist keine naturwissen-

schaftliche Frage, sondern eine im wesentlichen ethische bzw. philosophische (Breitenmoser 2000). Lediglich die Fragen "wie" und "wo" können beantwortet werden.

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CHAPTER II

The habitat suitability model[1]

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

Abstract

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 controversially in various locations. We present a habitat suitability model for lynx in this region as a basis for further management and conservation efforts aimed at recolonisation and population development.

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, introducing also variables that described the connectivity of forested and non-forested semi-natural areas on a larger scale than the map resolution.

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 km². This result is biologically meaningful, reflecting the absence of intensive human land use on the scale of an average female home range. Model testing at a cut level $P > 0.5$ 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.

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 a basis for further assessing population viability of species of conservation concern in suitable patches.

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 especially 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*. 2001; 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; Clevenger, 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 re-invading 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) (Figure 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 their 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 (1) identifying the broad distribution of suitable patches, (2) obtaining an estimate of possible lynx home ranges in Germany, and (3) providing a basis for a spatially explicit population simulation model to assess re-colonisation success and population development.

Methods

Habitat models using presence-absence data and logistic regression are useful in formalising 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 (e.g. Buckland & Elston 1993; FitzGibbon 1993; Wilson *et al.* 1997; Mace *et al.* 1999; Mladenoff, Sickley & Wydeven 1999; Palma, Beja & Rodrigues 1999; Rodríguez & 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 density to the German low mountain ranges. This model was then extrapolated to Germany (large-scale study area)
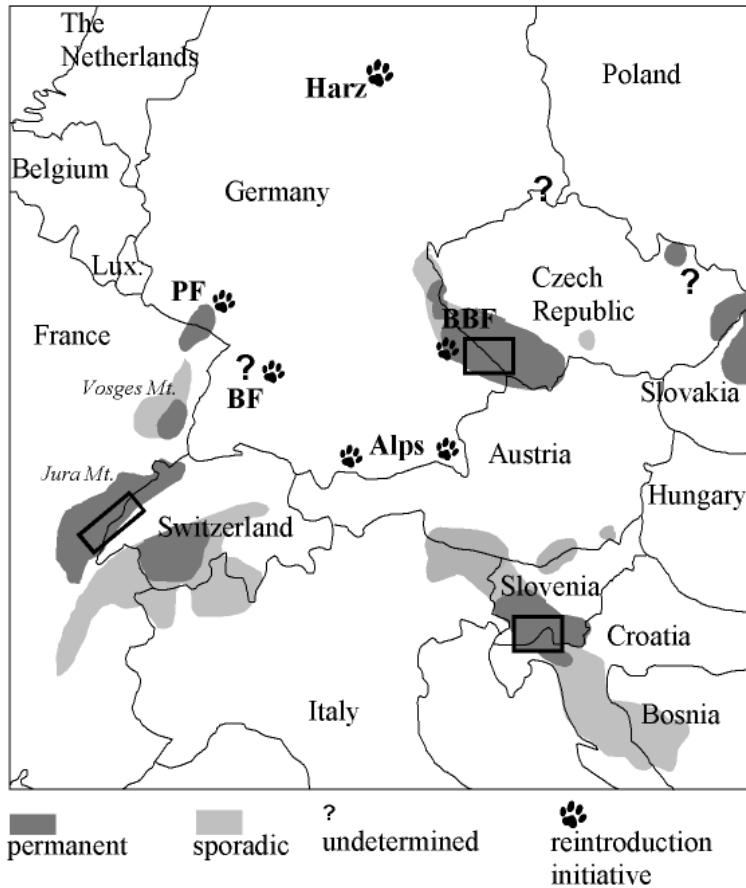
Figure 1. Permanent lynx populations in central Europe, sporadic and undetermined lynx occurrence (modified after Breitenmoser *et al.* 2000) and reintroduction initiatives for lynx in Germany. The black rectangles show the places from where we obtained telemetry data for developing the habitat model. PF: Palatine Forest, BF: Black Forest, BBF: Bavarian /Bohemian Forest.

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 pseudo-replication due to home range overlap. We

did not use single lynx location data, though we also used the telemetry data to gain insight into preferred land-use types. As the accuracy of the telemetry location data was 1 km², 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. The highlands are 53% covered by deciduous forest on the slopes, with coniferous forests on the ridges. Human population density reaches about 120 inhabitants per km², 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 - 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 altogether 5 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 km² for females (n = 5) and 263 km² for males (n = 3). For our analysis we defined the "closer 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 (Figure 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, Fichtelgebirge). Population density ranges from 20 to 100 inhabitants per km² (Červený & Bufka 1996; Wölfl *et al.* 2001) (Figure 1). From the Šumava National Park we used
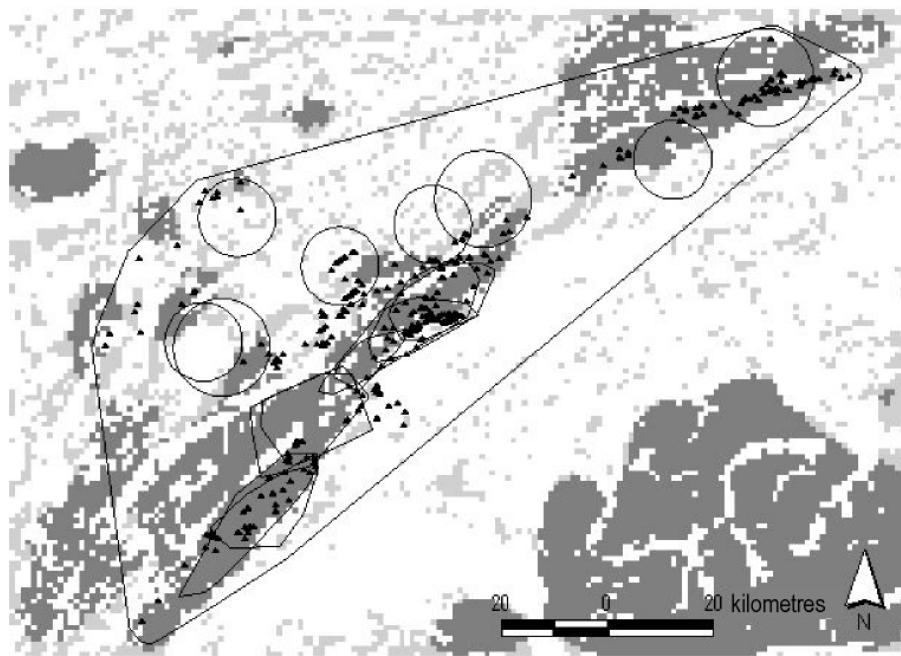
Figure 2. Swiss Jura Mountain chain: home ranges of resident lynx (polygons), random home ranges (circles) and locations of dispersing lynx (triangles) in the closer study area (CSA). Light grey are grid cells which contain more than 66.6% of extensively used land use types, such as forest or heathland (classed as PExt cells); dark grey are cells of the applied model with P > 0.5 (cf. results of logistic regression).

714 radio-location data from 5 lynx observed between 1997 - 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 - 1996 (Staniša 1998). The lynx were descendants of 6 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 (Figure 1). Elevations range from 300 - 1200 m, forest cover averages 90% and the dominating forest community is *Abieti-Fagetum dinaricum*. Human population density is low, averaging 22 inhabitants per km² 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 km² with an average population density of 230 inhabitants per km², which drops to about 100 inhabitants per km² in places such as the low mountain ranges (e.g. Black Forest, Palatine Forest, Thuringian Forest). Urbanisation 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 northeast. 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), that classify the following land use types on a 250 m grid. The CORINE classification names are provided in parentheses when different. (1) Urban areas (artificial territories), (2) agricultural land (strongly artificial vegetated areas), (3) pasture (less artificial vegetated areas), (4) forests, (5) non-wooded semi-natural areas, e.g. heathland, (6) wetlands, (7) water surfaces. Information on roads was digitised from 1:250 000 scale road maps. Roads include 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 (closer study area) in Switzerland. Each lynx home range was intersected with the raster map and descriptive environmental variables were extracted for each cell. We created 5 non-used home ranges for females and 3 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, 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 werethen buffered with a radius of 7334 m (= area of 169 km²) for females and 9150 m

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 $P < 0.01$ and (*) at a significance level $P < 0.05$, n = 16, df = 1. Retained variables (RV) for the logistic regression are marked with an *x*.

Variable		Biological interpretation		Random HR ± SD	Lynx HR ± SD	RV
PUrb (% of urban areas)		intensive human land use	(**)	3.3 ± 2.3	0.7 ± 0.3	
PAgr (% of agriculture)		intensive human land use		5.5 ± 8.8	10.2 ± 5.4	
PPast (% of pasture)		intensive human land use	(*)	39.5 ± 20.8	11.2 ± 5	
PFor (% of forest)		extensive human land use	(*)	40.9 ± 8.6	52.9 ± 2.5	*x*
PNat (% of natural areas)		extensive human land use	(**)	8.9 ± 4.1	24 ± 6.9	*x*
NPTot (total no. of polygons)		fragmentation		2.5 ± 0.4	2.5 ± 0.2	*x*
NPFor (no. of forest polygons)		extensive human land use	(*)	0.9 ± 0.1	1.1 ± 0.1	*x*
NPUrb (no. of urban polygons)		intensive human land use	(**)	0.1 ± 0.1	0 ± 0	*x*
PeriFor (perimeter of forest)		forest fragmentation	(*)	2614.5 ± 420.7	3220.5 ± 209.5	
R50 (density of major roads in km/ km²)		intensive human land use		0.6 ± 0.3	0.3 ± 0.2	*x*
R_A	radius 1 km	forest fragmentation	(**)	0.26 0.17	0.66 ± 0.1	*x*
	radius 3 km	forest fragmentation	(**)	0.22 ± 0.16	0.58 ± 0.1	*x*
	radius 5 km	forest fragmentation	(**)	0.2 ± 0.15	0.53 ± 0.1	*x*
	radius 7 km	forest fragmentation	(**)	0.19 ± 0.14	0.47 ± 0.1	*x*
R_C	radius 1 km	forest fragmentation	(**)	1.13 ± 0.26	1.7 ± 0.13	*x*
	radius 3 km	forest fragmentation	(**)	1.11 ± 0.23	1.62 ± 0.12	*x*
	radius 5 km	forest fragmentation	(**)	1.11 ± 0.19	1.51 ± 0.12	*x*
	radius 7 km	forest fragmentation	(**)	1.11 ± 0.16	1.43 ± 0.13	*x*

(= area of 263 km²) for males. The random home ranges of the different sexes overlapped in two cases (Figure 2).

Lynx biology and predictive environmental variables

To improve the biological interpretability of the final model, we avoided choosing many potential landscape predictors which *a priori* were not directly linked to the biology of the species, and orthogonalising 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 (e.g. 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.
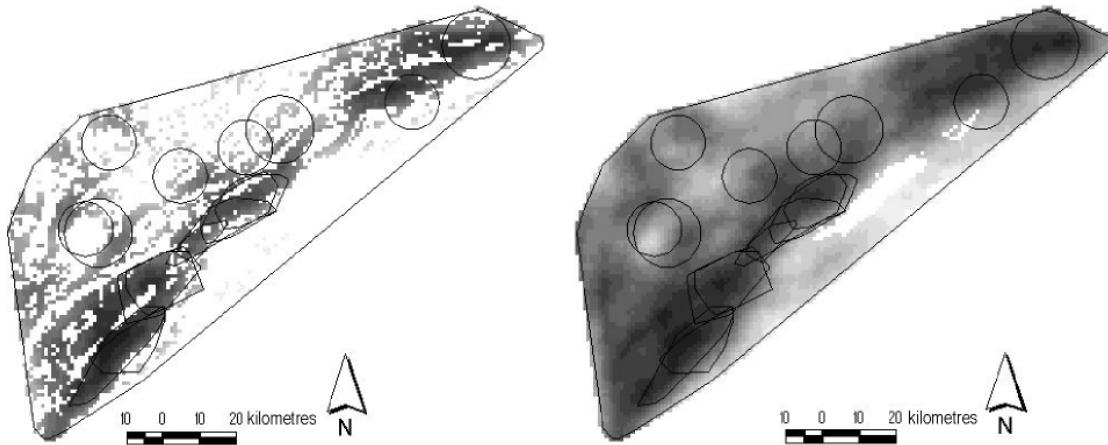
Figure 3. Example of the indices R_A (left) and R_C (right) with radii of 5 km each. R_A only uses the predefined cells with extensively used areas and calculates the percentage of more cells of that type around, R_C uses all cells and calculates the mean part of cells with extensively used areas around. 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.

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, *Peri-For*. 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 later 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 ≥ 66.6% (Table 1). With that we 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 (Figure 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,*
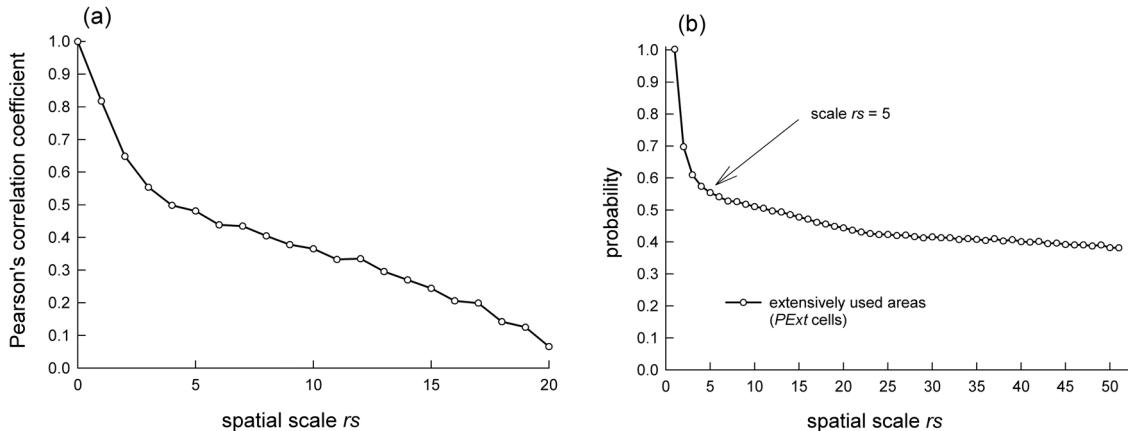
Figure 4. (a) Spatial correlation coefficient. The Pearson correlation coefficient between two variables v_i and m_i taken over all cells i of the closer study area, where v_i is the value of the variable "extensively used areas" in a given cell i, and m_i the mean value of this variable within a ring of radius r and width 2 around cell i. (b) Probability of finding an extensively used cell at distance rs away from an arbitrary extensively used cell within the closer study area.

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 $(x, y, r) \ll 1$ indicates that only 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 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 km² (Figure 3), we expected a high spatial autocorrelation in our dependent variable, that means the probability is very high, that a cell contains the same information as its neighbouring cell (Lennon 1999). Therefore, we could not include the data of all cells into the regression analyses as this would lead to pseudo-replication and to an overparameterised model adjusted too closely to the training data set. That means that 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, Figure 4a), and calculated the probability of finding an extensively used cell at distance *rs* away from an arbitrary extensively used cell (Figure 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 multicolinearity 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.). 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 which 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 case of similar AIC values, the one with the smaller number of predictors. The result is a model with the following formula:

$$\text{logit}(P) = \beta_0 + \beta_1 * V_1 + \beta_2 * V_2 + ... + \beta_n * V_n \qquad \text{eqn 1}$$

where *P* is the probability of a cell belonging to a lynx home range, β_0 is the intercept, the βs are the coefficients assigned to each of the independent variables during regression. The Vs represent the various independent variables. Probability values can be calculated based on equation 1, where e is the natural exponent:

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

We chose the model with the best classification of correctly predicted lynx home range cells (sensitivity) for methodical reasons: absences can not 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. A 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 $AUC_{crit} = 0.5$, 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 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 to occur (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 (99 km²) and the average core area size of male lynx (185 km²; Breitenmoser *et al.* 1993) to assess the possible number of lynx in Germany, and divided the suitable patches in Germany by these areas.

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. β_0 refers to the intercept.

Model	Model information					Model parameters				
	n	deviance	AIC	df	Sensitivity	Specificity	Variable	$\beta \pm se$	Wald χ^2	df	P
m1	62	74.5	78.5	60	74.3	48.1	R_A1	2.43 ± 0.81	8.93	1	0.0028
							β_0	-1.26 ± 0.59	4.63	1	0.0314
m2	62	69.8	73.8	60	85.7	51.9	R_A3	3.60 ± 1.06	11.5	1	0.0007
							β_0	-1.77 ± 0.68	6.71	1	0.0096
m3 (*)	62	66.7	70.7	60	91.4	55.6	R_A5	4.55 ± 1.28	12.65	1	0.0004
							β_0	-2.13 ± 0.77	7.75	1	0.0054
m4	62	64.0	68.0	60	88.6	59.3	R_A7	5.59 ± 1.55	13.10	1	0.0003
							β_0	-2.48 ± 0.86	8.43	1	0.0037
m5	86	104.2	108.2	84	74.4	65.1	R_C1	1.02 ± 0.28	13.35	1	0.0003
							β_0	-1.05 ± 0.37	7.76	1	0.0053
m6	86	103.4	107.4	84	76.7	62.8	R_C3	1.16 ± 0.31	13.93	1	0.0002
							β_0	-1.09 ± 0.38	8.14	1	0.0043
m7	86	101.4	105.4	84	76.7	60.5	R_C5	1.32 ± 0.34	15.42	1	0.0001
							β_0	-1.17 ± 0.39	9.01	1	0.0027
m8	86	100.7	104.7	84	76.7	62.8	R_C7	1.43 ± 0.36	15.90	1	0.0001
							β_0	-1.20 ± 1.39	9.31	1	0.0023

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, pastures) and a preference for forest ($\chi^2 = 2740$, df = 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 urbanised 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 to 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
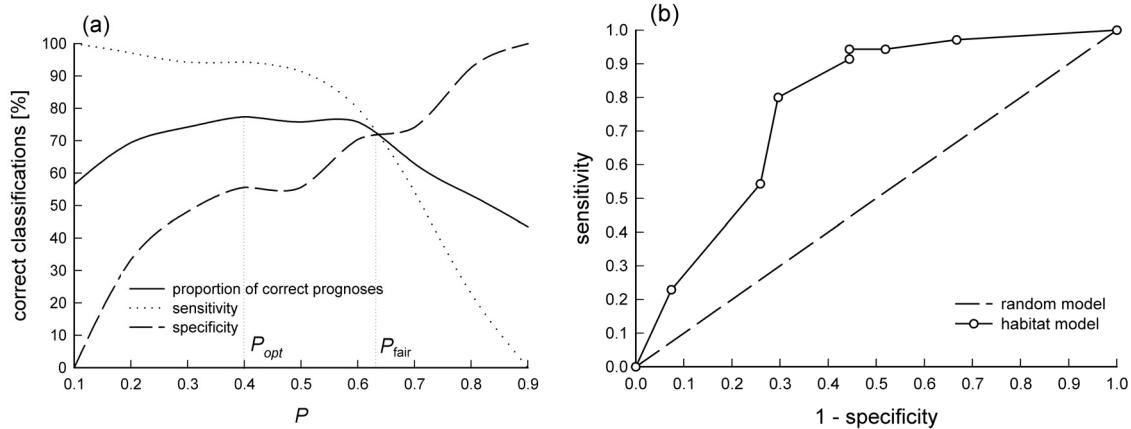
Figure 5. (a) Percentage of correct prognoses of the total model, sensitivity and specificity of the chosen model in dependence on *P*. (b) ROC plot for the chosen habitat model. The area under the ROC plot, AUC, is 0.77. The chance performance of a model (e.g. a random model) is AUC = 0.5, models that outperform chance have greater AUC values. AUC is a convenient measure for overall fit.

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; Figure 4a & b). Thus, to obtain a set of data which were spatially independent we removed neighbouring cells, retaining 1 of 25 cells (i.e. *rs* = 5) and hence obtaining a sample size of *n* = 62 (R_A-indices) and *n* = 86 (R_C-indices). For *rs* = 5 the spatial correlation coefficient of *PExt* was *c* = 0.5 (Figure 4a), and the probability of finding an extensively used cell in distance *rs* = 5 from an arbitrary *PExt*-cell in the closer study site was 54% (Figure 4b).

Correlation analysis

NPUrb and *PUrb*, and *PeriFor* and *PFor* were highly correlated, and therefore contained very similar information. The variables with the greatest explanatory effect in respect to the response variable, *NPUrb* and *PFor,* were retained. The indices for R_A and R_C of variable *PExt* 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 (Mac Nally 2000).

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. also Figure 1 & 6).

area	females (f) / males (m)	n HR	% observed HR cells correctly classified (SD)	n locs	% observed telemetry locations correctly classified (SD)
Swiss Jura Mts.	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)*

Logistic models

For the logistic regression using the R_A index we only used *PExt*-cells, which explains the reduced amount of cells (n = 62) in comparison to 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, that means 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 km², which is approximately the size of the core area of a female lynx's home range (72 ± 27 km²; 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 (Figure 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 (Figure 5).

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 level of $P > 0.5$, which is even higher than in the training data set (Table 3, Figure 2 & 6). The model classification accuracy of independent data was therefore high.
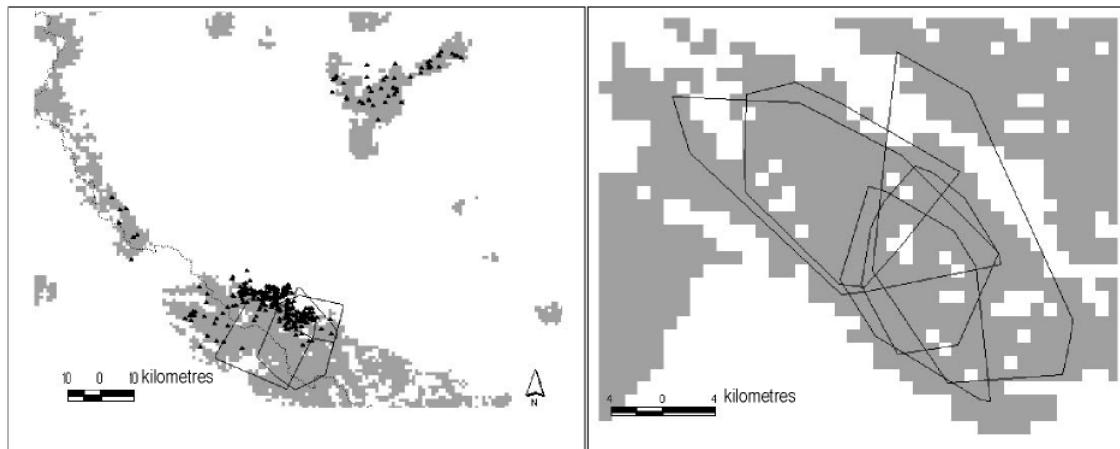
Figure 6. Independent model validation with data from the German-Czech border (left) and Slovenia (right). Grey cells show suitable areas for lynx home ranges based on the applied model, polygons show the home ranges of resident lynx, and triangles show locations of dispersing animals in the Czech Republic.

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, Figure 7), the forest of Lüneburger Heath (LH, Figure 7) and the large forests in the northeast (NF; Figure 7) and close to the Polish border. These big patches are surrounded by smaller suitable satellite patches.

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 km² a total of 29 105 km² (43%) reached a P-level above 0.5 (Figure 8). Considering only those areas with $P > 0.5$ that are $\geq$ 100 km², we obtained a total area of 32 266 km² for Germany and neighbouring forest areas in France, the Czech Republic and Poland, which is reduced to 24 119 km² for Germany only (Table 4, Figure 6 & 8); at typical home range size, this leaves space for about 370 resident lynx in the suitable patches in Germany.
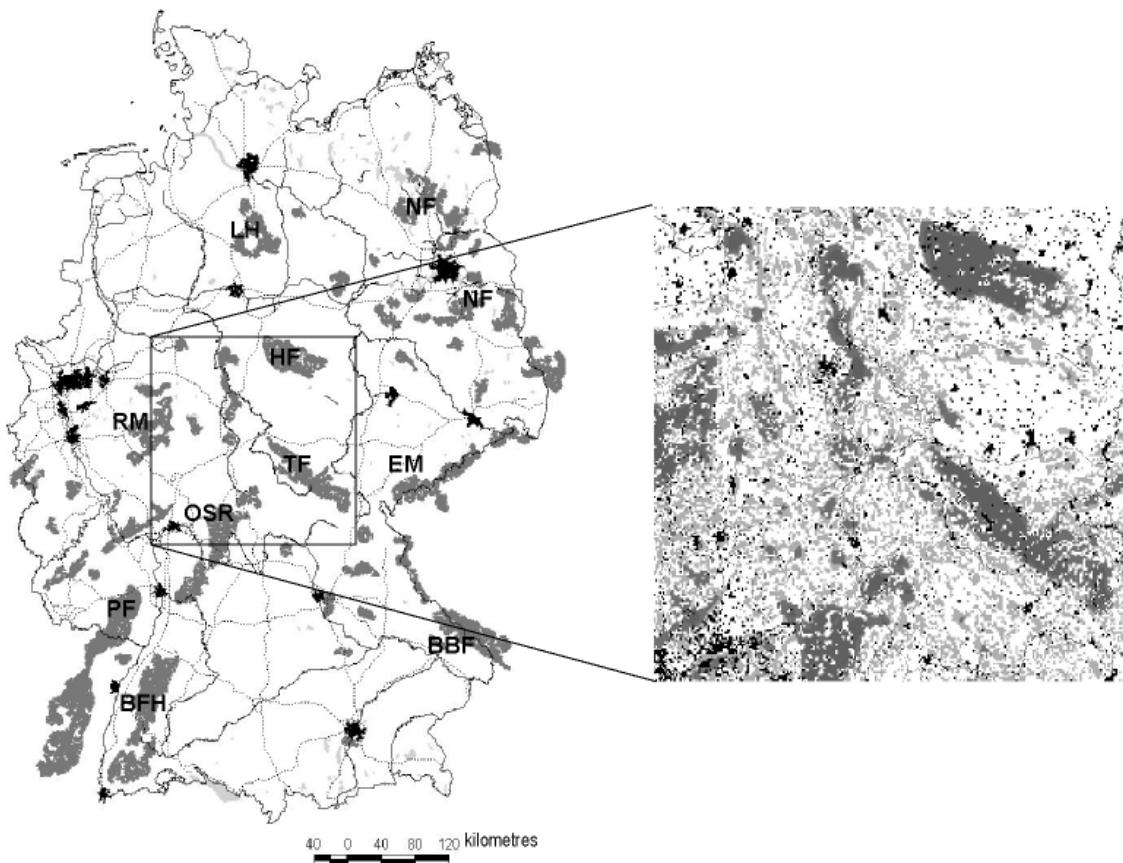
Figure 7. Favourable lynx home range areas in Germany with an area ≥ 99 km² and a P-level > 0.5 based on the logistic model (dark grey). Water bodies (light grey), rivers (solid black line), highways (dotted black line) show further influences that could minimise home range numbers by a fragmentation effect. Black polygons show the biggest urban areas. HF: Harz; NF: Northeastern 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, and dark grey: breeding habitat e.g. suitable cells based on the results of the logistic model.

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;

Table 4. Suitable patches in Germany (cf. also Fig. 7) based on the logistic regression model with patches bigger than 99 km² 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 km².

suitable patch		size [km²]	no. of female HR
Lüneburger Heath	LH	1193	12
Northeastern 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

a model which can be applied to similar kinds of landscapes, for example in Belgium, Scotland, The Netherlands or 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 (e.g. 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 depend also 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 were 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
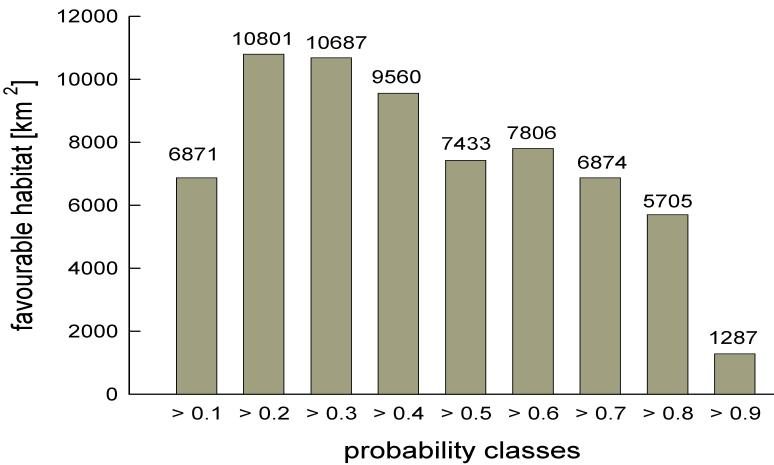
Figure 8. Favourable habitat area in Germany based on probability levels from the logistic regression model. Of a total area of 357 909 km² 328 804 km² (92%) were unsuitable for lynx home ranges.

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 (e.g. 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 significally different between lynx and random home ranges, but a variable comprising a regional scale (cf. also 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 intra-territory use and for dispersal than for predicting regional home range distribution.

An additional problem in the context of logistic regression is dealing with spatial auto-correlation of the dependent variable, which leads to overparameterised 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 significant 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 MCPs many cells with land use types which 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 (Rodríguez & Andrén 1999). If the transferability of the model is not examined and verified, only local applications are possible (Morrison, Marcot & Mannan 1992; Fielding & Haworth 1995; Rodríguez & Andrén 1999). General validity requires new applications in space and time (Brooks 1997; Schröder & 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 (Červený, Koubek & Anděra 1996) and with data from 1999 (Wölfl *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. But this is not in contrast with transferability to Germany.

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 (Lüneburger Heath, LH, Figure 7) or fragmented by highways or rivers (Odenwald-Spessart-Rhön, OSR, Figure 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 to 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, Knauer & Kaczensky 2000, 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 ± 3 home ranges when comparing the two modelling approaches. But the number of female home ranges is reduced by approximately 1/3 in the current model for the Rothaar Mountains and increased by approximately 1/3 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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CHAPTER III

The dispersal model

Fragmented landscapes, road mortality and patch connectivity: modeling dispersal for the Eurasian lynx in Germany

Abstract

The case of a re-invading large carnivore into Germany, the Eurasian lynx, *Lynx lynx* L., stands as an example for the fate of many endangered species in human dominated landscapes. Many reintroduction schemes have been discussed controversially in various locations, but no assessment has been launched whether the suitable patches in Germany are connected to allow expansion of the reintroduced population to other suitable patches. My aim is to assess (1) the connectivity of the patches that could be hot spots for interactions between potential lynx populations and (2) the influence of the dense German traffic system on inter-patch connectivity.

I introduce an individual-based, spatially explicit dispersal simulation model to assess the probability of a dispersing animal reaching another suitable patch in complex heterogeneous landscapes. The dispersal model is calibrated with telemetric data from the Swiss Jura landscape similar in fragmentation, forest cover and population density and based on a map of potential lynx habitat and dispersal habitat as forested areas. I found that the most important factor for determining lynx movement is the availability of dispersal habitat. My results were coincident with literature about lynx biology.

Applying the dispersal model to Germany, I found that within a 10-years dispersal run most of the patches are interconnected. However, when applying realistic levels of mortality risks on roads I can find that most of the patches are isolated except the patches along the German-Czech border. Consequently, it is not the distribution of dispersal habitat that limits patch connectivity in Germany but factors contributing to a high mortality like the dense traffic system. This leads to management implications such as reducing road mortality besides investing into habitat restoration. The model results can be used to assess the possible success of the single reintroduction initiatives in Germany as a basis for a nationwide action plan.

Introduction

Nowadays, in human dominated regions, many animal populations are relatively small and isolated due to habitat loss and fragmentation. If these populations contain only few individuals, the probability of local extinction is high. Dispersal is a key process in determining the survival of such spatially structured populations or metapopulations (e.g., Lima & Zollner 1996; Schippers *et al.* 1996; Collingham & Huntley 2000; Thomas, Baguette & Lewis 2000). The dispersal success depends on the connectivity of the landscape and is especially complicated in intensively used landscapes due to movement barriers imposed by humans, such as roads (Kaczensky *et al.* 1996; Clevenger & Waltho 2000; Saunders *et al.* 2002; Kerley *et al.* 2002) and destruction of habitat suitable for dispersal (Trombulak & Frissell 2000). But especially in these landscapes it is important to maintain exchange between sub-populations to reduce the risk of extinction and the loss of genetic diversity, and information on movement rates are critical for predicting extinction thresholds (Fahrig 2001).

The case of a re-invading large carnivore into Germany, the Eurasian lynx, *Lynx lynx* L., stands as an example for the fate of many endangered species in human dominated landscapes. Within the first half of the 20th century the lynx had completely disappeared from all of Central Europe west of the Slovakian Carpathians due to persecution, habitat destruction and fragmentation (Breitenmoser *et al.* 2000). However, changes in the public attitudes towards large carnivores as well as in the land-use during the second half of the 20th century are promoting the slow recovery of Eurasian lynx in several European countries (Breitenmoser *et al.* 2000). In Germany different locations have been discussed controversially for the reintroduction of lynx (Schadt *et al.* in press) (Figure 1). Meanwhile natural immigration occurred in the Bavarian Forest due to expansion of a reintroduced population in the Bohemian Forest, Czech Republic, and so far a new reintroduction program is being conducted in the Harz Forest (Červený & Bufka 1996; Wölfl *et al.* 2001).

Lynx, as other large, wide ranging carnivores, move long distances and require large home ranges. Especially in densely urbanised and populated Germany the only way to maintain viable populations of these species with large area requirements is within mixed-used landscapes. This complex, large-scale management problem requires knowledge on the extent, the spatial arrangement, and the connectivity of potentially suitable habitat. A first step has already been done with assessing the suitability of the German landscape for lynx (Schadt *et al.* 2002; chapter II this thesis), but before considering possible reintroduction it is important to assess the connectivity of the candidate patches of potentially suitable habitat to avoid short-term decisions that do not take into account individual exchange that is important for long-term survival of a population in small habitat patches.

In order to design conservation strategies for the lynx in Germany, it is also crucial to obtain insights in the relationships between dispersal and landscape characteristics. Clearly, the spatial structure of the landscape in which species are found must be explicitly considered, when landscape composition plays a role in determining patch connectivity (Tischendorf & Fahrig 2000). The key to understanding how landscape structure impacts dispersal is therefore to adopt a spatially explicit, organism-centered view of landscape structure (Lima & Zollner 1996). Models can be used to describe dispersal and estimate connectivity. The most recent developments in population viability analysis (PVA) have shown the usefulness of spatially explicit computer simulation and the integration of demographic and dispersal data with a detailed knowledge of the landscape geometry into a spatially-explicit population simulation model (SEPM) (Akcakaya & Sjören-Gulve 2000).

However, our poor understanding of the response of animals to the spatial pattern of the landscape through which they move limits our ability to assess management actions. This is crucial because the spatial pattern of habitats across landscapes is largely a result of human activities (Gustafson & Gardner 1996). In order to develop an understanding of the implication of resource management activities, we must improve our knowledge of the mechanisms underlying movement decisions made by wildlife species (Conroy *et al.* 1995). There is a general lack of empirical information on the behavioral responses of animals to landscape structure (Lima & Zollner 1996), by which the application of spatially-explicit models is hampered. Consequently, the dispersal modules of SEPMs are often placed on *ad hoc* assumptions on interactions between individuals and landscape structure and on the relevant spatial and temporal scales on which they take place. As a result, the initial enthusiasm about the use of such models has been dampened by critical voices, that criticize the immense data requirements of SEPMs, and emphasize especially on problems associated with parameterising the dispersal process.

For the case of the lynx in Germany we face the problem of data scarcity when parameterizing the model. To circumvent the arising uncertainty I use a pattern-oriented modeling approach (Grimm *et al.* 1996). Here, the information needed for developing and parameterizing a model must not necessarily be directly provided by field measurements, but can be indirectly revealed by comparing the model output with observed "patterns" (= results of analysis of telemetric field data).

I introduce a model to assess the probability that dispersing animals reach another patch in complex heterogeneous landscapes. The objective of this paper is to (1) parameterise a spatially explicit simulation model that in turn will be used to (2) assess the connectivity of patches that could be hot spots for interactions between lynx populations, to (3) investigate the influence of roads on connectivity and to (4) assess the possible success of the reintroduction initiatives on lynx in Germany as a basis for a nationwide action plan.

Methods

Modeling strategy

Model development

I use data from dispersing lynx in the Swiss Jura mountains for model calibration and parameterisation, as the landscape of this area is comparable to the suitable habitats in Germany. The analysis of telemetric data for model calibration and the model application are based on the same habitat map. Results from the analysis of the field data are "patterns" of the interday level (time laps separated by one day; e.g. distribution of net daily distance, use of different habitat types,...).

I develop a set of behavioral rules on the dispersal characteristics based on general knowledge about the process of dispersal and on movement analyses from the Iberian lynx (E. Revilla, unpublished analysis), and implement these rules in a spatially-explicit individual-based dispersal model (SEDM). The model is first implemented for the Swiss Jura Mountains for model calibration, and compares the model prediction of different movement types of increasing complexity with the patterns obtained from field data analyses.

I apply these rules during each model time-step corresponding with the active period of lynx (intraday level). This means, I use a top-down process from the interday level of the patterns to understand the intraday process, where the interaction of the animal with the landscape takes place. The smallest temporal scale of the patterns is a day to day period (interday) which already reflects the outcome of the interaction of the animal with its environment. I assume that movement rules (i.e. model structure) are similar to that of the Iberian lynx and use the pattern-oriented approach to estimate a plausible range of parameters for the Eurasian lynx, by using real data on the dispersal of the Eurasian lynx.

The model provides for each simulation run a simulated data set analogous to the set of field data of the Eurasian lynx in the Jura Mountains. I determine best model parameterisations and model processes by systematically comparing the patterns extracted from the observed data with the predicted patterns from the simulated data. The comparison requires simulations for a high number of different model parameterisations and different hypotheses on the behavioral dispersal rules and enables me to determine the most probable set of behavioral rules and model parameters.

I use linear regression of all parameterisations to assess the sensitivity of the model predictions to the parameters and also to the best parameter combination (that fitted all observed patterns simultaneously, cf. *"Movement patterns and parameter assessment"*). I scale the dependent (pattern) and independent (parameters) variables to values bet-

ween 0 and 1 and use the resulting regression coefficients β_i as indicators that describe the sensitivity of the model output to the parameters. A coefficient $|\beta_i| = 1$ indicates strong sensitivity while parameters with small values $|\beta_i| << 1$ have little impact on the model prediction.

Model application

I apply 100 randomly chosen parameterisations out of the best parameter combinations obtained through model calibration to be used for assessing connected habitat patches in Germany. In each source patch 100 lynx are released and allowed to disperse for 1, 3 and 10 years or until death according to the model rules under different mortality scenarios. Because of the stochastic character of the model each lynx has a different pathway leading to arrival in various target patches. Arrivals and mortality were registered. The connectivity between source and target patch is estimated to be the fraction of animals of the source patch which arrived in a certain target patch. When adding barrier mortality in a scenario, simulated lynx that leave the study area are deleted at the border of Germany, because I do not have digital information in the form of maps on the road system of the adjacent countries. With that I avoid making inference on the connectivity of patches that are linked via corridors outside of Germany, e.g. a connection of the Black Forest and the Palatine Forest via the French Vosges Mountains.

As I repeat the runs under different mortality scenarios with 100 parameterisations, I take the average *plus* standard deviation (as optimistic assessment) of these 100 simulation runs per mortality parameter to categorise the connectivity of the patches. Connectivity was classified in the following categories: *very low connectivity* (I) ranging between 1 and 5%, *low connectivity* (II) between 6 and 15%, *medium connectivity* (III) between 16 and 30%, *high connectivity* (IV) between 31 and 50% and *very high connectivity* (V) with more than 50% probability of reaching another patch. I also tested for relationships between inter-patch connectivity, Euclidean distance between patches, and minimum number of linear barriers that have to be crossed using non-linear regression, as connectivity is expected to be related with distance (Pokki 1981; Hanski 1994; Moilanen & Hanski 1998; Turchin 1998; Vos *et al.* 2001).

Study areas and telemetric data basis

Model development and calibration

For pattern derivation, parameter assessment and model calibration I used the telemetric data of dispersing lynx collected from 1988 – 1991 (Table 5) in the Swiss Jura Mountains (Breitenmoser *et al.* 1993), which are a secondary limestone chain between Switzerland and France. The altitude ranges from 372 m (Lake of Geneva) to 1679 m

Table 5. Telemetry locations of dispersing Eurasian lynx from Switzerland used to derive the patterns for model calibration (modified after Breitenmoser *et al.* 1993).

lynx	total observation period [days]	no. of locations	start of dispersal	last location	maximum distance from starting point [km]	fate
M16	78	74	03.04.90	19.06.90	28	dead
F17	44	23	10.04.90	23.05.90	51	dead
F20	284	121	24.03.91	31.12.91	64	still alive
F13	144	56	27.03.89	17.08.89	25	dead
F12	29	20	30.03.88	19.05.88	76	dead
F19	22	9	15.04.91	05.05.91	6	collar failure

(Mont Tendre). The highlands are covered to 53% by deciduous forest on the slopes and coniferous forests on the ridges. Human population density reaches about 120 inhabitants per km², and the area is intensively used for recreation. Cultivated areas are typically pastures (Breitenmoser & Baettig 1992; Breitenmoser *et al.* 1993).

Altogether I obtained 303 location data of 6 dispersing individuals (5 females, 1 male), separated by time laps of one day (interday level). One dispersing female established a home range during her observation period, so I excluded these radio-locations from my analysis. I did not consider radio-locations of subadults that were still together with their mother in their natal home range before separation. The accuracy of the telemetric location data is 1 km², so I define this as my spatial grain (Figure 9). I defined as the "closer study area" (CSA) the minimum convex polygon of all locations, including residents (cf. Breitenmoser *et al.* 1993).

Model application

Germany in total is very densely populated with 230 inhabitants per km² on average, which drop to about 100 inhabitants per km² in remote places such as the low mountain ranges (Black Forest, Bavarian Forest etc.). Urbanisation makes up to 5% of the total area, and only 30% of the total area is forested. 2.5% of the total area are protected with a National Park status. Germany also has a very dense traffic net consisting of 11 000 km of highways and more than 50 000 km of interstate and main roads.

The habitat suitability map

I obtained the habitat suitability map with a mesh size of 1 km² by logistic regression, as described in Schadt *et al.* (2002) or chapter II (this thesis). The habitat types can be summarised as breeding, dispersal, matrix and barrier habitat. Breeding habitat is formed by cells with a probability cut level $P > 0.5$ as calculated in the logistic regression
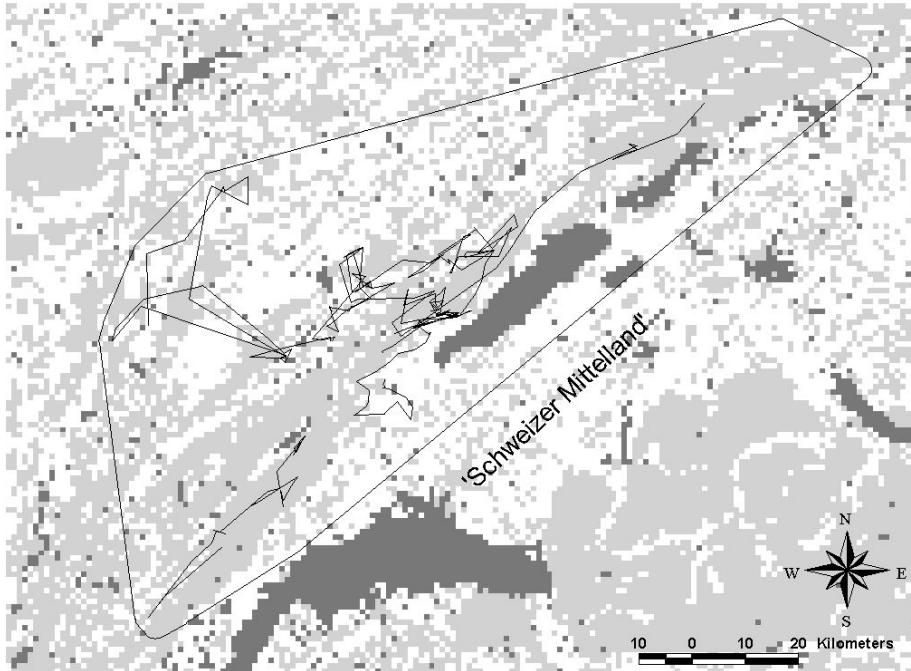
Figure 9. Dispersal pathes of the six dispersing subadult lynx in the Swiss Jura Mountains. Time laps between the locations are different and can be up to 20 days. Light grey is the distribution of dispersal habitat, dark grey are barriers. The polygon is marking the closer study area (CSA).

based on a variable containing extensively used areas (forest and other non-forested, semi-natural land use types, such as heathland) on a scale of about 100 km². To define dispersal habitat I assessed differences in the original 7 habitat classes ((1) urban areas, (2) forested areas, (3) pastures, (4) agriculture, (5) non-forested semi-natural land use types, (6) wetland, (7) water bodies) in the CSA between my telemetric locations and randomly distributed points with a log-likelihood ratio test. Random points were distributed in forest and other semi-natural, non-forested land use types to only 48.2% in comparison to 85.5% of the telemetric locations. Urban areas, wetlands and lakes contained no lynx observations. Considering only habitat classes with lynx observations revealed a departure from homogeneity between the four categories agriculture, pasture, forest and other semi-natural land cover ($G = 227$, $p < 0.01$, df = 3). I can therefore infer that dispersing lynx use forest significantly more often than open space. These results are coincident with results from Poland, where directions and routes of dispersing lynx were related to the contemporary distribution and availability of woodlands and forest cover (Schmidt 1998). So I define any forested area as well as breeding habitat as dispersal habitat.

I define barriers as areas never used by lynx, such as urban areas and lakes. The remaining areas, like pastures and agricultural areas, are summarised as matrix, which is
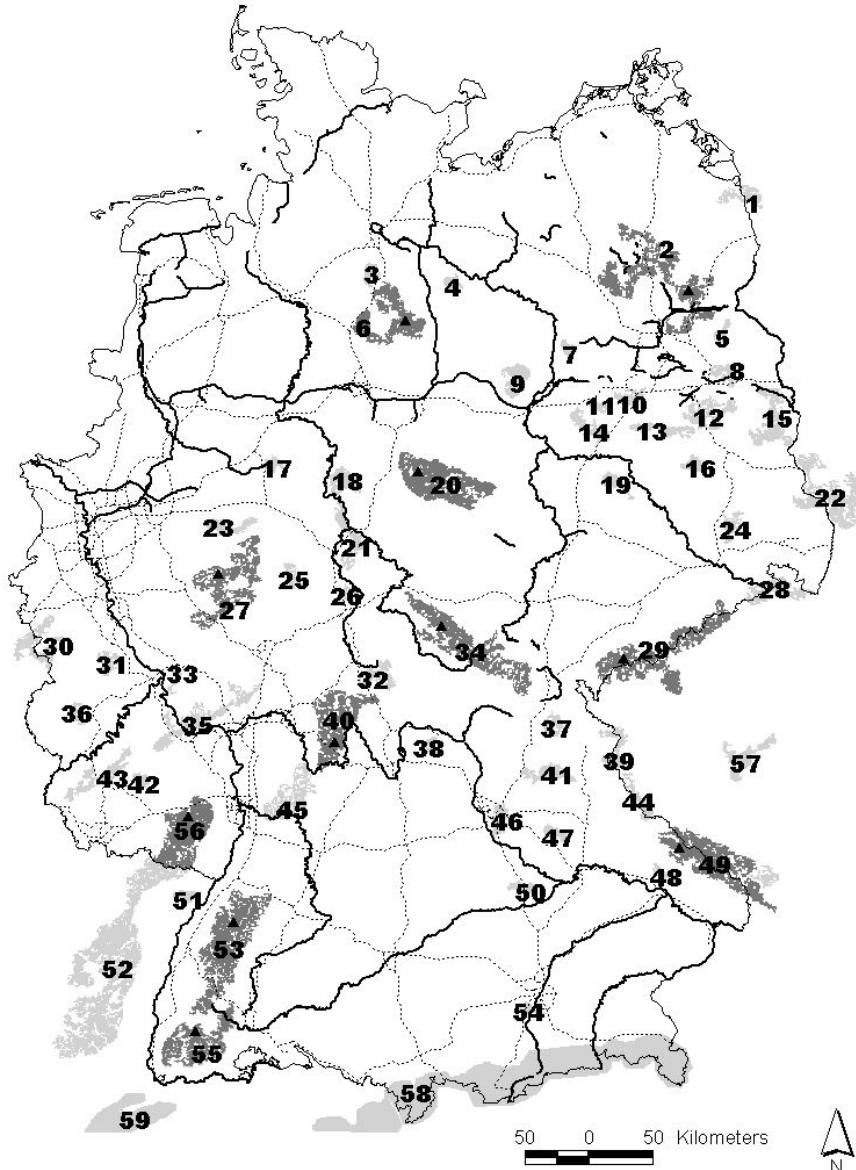
Figure 10. Source and target patches for measuring the connectivity of the German landscape. Dark grey are source patches, which are greater than 1000 km², light grey are target patches which are greater than 100 km². Dotted lines are higways, black lines are main rivers. The triangles indicate the starting points of the simulated animals. Connectivity between the patches for the different scenarios is given in Appendix 1.

avoided by dispersing lynx and only used occasionally. For simulating the effect of road mortality on connectivity, I create a second map with linear elements such as main roads, highways and large rivers. For simulating connectivity I define as source patches the major patches of special management interest (greater than 1000 km²) and as target patch each suitable area greater than 100 km² (Figure 10), which is the average home range size of a female lynx in the Swiss Jura Mountains (Breitenmoser *et al.* 1993).
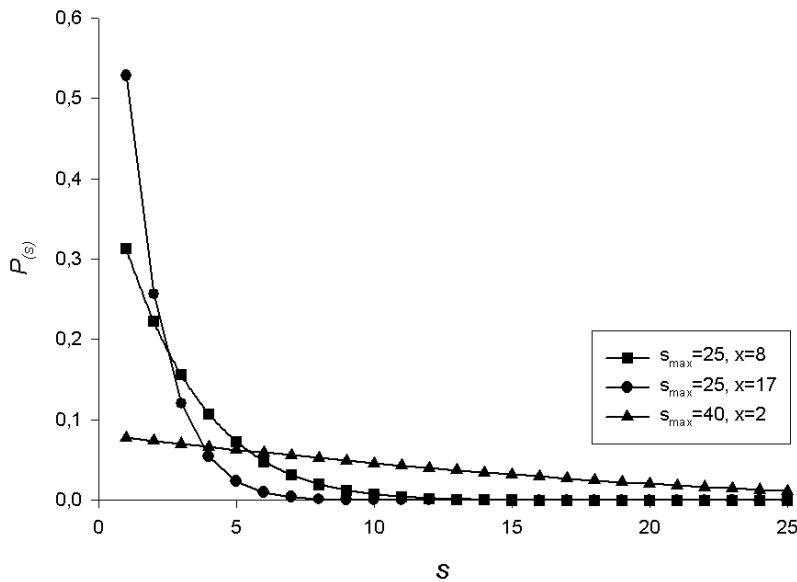
Figure 11. Intraday step distribution for different parameter values s_{max} (maximum number of intraday steps) and x (exponent of equation (1) as described in the text).

Patches separated by space laps of 1 km were considered as one patch, as this is the distance that lynx can perceive as connected (Haller & Breitenmoser 1986). Altogether I obtained 59 patches, of which 11 are source patches ((2) North-eastern forests, (6) Lüneburger Heath, (20) Harz Mountains, (27) Rothaar Mountains, (29) Erz Mountains, (34) Thuringian Forest, (40) Spessart, (49) Bavarian Forest, (53) Northern Black Forest, (55) Southern Black Forest, (56) Palatine Forest; Figure 10).

Dispersal model rules

Intraday number of steps

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

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

with an exponent *x* and parameter s_{max} that gives the maximum number of steps that a dispersing lynx can cover during one day and a normalisation factor φ (Figure 11). The parameter range for s_{max} was assessed by orientation on literature. In Poland the total distance covered by Eurasian lynx during the period of activity (intraday) was on

Table 6. Parameter ranges of the dispersal model for each movement type and the application to Germany. The probability giving the number of steps per day a lynx disperses is the same for each movement type, as well as the number of days a lynx can disperse during one simulation run.

unit	parameter	symbol	range
dispersal model adjustment	exponent of power function	x	1, 3.11, 5.22,..., 20
	Max. number of intraday movement steps	s_{max}	10, 20, 30, ..., 70
Movement types HDW (CHDW*) CHDW*	probability of stepping into matrix	P_{matrix}	0, 0.1, 0.2,..., 1
	probability for moving forward or backward	P_c	0.1, 0.2,... 1
application to Germany	Mortality probability on highways/rivers per crossing	$M_{highway}$	0, 0.15, 0.50, 0.75
	Mortality probability on main roads per crossing	M_{road}	0, 0.0005, 0.001, 0.002
	Natural mortality probability per day	M_{nat}	0, 0.0003, 0.0007, 0.001

* The movement types in parentheses means that the parameter is also used for another movement type.

average 2.6 to 4.5 times longer than distances between locations taken once daily, which led to possible maximum distances between 26 and 46 km per activity period (W. Jedrzejewski, unpublished analysis). Similar figures are also known from the Iberian lynx (*Lynx pardinus*). Here the total maximum distance was 38.7 km within the period of activity (E. Revilla, unpublished analysis). From my telemetric data analysis I can therefore expect values between 30 and 55 km, as the daily maximum distance was 12 km (n = 198). I set the parameter range for s_{max} between 10 and 70 km (Table 6). The exponent x of the power function was varied over a broad range to ensure a large variability in the step distribution (Table 6). Low exponent values yield linear distributions whereas high exponent values promote a higher probability of a small amount of movement steps (Figure 11). Lynx move one grid cell per step or stay in the cell, with the probability of moving to any of the 8 adjacent cells or to stay in the cell determined by a certain searching or movement type per step.

Habitat Dependent Walk (HDW)

I assume that dispersal direction depends upon local habitat quality as perceived by individual lynx. As a consequence, this process is determined through a set of rules which take into account local habitat quality. The next cell is chosen in preference for dispersal habitat and avoidance of matrix. The probability of randomly choosing one cell is 1/9 (I include the case that a lynx does not move or moves less than 1 km). Within this area of 3 by 3 cells (including the origin cell and its 8 surrounding cells) the number of matrix cells n_{mat} is counted. Thus, I assume that individuals survey their neighborhood and that their movement steps are based on this information. The probability of leaving dispersal habitat P_{leave} is then dependent on the number of matrix cells around the origin cell multiplied with a parameter P_{matrix}, and ranges from total avoidance of matrix (P_{matrix} =

0) to randomly choosing a surrounding cell (P_{matrix} = 1/(9-n_{barr}), where n_{barr} is the amount of barrier cells:

$$P_{leave} = n_{mat} \cdot P_{matrix}$$
<div align="right">eqn 2.</div>

Correlated Habitat Dependent Walk (CHDW)

This movement type differs from the habitat dependent walk in addition of a correlation factor P_c for keeping the previous direction within a day, which is supported by analyses of the Iberian lynx (E. Revilla, unpublished analysis). P_c gives a probability between 0.1 to 1 (note that the case $P_c = 0$ yields the former movement type) that the next cell is in the same movement direction, otherwise the next cell is chosen randomly. The hierarchy is preference of dispersal habitat (cf. above HDW) before correlation in movement direction. The first direction each day is chosen randomly.

Maximum residence in matrix cells

I measured in the parameterisations during model runs for model adjustment the total number of consecutive steps that the animal moved in matrix (P_{maxmat}). If a lynx is surrounded by matrix habitat, the probability of finding dispersal habitat again is very low, because the searching type is dependent on the number of surrounding matrix cells. The measure P_{maxmat} can therefore be seen as a memory to return to dispersal habitat after an excursion to matrix as does the Iberian lynx (E. Revilla, unpublished analysis). I included the rule in the model application to Germany that a lynx is turning back to the location where it had left the dispersal habitat when reaching the threshold value of P_{maxmat} (in my case 9 cells; cf. *"Results. Parameter range and sensitivity analysis"*). To assess the sensitivity of this parameter and its implication on the connectivity of German patches I set the value of the parameter to an unrealistically high value of 40 matrix cells and compared the outcome with the results of the connectivities gained by the adjusted value for P_{maxmat} with a linear regression.

Movement patterns and parameter assessment

Based on our habitat suitability map I can define a set of seasonal and daily patterns obtained by analysis of telemetric data that I aim to satisfy when simulating the active period. As I do not have any data of the active period, I varied the parameters over their full range, e.g. probabilities between 0 and 1 (Table 6). I defined threshold values above which the pattern was defined to be satisfied.

Pattern 1 "Habitat use"

Dispersing subadult individuals used dispersal habitat to 85.5% (n = 303) in the Swiss Jura Mountains (cf. *"The habitat suitability map"*). Randomisation of the telemetric

locations (10 000 samplings with replacement; Manly 1997) resulted in a distribution ranging from 78% to 92% (mean 84.34, SD 2.11) habitat use. As I know that matrix is avoided by dispersing lynx, I excluded the residual 5% in the lower tail and defined the pattern to be satisfied when the mean of the simulated pattern was above 81%.

Pattern 2 "Average Maximum Distance"

Maximum distance reached from the starting point of dispersal within the observation period was 76 km for Swiss dispersing lynx. The average maximum of the Swiss dispersers is 41.7 km ($\pm$ 26.5 km SD, n = 6) (Table 5). Total dispersal distances of subadult Eurasian lynx ranged between 11 km and 98 km (mean 43.4 km, n = 11) in the Swiss Jura Mountains (Zimmermann 1998). Similar figures are reported from Poland. Here the animals dispersed between 5 km and 129 km from their natal ranges (Schmidt 1998). As I have a high standard deviation in this pattern due to the different number of dispersal days of the subadults, I defined the pattern to be performed when the observed value of 41.7 km is inside the envelope (mean $\pm$ SD) of the simulation.

Pattern 3 "Study area"

I determined that a simulated lynx, that crossed the "Schweizer Mittelland", the densely populated, rather flat area between the Jura Mountains and the Alps (Figure 9), did not satisfy the pattern "study area". Since the beginning of the lynx project in the Jura Mountains, no lynx ever crossed this plain (U. Breitenmoser, personal communication).

Pattern 4 "Step Distribution"

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

$$\psi \;=\; \sqrt{\sum_{1}^{12} \left(\frac{data - sim}{12} \right)^2} \qquad\qquad \text{eqn 3,}$$

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

Methods for model calibration

I exactly simulate the time span of each of the six dispersing lynx in the Jura Mountains on the habitat suitability map. Each lynx is released in the same location where they started dispersal after separation from their mother. Each simulated lynx is run for the number of days it was observed in the field (Table 5). Hence, I can leave out demographic factors in this part of the model, which enables me to compare the output of the dispersal model with the results of the analysis of the telemetric data and to calibrate the model.

Simulation results are sampled and analysed analogously to the telemetric data pattern. For each model parameterisation I performed 100 replicate simulations to get a stabilised standard deviation (less than 1% variability). A model parameterisation was accepted when all four derived patterns were fulfilled simultaneously to allow for filtering plausible parameter combinations based on current knowledge.

Dispersal scenarios for Germany

Linking demographics to the landscape

The simulation for the demographic part includes different mortality risks per movement step (when crossing a linear barrier) or day (natural mortality occurring stochastically). For mortality on linear barriers I use the map with the linear elements of roads (main roads and highways) and rivers. I estimated mortality parameters for each of the two road types and rivers and the per day mortality probability with a second model calibration until I got results reflecting values of literature analyses (cf. *"Scenario III"* and Table 8). I additionally applied the rule not to cross more than 9 matrix cells (average + SD of P_{maxmat}, cf. "*Methods. Maximum residence in matrix cells"* and Table 7C) measured in the model calibration with the Swiss data, otherwise the lynx was set back to the place where it has started to leave dispersal habitat.

Scenario I "No mortality"

This is my reference or baseline scenario, as leaving out mortality for the simulation runs can give hints on possible corridors between patches depending on the landscape structure, landscape fragmentation and the amount of time dispersing.

Scenario II "Natural mortality"

Only imposing natural mortality enables distinguishing the influence of roads and linear barriers on the connectivity of patches in Germany. I take values for the daily natural mortality risk reflecting annual mortality rates of about 20% as given from literature analyses for dispersing animals ($M_{nat} = 0.0007$, cf. Table 8). E.g., in the protected population of Poland, annual mortality rate of subadult and adult lynx was on average

0.37. Poaching was the most important factor contributing 71% to the total annual mortality rate (Jedrzejewski *et al.* 1996). Hence, natural mortality rate in this population is about 12%. In a model on badgers (*Meles meles;* Schippers *et al.* 1996) the annual natural mortality rate of dispersers was estimated double as high (25%) as the one of residents, a value also supported by data from the Iberian lynx, where mortality without poaching and road kills was estimated to be about 22% (Ferreras *et al.* 2001).

Scenario III "Barrier mortality"

The occurrence of traffic casualties influences the connectivity of the study area because it lowers the number of successfully dispersing animals. Between 1988 and 1991 only one of five dispersing lynx in the Swiss Jura Mountains survived the first year of dispersal (Breitenmoser *et al.* 1993). Traffic accidents are the main cause of mortality of subadult lynx. Of 17 subadult lynx found dead between 1988 and 1997, about 45% died in traffic accidents, 25% were poached or captured, another 25% died of diseases or natural accidents, and 5% were found dead of unknown causes (Zimmermann 1998; Schmidt-Posthaus *et al.* 2002). Subadult mortality in the Jura Mountains was estimated to be about 44% per year and 56-60% per year in the Alps (Breitenmoser-Würsten *et al.* 2001). Total mortality rate for Iberian subadult lynx was estimated to be about 55% (Gaona, Ferreras & Delibes 1998; Ferreras *et al.* 2001). A suggestion for European badgers gives figures between 20 and 50% total mortality rate (including road mortality; Waser 1996). In a model for beavers (*Castor fiber*) total dispersal mortality was set to the lowest known value (14%) and the highest known value (57%; South, Rushton & Macdonald 2000). Similar figures are reported for nonresident wolves (*Canis lupus*) in north-central Minnesota (48%) and Alaska (62%; Waser 1996).

I expressed the crossing mortality of a barrier as the probability of death per crossing event. I varied the probability of being killed when crossing a highway/ river with probabilities of 0.15, 0.50 and 0.75. The mortality risk while crossing a main road was difficult to assess because resident lynx can have roads within their home ranges and cross them several times. I varied parameters for mortality events due to crossing linear barriers over some plausible range and accepted only model parameterisations that accorded with general knowledge on overall mortality rates for further analysis. I checked the outcome of the model to yield about 70% linear barrier mortality events (roads, rivers and highways together, $M_{road} = 0.002$, $M_{highway} = 0.15$, cf. Table 8) of the total mortality, the rest of 30% being natural mortality ($M_{nat} = 0.007$, cf. Table 8), to get a realistic picture on the situation in Germany. Hence, total annual mortality was set to about 50%.

Table 7 (A). Result of the calibration of the dispersal model. Each model parameterisation was repeated 100 times, and the mean taken from 100 replicate simulations was compared with the observed patterns. The result of the parameter range of these searching types is described in the second part of the table.

movement type	n parameterisations	pattern performance[%]				simultaneous fit of all 4 pattern [%]
		pattern 1 habitat use	*pattern 2 average maximum distance*	*pattern 3 study area*	*pattern 4 step distribution*	
HDW	840	76	45	58	26	11 (n = 90)
CHDW	8400	86	56	46	37	18 (n = 1535)

Table 7 (B). Parameter range of the best parameter sets (n = 1625), that fitted all four patterns simultaneously in the two habitat dependent random walks (HDW, CHDW). Only the probability of stepping into matrix P_{matrix} has been slightly restricted in its range.

	parameter symbol			
	x	s_{max}	P_c	P_{matrix}
mean total (±SD)	11 (± 5)	45 (± 17)	0.53 (± 0.30)	0.27 (± 0.18)
range total	1-20	10-70	0-1	0.0-0.9
mean HDW (±SD)	8 (± 5)	51 (± 15)	-	0.27 (± 0.18)
mean CHDW (±SD)	12 (± 5)	45 (± 17)	0.56 (± 0.28)	0.27 (± 0.18)

Table 7 (C). Range of the average maximum amount spent in matrix cells P_{maxmat} in the different movement types and also in the best parameter sets.

Movement type	simulation		simultaneously fitted parameter sets	
	Mean (±SD)	*range*	*Mean (± SD)*	*range*
HDW	14 (± 14)	0-80	6 (± 5)	0-21
CHDW	12 (± 10)	0-63	4 (± 4)	0-24
Best parameter set			5 (± 4)	0-24

Results

Model calibration

In the habitat dependent walk only 11% of all model parameterisations were in accordance with the data on lynx movement, i.e. satisfied all 4 patterns simultaneously. Adding correlation in movement direction to this sub-unit increased the percentage of simultaneous fits of all 4 patterns. This infers that habitat dependency is the most important factor for describing the movement of the Swiss Jura lynx, and that correlation in movement direction is plausible, but not obligate (Table 7A).

Parameter range and sensitivity analysis

Sensitivity analysis of the normalised dependent and independent variable of all parameterisations shows that all regression functions are highly significant ($P < 0.001$, Table 5). High r^2_{adj} values ($r^2_{adj} > 0.7$) for most patterns indicate that the linear regression models yield good approximations. The most sensitive model parameter clearly is the probability of stepping into matrix (P_{matrix}), followed by the maximum number of steps s_{max} and the exponent of the equation for the number of intraday dispersal steps x.

In parameterisations which fitted all 4 patterns simultaneously, only the probability of stepping into matrix P_{matrix} has been slightly restricted (Table 7B). The maximum number of intraday steps s_{max} is correlated with high exponent values x ($r = 0.67$), which leads to step distributions with very high probabilities of moving short distances and rare events of long distances during the period of activity. This could reflect the behaviour of lynx of staying up to one week close to the carcass of the prey and therefore moving only short distances, and then moving far distances within one night (Breitenmoser *et al.* 2000). The maximum number of intraday steps s_{max} (range 28 to 62 km) also reflects data which are known for the Iberian lynx (Ferreras *et al.* 1997; Palomares *et al.* 2000) and the Eurasian lynx in Poland (W. Jedrzejewski, unpublished analysis). Within the plausible parameterisations the measure for residence in matrix cells P_{maxmat} was restricted to 5 (SD ± 4) cells, which is supported by literature results of Iberian lynx: intraday maximum distance across matrix was 9.5 km (Eloy Revilla, unpublished analysis; Table 7C). Hence, the results can be seen in accordance with general knowledge on lynx dispersal.

When parameter P_{maxmat} was set to a very high value (= 40) in the 10 years run without mortality, connectivity values were highly related ($r^2_{adj} = 0.994$, SE = 0.9, P < 0.001, df = 1, n = 238):

$$C_{m40,scen1} = 1.4 + 0.96 \cdot C_{m9,scen1} \qquad \text{eqn 4.}$$

Of course there were additional connections to other patches, but the connectivity was very low (< 3%). The result is similar when comparing the connectivity values of scenario 3 in the 10 years run. Linear regression also showed highly related connectivity values ($r^2_{adj} = 0.995$, SE = 0.6, P < 0.001, df = 1, n = 56):

$$C_{m40,scen3} = 1.0 + 0.94 \cdot C_{m9,scen3} \qquad \text{eqn 5,}$$

also resulting in additional connections to other patches, but also with very low connectivity values (< 2%). This means, the difference in the connectivity values for the different maximum residence in matrix is on average not higher than 1.4% (e.g. for scenario 1), leading to the conclusion that the restricted value for $P_{maxmatrix}$ of 9 cells did not have any decisive effect on the model results.

Table 8. Result of model calibration for annual mortality rates (cf. also Table 6). For each parameterisation the total annual mortality rate was measured, as well as the proportion of the total mortality rate of animals that died naturally or while crossing a linear barrier. Shown are the parameter combinations that were used for the dispersal scenarios in Germany and their resulting annual mortality rates.

parameter			Results			
M_{nat}	$M_{highway}$	M_{road}		*Proportion of total annual mortality*		
			Total annual mortality rate (SD) (%)	*Natural death*	*Death crossing highways/ rivers*	*Death crossing main roads*
0	0	0	0	0	0	0
0.0007	0	0	20 (1)	100 (0)	0	0
0.0007	0.15	0.002	51 (5)	31 (4)	40 (4)	29 (5)

Linear regression of the best parameterisations (pattern as dependent variable, parameter as independent variable) revealed that all parameters are significant (p < 0.001, Table 9), but the fit of the regression function is only high for the pattern "habitat use" and "average maximum distance" (Table 9). I find that P_{matrix} is the decisive parameter for explaining the pattern "habitat use", whereas the patterns "step distribution" and "study area" strongly depend on the maximum number of intraday steps s_{max} and the exponent of the equation x.

The scenarios

Scenario 1 "No Mortality"

Considering connectivity values in class (I) "*very low connectivity*" in a one years' run I can only find indirectly connected source patches via target patches. This would link together the Black Forest with the Palatine Forest (53-51-56), the Thuringian Forest with the Spessart (34-32-40) and the Bavarian Forest with the Erz Mountains (49-44-39-29; Figure 10, Appendix 1). From the Southern Black Forest there would also be a connection into the Swiss Jura Mountains. *S*ource patches are also not directly connected with each other within one year considering connectivity values above 5% (*low connectivity (II))*, only can I find some interconnected source and target patches (Figure 10, Appendix 1). The only connected source patches (*good connectivity (IV)*) are the Northern and Southern Black Forest (53-55) with only having 3 km of distance in between them.

Increasing the simulation time to three years, we get an interconnected source patch system (above 5% connectivity) between the Spessart and the Thuringian Forest (40-34), the Erz Mountains and the Bavarian Forest (29-49) and also between the Palatine Forest and the Northern and Southern Black Forest (56-53-55). The connectivity of patches 49 and 57 (Bavarian Forest and Czech patch), known from field data of a dispersing subadult male (Bufka *et al.* 2000) was represented in 4% of the cases. Considering also very low connectivity, the Palatine Forest (56) would be connected with the Rot-

haar Mountains (27) via the Taunus (target patch 35), and also the Thuringian Forest (34) would be connected with the Rothaar Mountains (27) via patches 21, 25 and 26, and with the interconnected source patches along the German Czech border (29-49). The Rothaar Mountains (27) are also connected to the Harz Mountains (20) via the target patch 21. Still, the Lüneburger Heide (6) and the North-eastern forests (2) are connected with surrounding target patches, but not with any other source patch.

Running the simulations for 10 years we obtain 134 connections to other patches. Above 5% connectivity we get an interconnected source patch system Erz Mountains (29), Bavarian Forest (49), Thuringian Forest (34) and Spessart (40), and also Thuringian Forest (34) with the Rothaar Mountains (27) via patches 25 and 26 and Thuringian Forest with the Harz Mountains (20) via 18 and 21. Additionally the Rothaar Mountains are connected with the Harz Mountains (20) via patch 21. The Rothaar Mountains (27) would also be connected with the connected source patch system Palatine Forest (56), Northern and Southern Black Forest (53, 55) via patch 35. The known connection of the Bavarian Forest with the patch in the Czech Republic (49-57) was represented in 13% of the cases (Bufka *et al.* 2000). Below 5% all source patches are interconnected either directly or via target patches, but these are the most sensitive connections that disappear as soon as any mortality factors are introduced (see below). Time dependency of connectivity is clearly shown in the time increment from 1 to 10 years. I also find a relation between Euclidean inter-patch distance d_{net} and connectivity $C_{scen1,10}$ following an exponential decay function ($r^2_{adj} = 0.77$, df = 1, p < 0.0001, n = 134), when mortality was not considered:

$$C_{scen1,10} = 125 \cdot \exp(-0.03 \cdot d_{net})$$ eqn 6.

Scenario 2 "Natural Mortality"

Imposing a total annual natural mortality rate of about 20% does not change the picture I obtain from the simulation runs above (Appendix 1). After 10 years the connectivity between patches is the same, only the percentage of dispersers that reach another patch has decreased (Figure 12a). So has the connection between the Harz Mountains (20), the Lüneburger Heath (6) and the North-eastern forests (2) disappeared. The connectivity known from field data between the Bavarian Forest (49) and the Czech patch (57) has decreased from 13% to 9% in these 10 years and from 4 to 2% in 3 years. Connectivity $C_{scen2,10}$ is related with inter-patch distance d_{net} following an exponential decay function ($r^2_{adj} = 0.74$, df = 1, p < 0.0001, n = 134):

$$C_{scen2,10} = 106 \cdot \exp(-0.04 \cdot d_{net})$$ eqn 7.
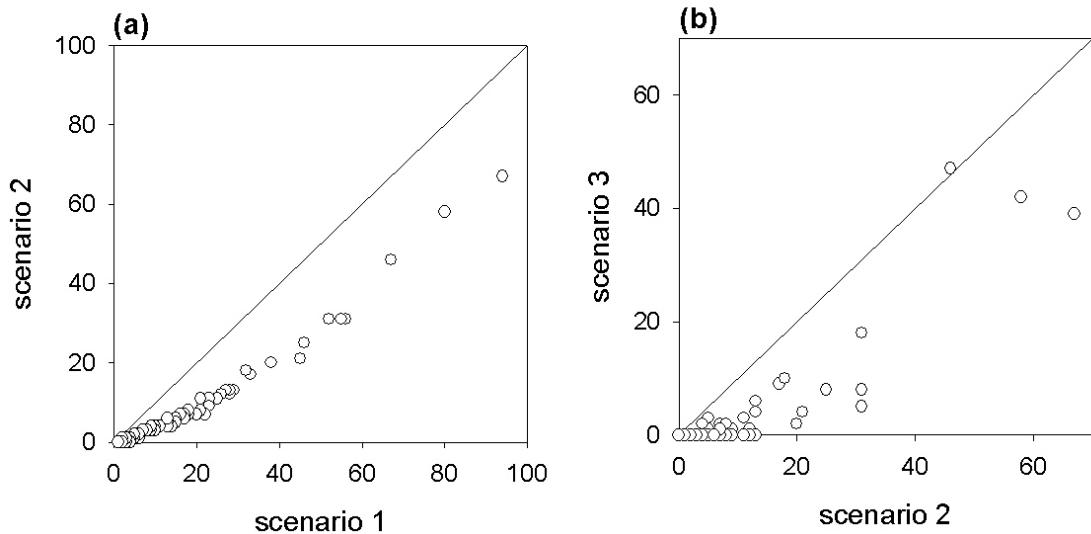
Figure 12. Connectivities of the scenarios plotted against each other. Adding only natural mortality (scenario 2) decreases connectivities almost linearly in comparison to scenario 1 without any mortality (a), but adding road mortality makes connectivity between patches unpredictable (b).

Scenario 3 "Natural and Barrier Mortality"

I considered total annual mortality rates of 51 (± 5 SD) %, with natural mortality of 31 (± 4 SD) % and traffic mortality of 69 (± 5 SD) % as supported by literature (Table 8). In the 10 year simulation runs, only the Northern and the Southern Black Forest (53, 55), the Spessart and the Thuringian Forest (34-40) and the patches along the German-Czech border (49-29) are interconnected (Figure 10, Appendix 1). It is important to note that the 3 years run almost shows the same connectivity as the 10 years run, only that the patches along the German-Czech border are separated. This low connectivity of the German landscape due to traffic mortality in comparison with the simulation results of the scenarios without road mortality (Figure 12b) illustrates the impact that roads can have on dispersal success. In the 10 years run patch-size of the target patch and least number of highways or rivers to be crossed did not play a role for connectivity. Connectivity $C_{scen3,10}$ is related with inter-patch distance d_{net} following an exponential decay function ($r^2_{adj} = 0.71$, df = 1, p < 0.0001, n = 134):

$$C_{scen3,10} = 167 \cdot \exp(-0.08 \cdot d_{net}) \hspace{3cm} \text{eqn 8.}$$

If I additionally consider the influence of linear barriers (distance multiplied by least number of highways and rivers $n_{linbarr}$ that have to be crossed for reaching another patch) I get an even better fit ($r^2_{adj} = 0.79$, df = 1, p<0.0001, n = 131):

$$C_{scen3,10,linbarr} = 106 \cdot \exp(-0.04 \cdot (d_{net} \cdot (n_{linbarr}+1))) \hspace{2cm} \text{eqn 9.}$$
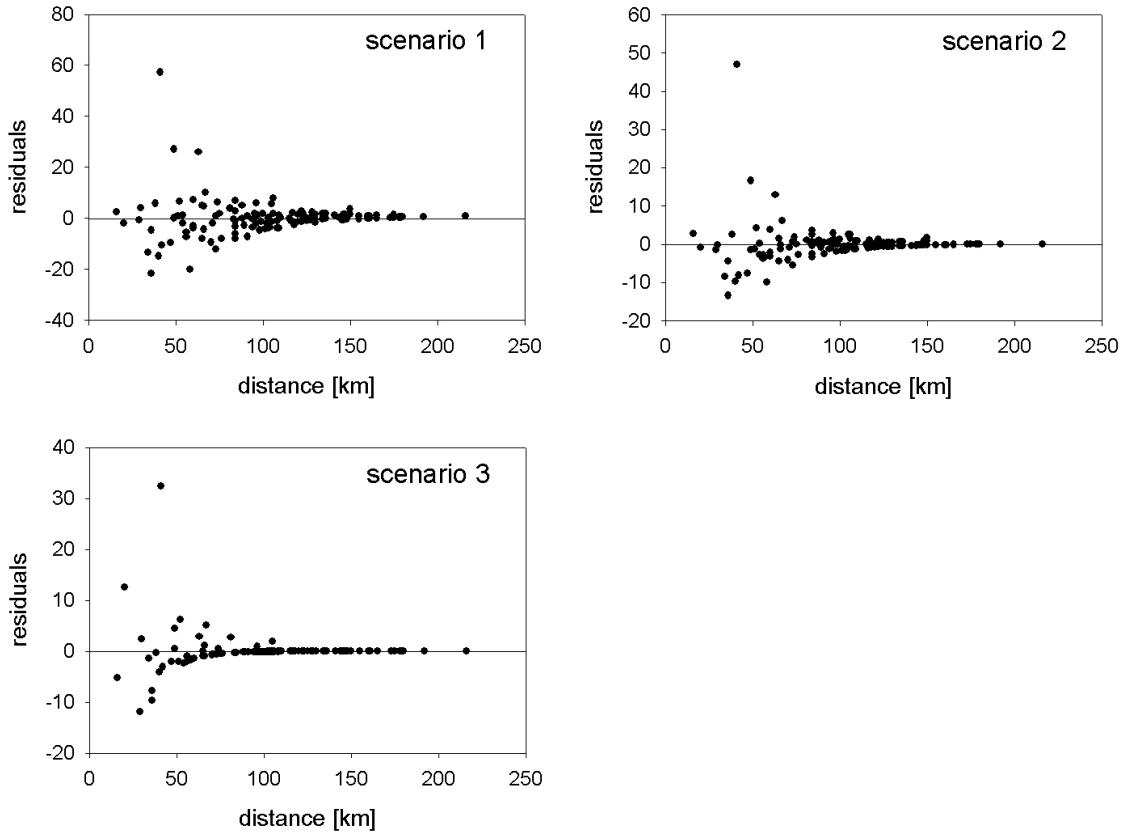
Figure 13. Residuals of the exponential decay functions (6) - (8) relating connectivity and distance as described in the text. Residuals vary extremely strong for short distances, showing the importance of landscape structure (distribution of matrix and dispersal habitat) and roads on dispersal success.

Altogether I found a relatively high fit of all regression functions ($r^2_{adj} > 0.7$ for eqn. 6-9), but the high fit is mainly due to the many zeroes for far distances (no connectivity). But the residuals show an extremely high variation for short distances (Figure 13). This finding is extremely important for conservation of populations, where connectivity is often assessed only by a function of distance.

Discussion

The modeling approach

The model demanded quantification of several parameters. The data necessary for exact quantification are usually assumed to be insufficient (Turner *et al.* 1995; Lima & Zollner 1996), and critical voices against the use of SEDM's have remarked the 'immense data requirements' (Beissinger & Westphal 1998) and emphasised the problems associated with parameterising dispersal processes (Doak & Mills 1994; Ruckelshaus, Hartway & Kareiva 1997; Beissinger & Westphal 1998). I faced these problems in first

calibrating the model with field data in the sense of *understanding* the landscape- and individual-level processes before *forecasting* any effects of human activities (*sensu* Conroy *et al.* 1995). As I have to address the stochastic problem of only having data from six animals, I varied the parameters across a broad range and used only plausible parameterisations that were coincident with data from Poland and Spain.

An important limitation of the model is that I had to base the intra-day movement rules on literature and analyses of the Iberian lynx and could have forgotten important rules. But considering the limited information that I had the model is reasonable. Even for a rather simple approach of a habitat dependent random walk I found that 18% of all model parameterisations produced a model behavior that accorded with the pattern information. I can therefore infer that time and habitat are the most important factors for predicting the movement patterns.

The model application to Germany should also be fine tuned to higher degrees of accuracy in the barrier maps, which presently do not contain existing highway underpasses, viaducts or green-bridges or information on traffic densities, which could alter the connectivity values. Adult large carnivores tend to avoid roads (Kaczensky *et al.* 1996; Gibeau *et al.* 2002). But that subadult lynx try to avoid crossing a highway until they have found an underpass is lacking evidence so far with the data I had. The approach is an example of assessing the influence of linear barrier and natural mortality on patch-connectivity in fragmented landscapes, that can also be used for other species of conservation focus, especially for assisting in investigations of conservation issues surrounding species introductions (cf. Cramer & Portier 2001).

Connected patches and management conclusions

The connectivity of patches has often been considered only as a function of distance (cf. Ricketts 2001; Verboom *et al.* 2001), but there is a need of adding realism to theoretical models and to include the behavioural ecology of the target species and the landscape structure. The analyses support that connectivity is the outcome of multiple factors related with landscape composition, e.g. effective isolation through matrix and linear barriers. This could be crucial in applied biology, especially when assessing the success of a reintroduction scheme in a certain place, where often local populations have to be linked. Understanding the factors that determine the variability in patch connectivity may not only further our ecological understanding of fragmented landscapes but also improve our ability to conserve species inhabiting them (cf. Ricketts 2001).

Landscape structure has a very constraining impact on the movement directionality in Germany, as the long simulation runs over 10 years considering only natural mortality, have shown. Matrix habitat isolates the Lüneburger Heide (6) and the North-eastern forests (2) from the rest of the source patches. Matrix also hinders connectivity between

Table 9. Sensitivity analysis of model predictions based on all model parameterisations ($n = 9240$) and on the best parameter set ($n = 1625$). I scaled the dependent (pattern) and independent (parameters) variables to values between 0 and 1 and use the resulting coefficients β_i of the linear regression as indices that describe the sensitivity of the model output to the parameters. A coefficient $|\beta_i| = 1$ indicates strong sensitivity while parameters with small values $|\beta_i| \ll 1$ have little impact on the model prediction. If not marked in the table, the p-value for the parameter coefficients is p <0.001. Bold are high coefficient values $|\beta_i| > 0.7$, and italic are coefficient values $|\beta_i| > 0.4$.

pattern	n	mean ± SD	range	r^2_{adj} (df = 4)	p	Parameter Coefficient β_i ± SE intercept	x exponent of equation (1)	s_{max} maximum no. of intraday steps	P_c autocorrelation probability	P_{matrix} probability f stepping into matrix
Habitat use	9240	90.3 ± 7.5	69.06-100	**0.95**	<0.001	1 ± 0.002	0.08 ± 0.002	-0.08 ± 0.002	-0.01 ± 0.002	**-0.75 ± 0.002**
Step distribution	9240	0.03 ± 0.02	0.009-0.095	**0.14**	<0.001	0.35 ± 0.006	-0.2 ± 0.006	-0.01 ± 0.006 (p=0.16)	0.04 ± 0.006	0.03 ± 0.006
Avg. Max. distance	9240	39.9 ± 8.5	13.15-83.77	**0.90**	<0.001	0.18 ± 0.002	*-0.43 ± 0.002*	*0.41 ± 0.002*	0.26 ± 0.002	0.15 ± 0.002
Study area	9240	4.9 ± 3.4	0-10	**0.75**	<0.001	0.06 ± 0.006	*-0.44 ± 0.006*	*0.46 ± 0.005*	0.22 ± 0.006	*0.61 ± 0.006*
Habitat use	1626	96.1 ± 3.9	81.43-100	**0.97**	<0.001	1 ± 0.004	0.04 ± 0.005	-0.04 ± 0.006	-0.02 ± 0.004	**-0.9 ± 0.005**
Step distribution	1626	0.020 ± 0.006	0.009-0.037	**0.63**	<0.001	0.15 ± 0.02	**-0.88 ± 0.02**	**0.86 ± 0.02**	0.30 ± 0.02	0.14 ± 0.02
Avg. Max. distance	1626	36.7 ± 6.3	15.6-59.7	**0.77**	<0.001	0.41 ± 0.008	*-0.55 ± 0.009*	*0.65 ± 0.01*	*0.46 ± 0.007*	0.23 ± 0.008
Study area	1626	2.5 ± 0.6	1-3	**0.29**	<0.001	0.13 ± 0.03	**-0.76 ± 0.03**	**0.86 ± 0.04**	*0.60 ± 0.03*	*0.65 ± 0.03*

the Spessart (40) and the Palatine Forest (56) and the North-eastern forests (2) and the Erz Mountains (29), though the direct distance between point of release and arrival in a target patch is shorter than between other connected patches.

The model results have shown that patch connectivity is also time dependent, a very important point in modeling dispersal, because in many models time is not explicitly considered and inherently modeled in a number of maximum steps the individual can make. This may sound trivial but has strong consequences for management. Even when mortality was not considered, within a time lap of one year - the normal natal dispersal time of lynx - almost none of the source patches were directly connected. Only when running the simulations for at least 3 years without mortality do we obtain an interconnected patch system as described in the results. After a 10 years run week connections were linked with very low connectivity values due to lack of dispersal habitat (e.g. 6-20, 2-6, 2-29 and 44-56). This time dependency of the patch connectivity shows how important it is that the dispersers survive to settle in target patches, which can in this way play a crucial role for the connectivity of the source patches. It also shows, that connectivity between patches can be enhanced when enough dispersal habitat is available, which recommends investing into land restoration and reducing fragmentation of connected forests that resemble dispersal habitat (*sensu* Simberloff *et al.* 1992).

However, for management implications in Germany it is important to recognise that most of the patches are connected when running the simulations for a long time without mortality. Even when considering natural mortality of 20% per year, we still retain an interconnected patch system. This leads to the result that in Germany it is not only the distribution of dispersal habitat that limits patch connectivity but factors contributing to a high mortality like the dense traffic system. This finding is supported by (Ferreras *et al.* 1992) for the Iberian lynx in Doñana, Spain. In fact, when applying mortality risks on roads we can find that most of the patches are isolated except the patches along the German-Czech border. Road mortality is therefore a very sensitive parameter in the scenarios.

The results are widely held by a previous analysis based on a completely different approach, a static landscape analysis with a GIS where connections between patches were assessed with a cost-path analysis (Schadt, Knauer & Kaczensky 2000; Schadt *et al.* in press). Here the only promising connection of source patches is along the German-Czech border with the Thuringian Forest. In the model a connection to the Thuringian Forest could only be achieved without considering the influence of roads. This backs up the suggestion, that management should concentrate on enhancing a link between these patches, if the already established population along the German-Czech border should have a chance for spreading into other suitable patches in Germany.

This does not mean that there is no future for a lynx population elsewhere in Germany. E.g., many of the source and target patches of the North-eastern forests (2) are connec-

ted, but to which degree these patches have a source-sink dynamic or a metapopulation structure and are viable without immigration can only be assessed with a population viability analysis. In summary, the simulations suggest in accordance with other findings (e.g., Fahrig 2001) that habitat preservation and restoration is important to enhance a more direct connection between the patches. As connectivity has shown to be time dependent, direct dispersal habitat links between patches can increase connectivity. Going hand in hand with this a reduction in road mortality is absolutely necessary, as this was the main factor hindering patch connectivity, independent of time. Very expensive habitat restoration could be useless, if there is no reduction in road mortality.

Proposals for future applications and research

The model can be applied for a variety of assessments of the effects of land use changes (incl. road construction) and management scenarios on landscape connectivity (e.g., White *et al.* 1997), on the use of corridors as enhancing links between patches or not (cf. reviews of Simberloff *et al.* 1992; Rosenberg *et al.* 1997; Beier & Noss 1998; Haddad *et al.* 2000) and also as a basis for analysing neutral landscape models and finding thresholds in fragmented landscapes (Gustafson & Gardner 1996; Keitt, Urban & Milne 1997; With 1997; King & With 2002). On such a basis the model could then be used to derive ecologically scaled landscape indices for lynx that could quickly be applied to other landscapes without having to develop and calibrate a new simulation model (Verboom *et al.* 2001; Vos *et al.* 2001).

Of course, the forecasts from the SEDM can only be used to generate initial qualitative hypotheses on connectivity, because due to lack of independent data the model can not be validated. I therefore strongly recommend to promote field studies analysing dispersal for gaining more insight into dispersal behavior in fragmented landscapes. There is also a strong evidence for sex-biased dispersal, that means females are much more philopatric and disperse smaller distances than males (Waser 1996; Swenson, Sandegren & Söderberg 1998; Perrin & Mazalov 2000). This could also have an important effect on the connectivity of the patches, as the model is mainly based on female dispersal data. However, females are more important for establishing a population and are therefore the limiting factor.

There is a variety of questions that can not be answered with the connectivity model. For example, the long-term viability of a population also depends on genetic effects as causes of extinction (Lande & Barrowclough 1987). Detecting a metapopulation structure can be very important for managing a viable lynx population, as success of reintroductions does not only depend on patch size, but also on extinction and colonisation dynamics of small but locally connected patches (McCullough 1996). The probability of reproduction of an immigrant in a new patch and the effects of genetic stochasticity can only be assessed with demographic population viability analyses (PVA) (Boyce 1992). Given the assumption of more or less isolated patches as referring to the simulation re-

sults, a PVA would also be a necessary requisite to assess the viability inside these isolated patches.

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Appendix 1

Connectivities (%) for the different scenarios. The numbers of the source and target patches are pictured in Figure 10.

Source	Target	Patchsize*	Distance**	Highways/ rivers***	Scenarios 10 years No mortality	Natural mort.	Barrier mort.	1 year No mortality	Natural mort.	Barrier mort.
2	1	287	76	0	5	2				
2	10	210	84	3	2					
2	11	100	108	4	1					
2	12	672	83	3	10	4				
2	13	115	104	3	2					
2	14	305	125	4	2					
2	15	639	91	3	9	3				
2	16	130	127	3	2					
2	22	1120	155	3	2					
2	5	116	36	2	38	20	2	6	5	2
2	7	104	98	3	2					
2	8	187	60	2	18	7				
20	17	132	105	2	4	1				
20	18	307	47	1	21	8	2	1		
20	21	378	66	1	22	7	2			
20	23	295	130	3	2					
20	25	144	120	3	2					
20	26	104	103	2	6	1				
20	27	1256	134	3	2					
20	32	287	148	2	1					
20	34	1676	94	1	4	1				
20	40	1199	175	3	1					
20	6	1047	103	6	2					
20	9	350	91	2	1					
27	17	132	89	1	6	2				
27	18	307	110	2	5	2				
27	20	1566	161	3	1					
27	21	378	95	2	9	3				
27	23	295	30	0	55	31	18	13	11	9
27	25	144	52	0	33	17	9	5	4	4
27	26	104	94	2	7	3				
27	30	536	130	4	1					
27	31	208	99	4	5	2				
27	32	287	135	3	4	1				
27	33	108	75	2	15	5				
27	34	1676	146	4	2					
27	35	764	84	1	17	7				
27	36	110	145	4	2					
27	40	1199	123	2	5	1				
27	42	120	165	4	2					
27	43	471	150	4	3					
27	45	665	160	4	1					
29	24	177	118	2	1					
29	28	473	105	0	11	4	2			
29	32	287	179	2	1					
29	34	1676	73	2	15	6				
29	37	185	67	0	27	13	6	2	2	
29	38	123	155	2	1					
29	39	310	51	0	28	12	1	1	1	
29	41	332	96	0	13	5	1			

29	44	226	88	0	14	4				
29	46	220	147	0	3					
29	47	154	141	1	3					
29	48	105	161	0	2					
29	49	1849	136	0	4	1				
29	57	-	100	-	8	3				
34	18	307	123	2	3	1				
34	20	1566	94	1	4	1				
34	21	378	84	2	13	6				
34	23	295	165	4	1					
34	25	144	115	4	4	1				
34	26	104	71	3	13	5				
34	27	1256	148	4	2	1				
34	29	1674	122	2	6	2				
34	32	287	49	1	29	13	4	3	2	2
34	37	185	106	1	7	3				
34	38	123	84	1	7	3				
34	39	310	146	1	3					
34	40	1199	74	2	20	7	1			
34	41	332	128	1	5	1				
34	44	226	180	1	1					
34	45	665	150	4	3	1				
34	46	220	144	1	2					
34	47	154	173	2	1					
40	18	307	192	4	1					
40	21	378	134	2	4	1				
40	23	295	178	2	1					
40	25	144	125	2	3	1				
40	26	104	109	3	6	2				
40	27	1256	127	2	3	1				
40	32	287	49	1	56	31	8	10	8	5
40	34	1676	106	2	13	4				
40	35	764	73	3	2					
40	38	123	70	2	6	2				
40	45	665	29	2	52	31	5	14	12	4
40	53	1934	128	5	2					
49	29	1674	120	0	5	1				
49	37	185	130	0	4	1				
49	39	310	81	0	15	5	3			
49	41	332	97	0	8	3				
49	44	226	34	0	32	18	10	7	6	4
49	46	220	135	2	3					
49	47	154	88	1	9	3				
49	48	105	20	0	67	46	47	29	27	29
49	50	105	116	3	3					
49	57	-	66	-	13	6				
49	58	-	148	4	2					
53	35	764	146	3	1					
53	40	1199	136	5	2					
53	42	120	125	3	2					
53	43	471	145	3	2					
53	45	665	84	3	4	1				
53	51	137	36	2	21	11		3	3	
53	52	5232	54	2	23	9				
53	55	1040	63	1	45	21	4	3	2	1
53	56	4957	56	2	18	8				
53	58	-	175	4	2					
53	59	-	150	2	5	2				
55	51	137	102	2	4	1				

		*	**	***						
55	52	5232	60	2	17	6				
55	53	1934	16	1	80	58	42	40	35	31
55	56	4957	130	2	4					
55	58	-	117	2	6	2				
55	59	-	60	1	28	13		2	2	
56	27	1256	145	5	1					
56	30	536	160	3	2					
56	31	208	125	3	3	1				
56	33	108	96	3	5	2				
56	35	764	56	3	16	7	1			
56	36	110	108	2	4	1				
56	40	1199	109	6	1					
56	42	120	40	1	23	11	3	2	2	
56	43	471	65	1	23	9	1			
56	45	665	58	3	2					
56	51	137	54	-	26	12		2	2	
56	52	5232	41	0	94	67	39	42	38	29
56	53	1934	65	2	10	3				
56	55	1040	148	2	2					
56	59	-	216	2	1					
6	20	1566	101	3	2					
6	3	146	38	1	46	25	8	8	7	5
6	4	115	42	1	25	11	3	2	2	
6	7	104	122	2	2					
6	9	350	84	1	9	4				

*   patchsize (km²) of the target patch. Patch size was only calculated when the patch is inside Germany.

**   euclidean distance (km) between source and target patch

***   least number of highway and river crossings between patches (note that there is additional mortality on roads!)

CHAPTER IV

The population simulation model

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

Abstract

Lynx are slowly recovering in Germany after an absence of about 100 years and additional reintroduction programs are launched. Suitable habitat for populations is distributed in different degrees of fragmentation in Germany, and it is not known, which patches could host a viable population or contribute to the potential spread of a lynx population.

I combined spatial and demographic scenarios with a spatially-explicit population simulation model to predict viability and colonisation success of the populations in the different patches and to give guidelines for species reintroductions. The spatial basis for the model is a validated habitat model for the lynx in Germany consisting of barriers, matrix, dispersal and breeding habitat. The dispersal module stems from a calibrated dispersal model, and the demographic module uses published information on lynx' life history.

The results indicate that in principal a viable population is possible in Germany, but that the source patches are not interconnected except along the German Czech border, and that about 10 females and at least 3 males are required for a starting population that is likely to become viable. The survival rate of adults with territories was the most sensitive parameter, and the best management strategy for the success of a reintroduction would be reducing mortality of residents in the source patches.

Introduction

Species reintroduction is increasingly seen as a valuable tool for conservation, e.g. to save species from extinction or to reinstate species that have become locally extinct (Leaper *et al.* 1999). Due to a change in people's attitude towards wildlife in the middle of the 20th century, species reintroductions have been increasingly considered (Breitenmoser & Haller 1987b; Wotschikowsky 1992; Böer, Smielowski & Tyrala 1994; Frković 1998; Leaper *et al.* 1999; Sarrazin & Legendre 2000; South, Rushton & Macdonald 2000; Breitenmoser *et al.* 2001; O'Toole, Fielding & Haworth 2002). In human-dominated landscapes of Germany, reintroductions of lynx have been controversially and vehemently discussed since the 1970ies (van Acken & Grünwald 1977; Plän 1988; Goßmann-Köllner & Eisfeld 1989; Kluth, Wotschikowsky & Schröder 1989; Thor & Pegel 1992; Pohlmeyer 1997a). A recent example is the release of lynx into the Harz forest in 2000 (Wotschikowsky, Kaczensky & Knauer 2001). Lynx are also slowly re-colonising the Bavarian Forest and the adjacent low mountain ranges due to a reintroduction of lynx in the Bohemian Forest on the Czech side (Figure 10; chapter III this thesis).

Carnivore reintroductions in particular are extremely lengthy, costly and complex processes (IUCN/SSC 1995), and there is a clear need to improve the efficiency of carnivore reintroductions (Breitenmoser *et al.* 2001). The future development of a reintroduced lynx population and the success of potential reintroduction initiatives are difficult to assess because of the great spatial requirements of a lynx population and because the dynamics of small expanding populations in fragmented landscapes are not well understood. Questions such as for the minimum number of individuals that should be released and the influence of factors leading to a higher mortality on the population development remain unanswered. For example, the increased killings by humans in fragmented landscapes due to habitat contraction and modification, poaching and road mortality are major factors contributing to the failure of reintroductions (Kaczensky *et al.* 1996; Trombulak & Frissell 2000; Ferreras *et al.* 2001), but their consequences for population dynamics are difficult to assess without advanced modelling tools.

Another aspect is a change in the land use scheme on the development of a population. Afforestation of set-aside land could increase the dispersal medium for subadult lynx, and the construction of green-bridges across highways could minimise the mortality, thus enhancing a linkage between populations which could avoid inbreeding depression or even lead to the colonisation of other patches. On the contrary, additional highway constructions could lead to a higher mortality and thus making the exchange of individuals either impossible or even the habitat patch unsuitable for a viable population.

The assessment of human impact on the survival of species (such as fragmentation due to roads, other landscape changes) increasingly relies on population viability analyses (PVA), which use demographic models incorporating various aspects of the ecology and

behaviour of the species (Boyce 1992; Akcakaya & Raphael 1998). Despite some problems (Beissinger & Westphal 1998; Wiegand, Revilla & Knauer 2002) spatially explicit population simulation models are virtually the only means of finding an answer for distinct questions of population development under different landscape and demographic scenarios. For this purpose generic population viability analysis tools like VORTEX or RAMAS/GIS would be too unspecific (Akcakaya 1995; Brook, Burgman & Frankham 2000b).

In this article, I perform a PVA with a spatially-explicit population simulation model to answer the question under which scenarios a lynx population would be viable in Germany. The aim of the study is to formulate management strategies and to give guidelines of how habitat patches should be evaluated before releasing animals to follow the demanded improvement of future species reintroductions. For this, I test the impact of realistic land use changes and demographic scenarios (i.e. different mortality scenarios) on the development of the population and hence on reintroduction success. In this context, questions such as of the requirements for a successful spreading (e.g. size of suitable habitat, numbers and sex of individuals) and of connectivity among the populations were also of special interest. The specific questions are:

- Can the patches sustain a viable lynx population, and if so,
- what would be the minimum release population?
- What would be the most efficient (economic) ratio of females vs. males?
- Can other patches be colonised?
- If not, under which landscape scenarios (increase of dispersal habitat, decrease of mortality, e.g. by green-bridges) can a colonisation be achieved? Or is a connected lynx population unrealistic under current land development prognoses?

I exemplify these questions explicitly for Germany. I am interested in the population development in the Harz Forest and a possible linkage via the Thuringian Forest with the population in the Bavarian Forest. The Thuringian Forest, often cited as having a key position in the network of suitable lynx habitat in Germany – could be colonised from the Harz Forest or from the already established population in the Bavarian Forest. Additionally, I assess the population development in other patches considered as suitable, e.g. the Black Forest and the Palatine Forest (Figure 7).

Methods

I use an individual based and spatially explicit model to simulate the spatio-temporal population dynamic of lynx in Germany and to test their viability under the different demographic and land use change scenarios. The basis for the model is a GIS habitat suitability map for Germany. Model rules and parameters are derived from published data of lynx demography in Europe (Table 10). Sensitivity analysis was conducted to assess the influence of model parameters on the model results against a realistic reference scenario. Sensitivity was considered to be high, when the deviation from the reference scenario was > 20% (Huth, Ditzer & Bossel 1998).

I did not include environmental stochasticity (e.g. good years with a higher birth probability and vice versa) as the roe deer density in Germany is very high, so that food limitation is not assumed to play a role in population development (cf. chapter II this thesis).

Life history of Eurasian lynx

In central Europe, lynx are mostly bound to forested habitat, and their main prey are ungulates, especially roe deer. Lynx are solitary living animals except for females with the offspring of the year. Their home ranges (or territories) are intrasexually exclusive, and possession of a home range seems to be required for adults to reproduce (Ferreras *et al.* 1997; Breitenmoser *et al.* 2000). Generally, adult males share their home ranges with one or two females. Males usually occupy larger home ranges than females.

Mating takes place in spring, and litter sizes are on average 2 kittens (Breitenmoser-Würsten *et al.* 2001). Subadults leave their mother territory at an age of about 10 months to search for their own home ranges (Zimmermann 1998). Adults can also disperse when breeding areas are saturated (Ferreras 1994 after Gaona, Ferreras & Delibes 1998). Mortality during dispersal is higher than for resident individuals with total annual mortality rates of about 50% (Ferreras *et al.* 1992; Jedrzejewski *et al.* 1996; Gaona *et al.* 1998; Breitenmoser-Würsten *et al.* 2001; Ferreras *et al.* 2001).

Females are usually mature at the age of two years. Lynx can be sexually active almost until their expected lifetime. In nature, lynx were reported to live up to 17 years (Breitenmoser *et al.* 2000). Lynx suffer high mortality rates due to human-related factors such as poaching and road casualties, resulting in total annual mortality rates between 20 and 30%. In protected areas, mortality rates for residents average about 10% (Ferreras *et al.* 1992; Jedrzejewski *et al.* 1996; Zimmermann 1998; Breitenmoser-Würsten *et al.* 2001).

Table 10. Model parameters for each submodel. The mortality probabilities for each model step are given in each submodel and were assessed with indirect parameter adjustment to reflect published data on annual mortality rates. The values of the habitat suitabilities are explained in the text (cf. "Landscape submodel").

submodel	symbol	Published value	model parameter value or range
demographic submodel			
■ no. of cells for non overlapping core areas of female home ranges	CA_f	70 (SD ±30) km² [1]	40 - 100 km²
■ no. of habitat cells ($p > 0.5$) of non-overlapping home ranges of			
females	HR_f	85 (SD ± 38, n = 4) [2]	55-127 km²
males	HR_m	119 (SD ± 7, n = 3) [2]	
■ males overlapping females	RES_m	1 or more [1], 1-2 [6,7]	up to 3
■ surviving subadults starting to disperse per reproductive female		1.6 [7], 1.0-1.1 [7]	1 - 2
■ sex ratio of kitten	$ratio_s$	1:1 [3,7]	1:1
■ reproduction rate (= prob. of giving birth)	P_{birth}	0.75 [3], 0.88 [7]	0.5, 0.75, 0.95
■ mortality rates of residents	MR_{res}	0.6 ± 0.12 SD; 0.8 ± 0.12 SD [4] 12% [3] p.a., 10-30% [4] p.a. 13% [7] p.a. Jura Mts., 22-28% [7] p.a. Alps, 13-19% [8]	0.07, 0.18, 0.25 (results p.a. cf. Table 11)
■ number of released males and females	N_{rel}	-	1-18,20,22,25,30
dispersal submodel			
■ correlation factor (dispersal)	P_C	[5]	0.5
■ probability of stepping into matrix	P_{matrix}	[5]	0.3
■ maximum number of intraday steps	s_{max}	[5]	45
■ exponent of step distribution of equation (2)	x	[5]	11
■ mortality rates of dispersers	MR_{disp}	55% [4] p.a., 44% [7] p.a. Jura Mts., 56-60% [7] p.a. Alps, 19-38% [8]	(results p.a. cf. Table 11)
■ daily mortality rate of dispersers	M_{daily}	[5]	0.0001, 0.0006, 0.0014
■ mortality rate per crossing event of highway/ river	$M_{highway}$	[5]	0, 0.09, 0.14
road	M_{road}	[5]	0, 0.0009, 0.0019

[1] Breitenmoser et al. 1993; [2] Schadt et al. 2002 or chapter II this thesis; [3] Jedrzejewski et al. 1996; [4] Gaona et al. 1998; [5] cf. chapter III this thesis; [6] Breitenmoser et al. 2000, [7] Breitenmoser-Würsten et al. 2001: Please note that the authors state that their statistics are very weak due to small sample sizes; [8] Andrén et al. 1997

Study area

Germany comprises an area of about 358 000 km² with an average human population density of 230 inhabitants per km², which drops to about 100 inhabitants per km² in places such as the low mountain ranges (e.g. Black Forest, Palatine Forest, Thuringian Forest). About 30% of the total area is forested, with large local differences (e.g., Bundesland Hessen with about 41%, Bundesland Schleswig-Holstein with about 10%, BVEL 2001). The forests are clustered in areas formerly unsuitable for agricultural activity in the low mountain ranges and in areas with poor soils in the north-east. In the last 40 years forest areas increased by 1.2% of the total area, which refers to about 500 000 hectares (BVEL 2001). 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. I included neighbouring forest areas in Poland, the Czech Republic (e.g. Bohemian Forest), France (e.g. northern Vosges Mountains) and Belgium in the large-scale study area (Figure 7).

The model components

Landscape submodel

I obtained the habitat suitability map for resident individuals by logistic regression with a mesh size of 1 km², as described in (Schadt *et al.* 2002; chapter II this thesis). The model contained only one variable, the proportion of extensively used areas in a 5 km circular neighbourhood. The landscape map gives the habitat suitability HS of a cell. The habitat types can be summarised as breeding, dispersal, matrix and barrier habitat. Breeding habitat are areas with non-fragmented forest and other natural and semi-natural land use types with a p-value above 0.5 as calculated in the logistic regression model (HS = 4). Any forested area as well as breeding habitat is dispersal habitat (HS = 3). Barriers consist of urban areas and lakes, and are never used (HS = 0). The remaining areas, like pastures and agricultural areas, are summarised as matrix, which is not strictly avoided by dispersing lynx, but only used occasionally (HS = 2).

In order to simulate the effect of roads on mortality, I created a second map with linear elements such as main roads, highways and main rivers (> 100 m wide). For simulating connectivity I define as source patches the major patches of special management interest (bigger than 1000 km²) and as target patch each suitable area bigger than 100 km² (Figure 10). This is the average home range size of a female lynx in the Swiss Jura Mountains (Breitenmoser *et al.* 1993). Patches separated by gaps of 1 km were considered as one patch, as this is supposed to be the distance that lynx can perceive as connected (Haller & Breitenmoser 1986). Altogether, I obtained 59 patches, of which 11 are source patches ((2) North-eastern forests, (6) Lüneburger Heath, (20) Harz Forest, (27) Rothaar Mountains, (29) Erz Mountains, (34) Thuringian Forest, (40) Spessart,

(49) Bavarian Forest, (53) Northern Black Forest, (55) Southern Black Forest, (56) Palatine Forest; the numbers in parenthesis refer to the number of the patches; Figure 10). Suitable patches outside Germany connected with suitable patches inside, e.g. the Bavarian Forest with the Bohemian Forest, were also considered in the study area (cf. *"Study area"*). Animals leaving the study area in the simulations are deleted because emigrated animals do not further influence population development. I did not consider re-immigration of these individuals either.

Population submodel

One simulation run (Figure 14).— At the beginning of each model time step (year) we determine the number of resident males and females and the number of dispersers. All nonresidents older than one year disperse (rule 1) and search for home ranges (rule 2). The spatially explicit processes of dispersal and home range selection in the model depend upon local habitat quality, as perceived by individual lynx as they move through the landscape. As a consequence, these processes are determined by a set of rules, which take into account local habitat quality. If dispersing individuals survive they settle or continue dispersal in the next year. Next, we decide for each resident female older or equal 2 years and overlapped by a male territory whether these females reproduce (rule 3). In the final step we update the demographic variables for each surviving individual (age and status, i.e. disperser or resident). Each parameter set is repeated 100 times.

Plausible parameter ranges.— The demographic parameters of the model are mainly based on published data from Switzerland, Spain and Poland. The data are based on long-term field studies of a reintroduced lynx population in the Swiss Jura Mountains (Breitenmoser & Baettig 1992; Breitenmoser *et al.* 1993) and the Swiss Alps (Haller & Breitenmoser 1986; Haller 1992; Breitenmoser-Würsten *et al.* 2001) and a native population of lynx in the Białowieża Primeval Forest (Jedrzejewski *et al.* 1996; Schmidt, Jedrzejewski & Okarma 1997). Data from Spain are also based on long-term field studies of the Iberian lynx (Lynx pardinus, Gaona *et al.* 1998; Ferreras *et al.* 2001). Though this is a different species, I use published information to constitute the range of the model parameters. Model rules include detailed information about life-history attributes, family structure, mortality rates and reproduction.

Mortality rates are influenced by the status of the animal (e.g. disperser or resident). I introduced three different schemes where death can occur for a simulated individual (mortality scheme) to include the influence of the fragmented landscape realistically: 1. A daily mortality probability for dispersing lynx, 2. a mortality probability per linear barrier (road, highway, river) crossing event for dispersers, and 3. an annual mortality probability per resident individual (Figure 15).
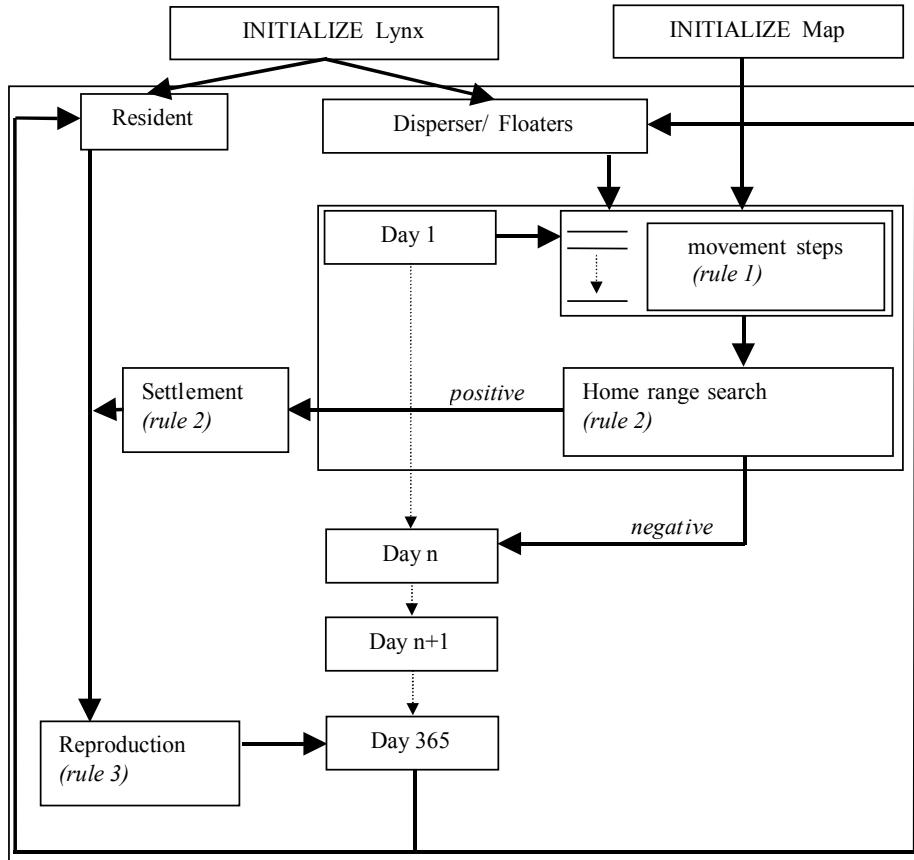
Figure 14. Flow chart of one year iteration in the spatially explicit simulation model. The rules are explained in the text.

Mortality parameters for each scheme were adjusted for the Harz Forest with indirect parameter assessment to produce a plausible range for annual mortality rates as known from literature (cf. chapter III this volume). I test 9 different mortality scenarios (low (~ 10%), medium (~ 20%) and high (~ 30%) total annual mortality for residents and low (~ 30%), medium (~50%) and high (~ 70%) total annual mortality rates for dispersers each, Table 11). Please note that for dispersers the mortality rates can change due to differing road and highway densities in the different patches.

Rule 1: Dispersal. — By definition, starting (released) animals are dispersers as long as they do not occupy a territory (cf. rule 2). Otherwise dispersal starts in the second year after separation of the mother. I did not distinguish dispersal rules of males or females. For movement rules cf. "*dispersal submodel*".

Rule 2: Settlement. — I use two different home range selection mechanisms for males and females. Females are the basic unit in the model that react to the landscape structure, because they have more detailed objectives for home range selection (e.g. no
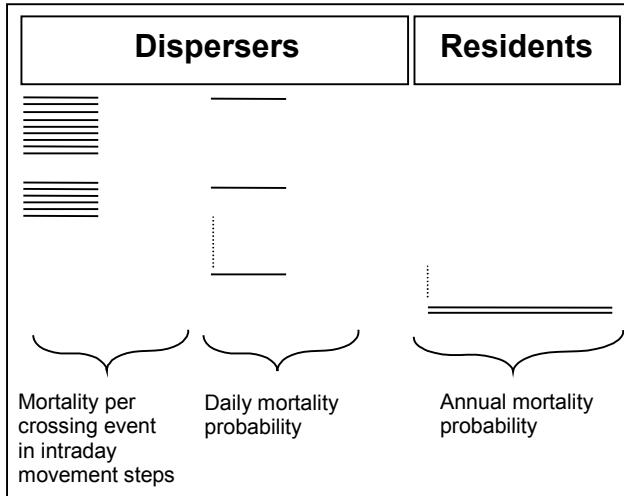
Figure 15. Model time steps and different mortality rates per time step and lynx's status. I use three different time resolutions: years for the main processes of the demographic submodel, days for the mortality during dispersal and home range searching behaviour and intraday steps for the movement direction and mortality per linear barrier crossing event.

highways or rivers inside, as known for other large carnivores, e.g. Kaczensky *et al.* 1996). Males are overlapping contiguous female territories, i.e. in the model they search for occupied female home ranges. For each time step (day), I applied the procedures for territory selection to dispersing individuals.

Once a female finds a cell of breeding habitat (HS = 4), it searches the area for contagious cells of HS = 4. If it finds at least 85 ± 38 cells (= km²) of HS = 4, it can occupy a home range (after analysis of female lynx territories with data of Breitenmoser *et al.* (1993, n = 5, Table 10). That means, for each individual a random number of cells within the given range is diced to include stochasticity in home range size. A simulated female then has to use this amount of cells as territory size. Once occupied, home range cells can not be used by other females. In unoccupied areas the female that "comes first" has the best chance of occupying a territory. Shifts of territories were not considered in the model, as lynx normally have fixed home ranges (Breitenmoser *et al.* 1993). The male search strategy is for occupied territory cells of neighbouring females. Once a male has occupied a territory belonging to females, this female is not accessible for other males (following the intra-sexual exclusivity of territories, Breitenmoser *et al.* 1993). Males can overlap up to three females in the model. The home range size (non-overlapping cells of breeding habitat) of male lynx is in the range of 119 (SD ± 7) km² (after analysis of male lynx territories with data of Breitenmoser *et al.* (1993, n = 3, Table 10). Please note that the male home range size was not a parameter in the model but measured as a control variable in the model results.
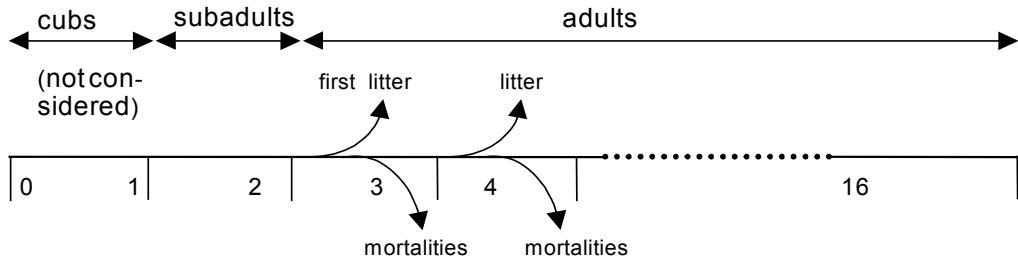
Figure 16. Life history traits of lynx as considered in the model. Cubs are staying the first year with the mother and this life stage is not explicitly modelled. Subadults are starting as dispersers, and adults can either be dispersers or residents. Females can only reproduce when they are territorial and when a male is occupying their territory. The maximum age is 16.

Rule 3: Reproduction. — Only females occupying a territory (age ≥ 2) and overlapped by a male can reproduce. Field studies show that litter size can be up to 4 cubs, but the kitten mortality rate is at least 50% (Breitenmoser *et al.* 1993; Jedrzejewski *et al.* 1996). Thus, about one or two subadults per reproductive female start dispersal in their second year (Figure 16). Therefore, I set the probability of having one or two dispersers starting to 0.5 and the sex ratio to 1:1 (Jedrzejewski *et al.* 1996). The probability of reproduction of each female per year was 0.75 (Jedrzejewski *et al.* 1996).

Dispersal submodel

The smallest space and time unit in the dispersal model is one movement step. I assume that individuals survey their neighbourhood and that their movement steps are based on this information. Basically, the next cell is chosen in preference for dispersal habitat and avoidance of matrix. If the neighbourhood of a dispersing lynx, comprising the origin cell and its 8 neighbours, contains only matrix or dispersal habitat cells, then the probability of choosing one of these cells is random (i.e., 1/9). However, if the neighbourhood is a mix of dispersal habitat and matrix, I consider preference of dispersal habitat in the following way: Within the neighbourhood the number of matrix cells n_{mat} is counted. The probability of leaving dispersal habitat P_{leave} is then dependent on the number of matrix cells around the origin cell multiplied with a factor P_{matrix} (e.g., $P_{matrix} = 1/(9-n_{barr})$ for a random walk), where n_{barr} is the amount of barrier cells never used:

$$P_{leave} = n_{mat} \cdot P_{matrix} \qquad \text{eqn 1.}$$

I included a correlation factor P_c for keeping the previous direction within a day, which is supported by data of the Iberian lynx (E. Revilla, unpublished analysis). P_c gives the probability that the next cell is in the same movement direction, otherwise the next cell is chosen randomly. The first direction of every next day is also chosen randomly (E.

Revilla, unpublished analysis). The hierarchy is preference of dispersal habitat over correlation in movement direction.

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

$$P(s) = \varphi \cdot (1-(\frac{s-1}{s_{max}-1}))^{x}$$
eqn 2

with an exponent x and parameter s_{max} that gives the maximum number of steps that a dispersing lynx can cover during one day and a normalisation factor φ. $P(s)$ is a good descriptor of the empirical distribution of daily movement distances. The parameter values were taken from a calibrated dispersal (mean of all suitable parameter combinations) model for the Eurasian lynx (Table 10, chapter III this thesis).

Management scenarios

Population scenarios

Scenario 1: Evaluation of the lynx reintroduction schemes in the most important source patches.— I release lynx in the patches considered for reintroductions (Black Forest (53), Palatine Forest (56), Bavarian Forest (49), Harz Mountains (20), North-eastern forests (2) and Thuringian Forest (34); Figure 10). Under the different mortality scenarios I want to assess

a) the minimum number of female and male lynx required for a successful reintroduction. I define this "minimum release population" (MRP) as the population size where the chance of survival is > 95% (measured as the percentage of extinction P_{ext} < 5%) if it were to survive at least 50 years. As females are the basic unit, I increase the number of females and keep the number of males fixed to the amount of released females (Table 10). To assess the minimum number of males needed for a MRP, I use the obtained minimum amount of females necessary for a MRP as a fixed parameter and vary the number of males.

b) isolation or connectivity of the patches, expressed as the probability P_{col} of settling and reproducing in other patches. The population development in other patches is measured as the arithmetic mean of the observed exponential rate of increase $\bar{r}$ during population persistence time T_P of all simulation runs n. t is time, N_{t+1} is the number of animals (residents + new-borns) in a certain patch in the current year, and N_t the number of animals of the previous year in the same patch (geometric mean within the time of persistence; Caughley 1980):

$$\bar{r} = \frac{\sum\limits_{1}^{n} \dfrac{\sum\limits_{t}^{T_P} \ln\left(\dfrac{N_{t+1}}{N_t}\right)}{T_P}}{n} \qquad\qquad \text{eqn 3}$$

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

$$\bar{\lambda} = \overline{e^r} \qquad\qquad \text{eqn 4,}$$

the population has increased. I used the z-score to calculate the proportion of the one-tailed normal curve that lies beyond (i.e. is more extreme than) a given normal deviate, with $Z = (\bar{r}-\mu)/\sigma$ (Zar 1999); in this case it was the proportion of the curve that lies beyond the stable state of population development (i.e. $\mu = 0$, no growth). I distinguish different probability classes of increasing population trend P_{col}, that is (1) >75%, (2) >50 % and <75%, (3) >25% and <50%, (4) >5% and <25%, (5) >1% and <5% and (6) <1%. For example, probability classes of (2) have in more than 50% a positive population trend. Probability classes of (6) indicate, that at least one female in 50 years and 100 repeated simulations has settled in the patch ($p = 0.0002$). Please note that these are extreme cases. I define patches linked with probability class (6) as connected.

Scenario 2: A confirmation of the model scenarios with the population spreading along the German-Czech border.— In the early 1970ies lynx were illegally released in the Bavarian Forest, but the exact number is not known. Estimates range between 5 to 9 individuals. These individuals have been tracked since 1985 and could have supported the lynx population released on the Czech side (Zachariae, Elstrodt & Hucht-Ciorga 1986), where 18 lynx had additionally been released into the Bohemian Forest in the 1980ies. The joined population is believed to have increased to about 70 resident individuals along the German-Czech-Austrian border, but recently with a declining tendency on the German side. Irregular occurrence of lynx is reported up to the Erz Mountains (29), the Fichtelgebirge (37), the Pegnitz region (41) and Outer Bavarian Forest (47 and 48), whereas in the Oberpfälzer Forest (39 and 44) even reproduction has been confirmed, but more towards the Czech side (Wölfl *et al.* 2001). Animals sighted in the Erz Mountains (29) could also be remnants from a small population in the Elbsandsteingebirge (28) that was established in the 1950ies probably due to immigration from the Slovakian Carpathians (Červený, Koubek & Anděra 1996).

To assess whether the model parameters and processes point into the right direction and whether the model reflects the current development of the lynx population in this region, I define criteria from the knowledge about the above mentioned population development in the Bavarian/ Bohemian Forest. To this end, I release 15 females and 10

males there, run the simulation for 20 years, which resembles the total number of released lynx in that area and the same time span. Please note that I only consider a patch to be colonised when a female lynx has reached the patch, as simulated males only establish home ranges when they have found a resident female. Thus, irregular sighting data can not be compared with the model outcome, only the places of confirmed reproduction. The criteria for comparing the model results with the known development are, that (1) the simulated lynx population did not go extinct, and that (2) reproduction has occured in the Oberpfälzer Forest (patches 39 and 44).

Landscape scenarios

Scenario 3: Increase in dispersal habitat.— The present tendency in land tenure and agriculture predicts that within the next 50 years forest areas will increase, as there was a tendency to increase up to 1.2 % in the last 40 years (BVEL 2001). I test for an increase in dispersal habitat of 3%, 10% and 20% of the total study area having an influence on connectivity and population development (cf. Scenario 1, Figure 17). As an example, I study the effects for a simulated population released in the Thuringian Forest (34) to assess how connectivity to other patches is changed when landscape changes. The Thuringian Forest is a patch located in the centre of Germany and therefore has a key position in a possible network of connected patches.

The maps of landscape change were calculated by summing the total amount of the cells in the study area. Increase in dispersal habitat was calculated as the proportion of the total amount of cells. Then cells with dispersal habitat were randomly chosen in the basic map, and if they had matrix cells in their neighbourhood, a matrix cell was changed into a dispersal habitat cell. With that, I simulated a spreading of forest in areas where there is already forest existing.

Scenario 4: Permeability of highways due to underpasses, green-bridges and viaducts.— For testing the influence of green-bridges or underpasses on patch connectivity I assume no mortality for crossing a highway or river. To assess the recolonisation success of the Thuringian Forest (34) via the Bavarian Forest (49) and the Harz Forest (20), I apply this scenario for a population in the Thuringian Forest under the current distribution of dispersal habitat (Figure 17).
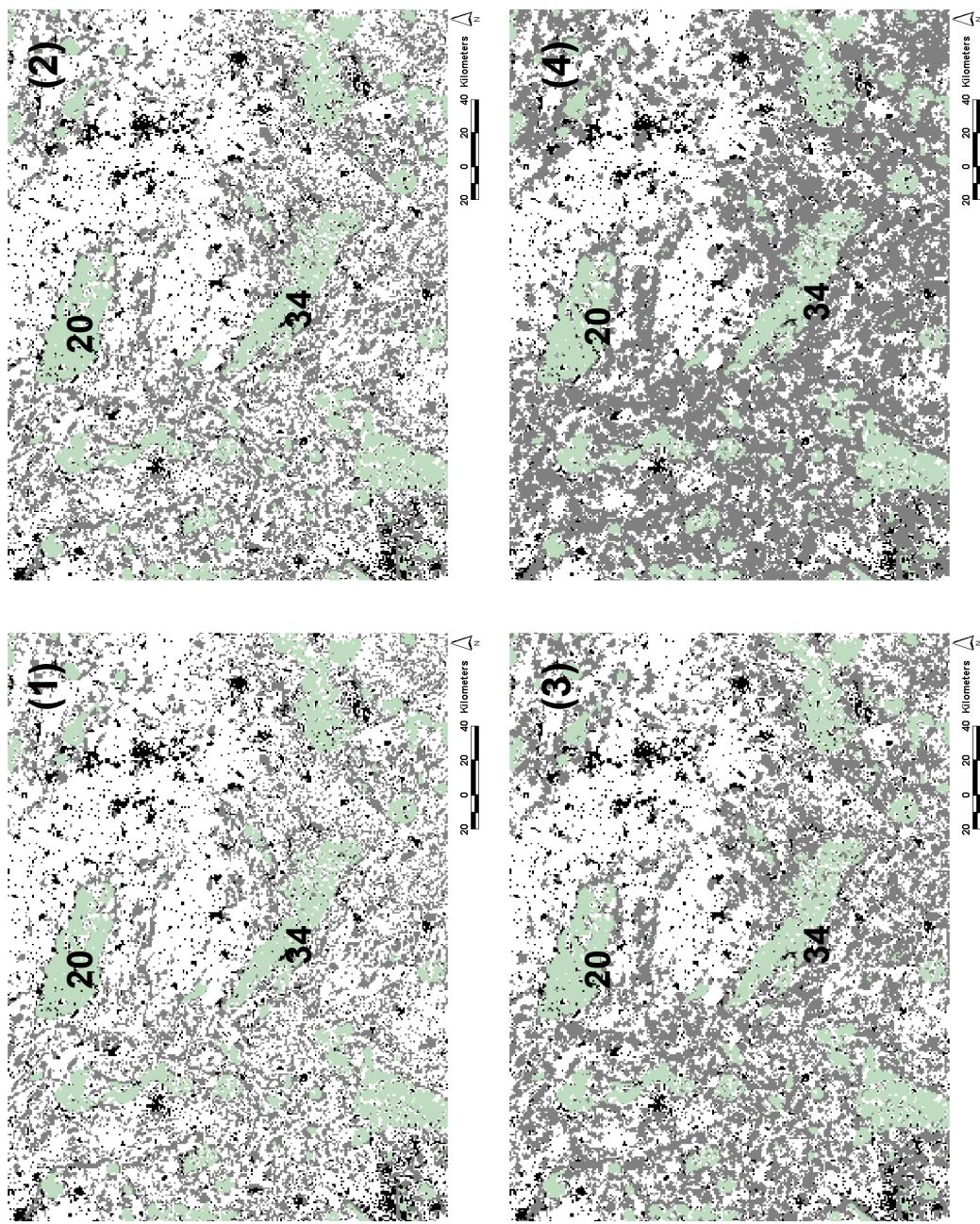
Figure 17. Increasing amount of dispersal habitat (medium grey). White is matrix, black are urban areas, and light gray is breeding habitat. (1) Current distribution of dispersal habitat, (2) increase in dispersal habitat of 3% of total study area, (3) increase of 10% and (4) increase of 20%.

Table 11. Simulated mortality rates resulting from the different mortality scenarios for the Harz Forest Mountains under given landscape conditions, when releasing more than 8 females and 8 males. Birth probability was set to 0.75. Scenario 5 for example, with a total annual mortality rate of 37 % resembles a realistic mortality scenario known for example from Poland or Spain, where poaching and road casualties occur.

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

Results

Sensitivity analysis

For the sensitivity analysis I simulated an increasing amount of females and males in the Harz forest with different parameter values for reproduction and for the nine mortality scenarios (Table 10). I took mortality scenario 5 (P_{birth} = 0.75, MR_{res} = 20%, MR_{disp} = 50%; Table 11) as reference scenario, because it yielded the current knowledge on overall mortality rates (cf. *"Plausible parameter ranges"*).

Deviations from the 20% envelope occur with different mortality rates for resident individuals and different birth rates. If more than five females and males (or the MRP) are released, also the mortality rate of dispersers plays a role (Figure 18), as dispersers have to fill the gaps in the reproducing part of the population, especially when birth probability is low. The difference in extinction probability is not so high in the scenarios 2, 5 and 8 (fixed resident mortality but increasing dispersers' mortality) with a high birth probability (Figure 18c).

A higher birth probability of 0.95 affects the minimum number of females needed for establishing a viable population in thus that it is decreased to 6 males and females (Figure 18). For a birth probability of 0.5 only mortality scenarios with very low mortality rates for residents and dispersers show a trend to reach the MRP with at least 10 to 20 males and females. Therefore, I can state that the survival of residents is the most important factor for establishing a viable population, which is also held by analyses of other predator species such as bears, cheetahs, badgers and vultures (e.g. Crooks, Sanjayan & Doak 1998; Gaona *et al.* 1998; van Appeldoorn *et al.* 1998; Sarrazin & Legendre 2000). In extreme cases, i.e. a population with a low birth probability or a higher resident mortality, the survival rate of dispersers plays an important role for the overall viability of the population.
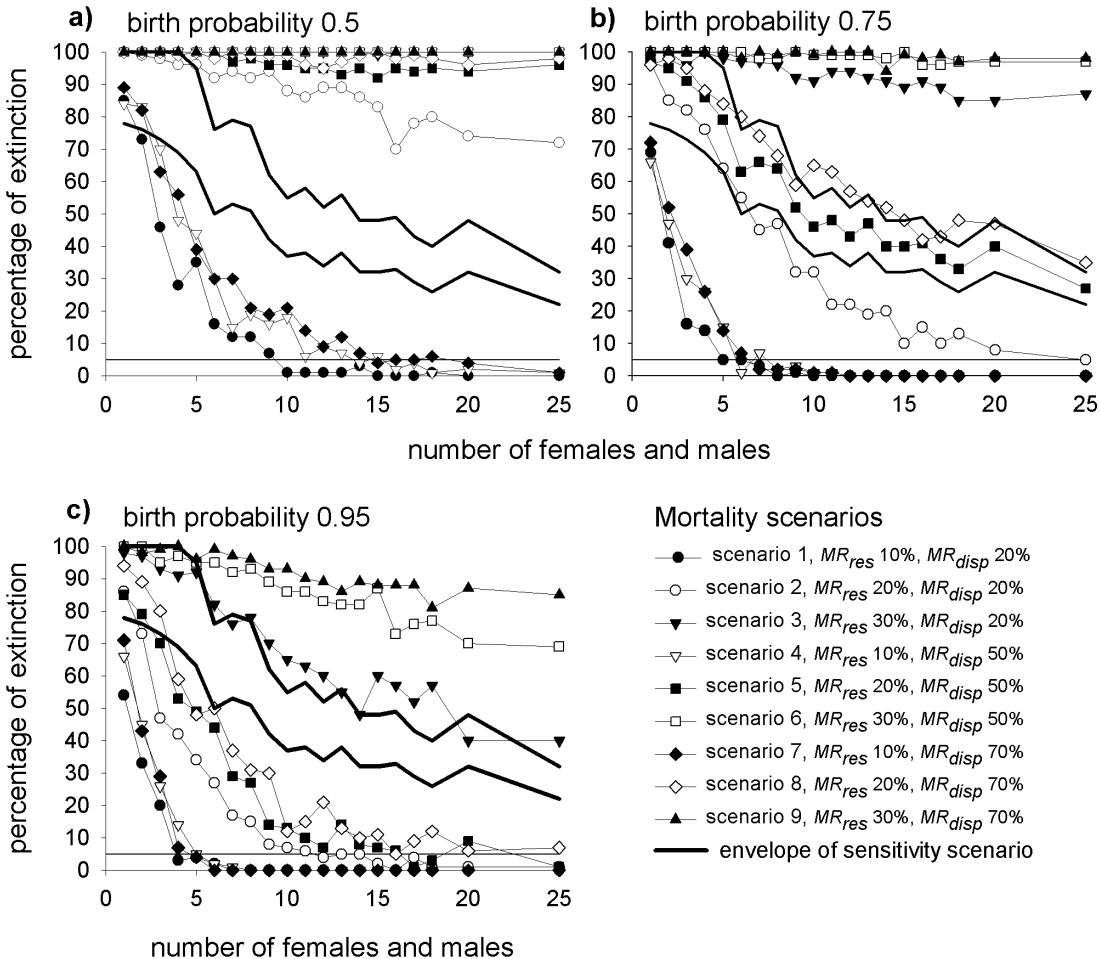
Figure 18. Extinction probability of the Harz population under different mortality scenarios and birth probabilities when the same number of females and males was released. Only scenarios having low mortality values for residents MR_{res} reach a viable population within a time horizon of 50 years. The envelope of the reference scenario 5 (b) shows that the most sensitive parameters are the birth rate and mortality rate of residents. The lower the birth probability, the more important becomes the initial number of released animals.

Population Scenarios

Scenario 1: Evaluation of the lynx reintroduction schemes

a) Assessing the minimum release population (MRP). — If an overlap of one to three female territories per male is assumed, the Harz Forest (20) has a carrying capacity of 15 ± 2 female resident lynx and 9 ± 1 male resident lynx. This results in a density of about 1 female resident lynx per 100 km² of breeding habitat, which also holds for the other source patches with the exception of the north-eastern forests (2) (Table 12). The later is fragmented by two highways.

For low mortality rates of residents in the Harz Forest (20) (mortality scenarios 1, 4, 7; Table 11 & Table 12) and a realistic birth probability of 0.75 per resident female, the probability of extinction drops relatively fast below 0.05 with an increasing number of females, i.e. for at least 8 released females (and 8 released males) I reach the requirements for a MRP. Mortality rates of dispersers did not play a role for the viability of the population if the resident mortality was very low (Figure 18b). With less than 8 lynx released in pairs (i.e. 8 females and 8 males) the maximum growth rate was not met due to demographic stochasticity (Figure 19). Lynx pairs releeased in addition to 8 pairs did not have an influence on population development. The optimal sex ratio for scenarios reaching a MRP (scenarios 1, 4, 7) was reached with about 8 females and 5 males in the Harz Forest (Figure 20).

Assuming higher mortality rates of residents of about 20%, which are realistic figures known from lynx populations in unprotected areas with high poaching probability or expected road casualties (Jedrzejewski *et al.* 1996; Gaona *et al.* 1998; Ferreras *et al.* 2001), the requirements for a MRP are by far not met (Figure 18b). However, the mean persistence time of a population with resident mortality of about 30% (scenarios 3, 6 and 9) was about the life span of an individual lynx (in years ± SD: e.g. for the Harz Forest (20): 17 ± 7 in scenario 3, 14 ± 5 in scenario 6, 12 ± 4 in scenario 9). This indicates that monitoring programmes should be launched for a long time period before the success of a species reintroduction can be assessed.

I obtain similar requirements for a MRP for the Northern Black Forest (53), the Palatine Forest (56) and the Thuringian Forest (34) in all cases. A release of 6 to 10 females is required, and it is only the scenarios with low resident mortality that yield viable populations (Table 12). However, in the Bavarian-Bohemian Forest (49) a viable population can even be obtained with a higher resident mortality, but only if the number of released females is high (scenario 2, Table 12). In contrast to that, the north-eastern forests (2) only obtain a viable population with a high number of initially released females and for very low mortality rates of both residents and dispersers. The differences between these patches are due to different mortality rates of the dispersing animals (Table 13). Even for low dispersal mortality scenarios (scenarios 1, 2 & 3), the total annual mortality rates of dispersers are up to 3 times higher in the north-eastern forests (2) than in the Harz Forest (20). This is because 2 highways cut and 1 highway flanks this habitat (Figure 10). In contrast to that, the road density in the Bavarian-Bohemian Forest (49) is very low and with that also the annual mortality rates of dispersers (Table 13).
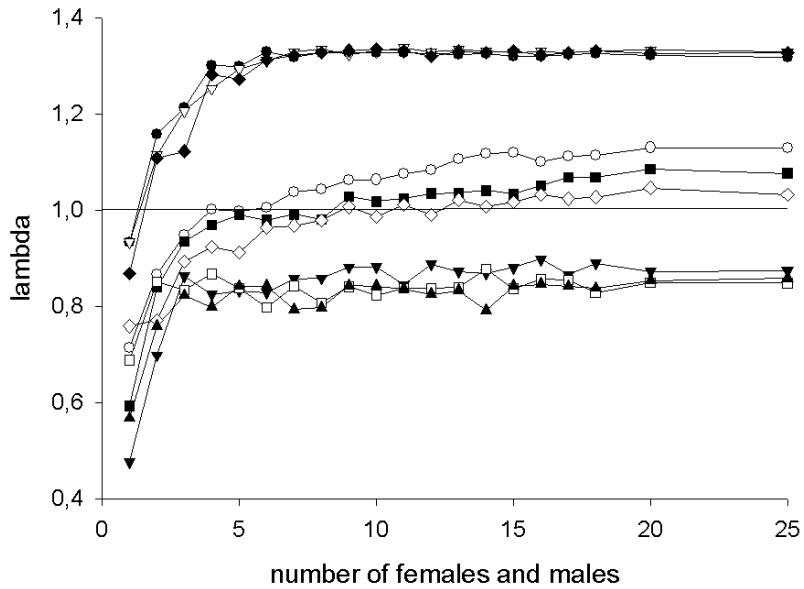
Figure 19. Population development in the Harz Forest over a time horizon of 50 years and a fixed birth probability of 0.75. Values of lambda above 1 indicate positive population development, whereas values below one indicate population decrease. Only for mortality scenarios 1, 4 and 7 (legend cf. Figure 18) was lambda above 1 when subtracting 1 standard deviation.
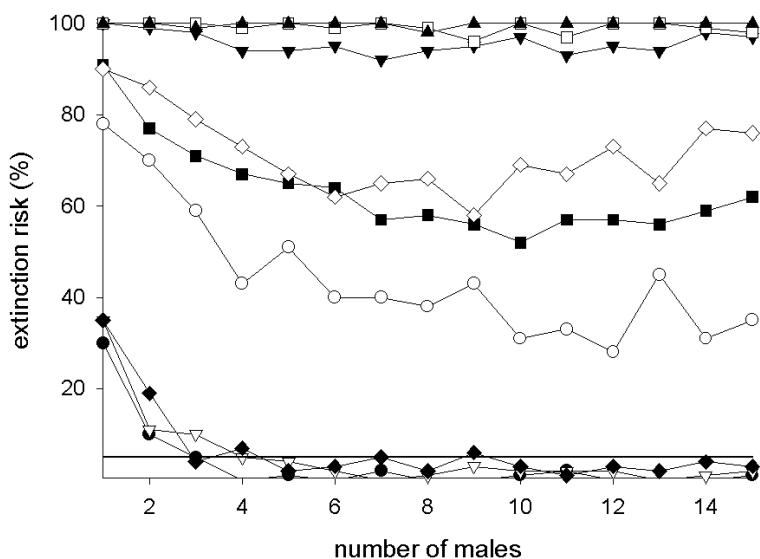
Figure 20. Influence of an increasing number of male lynx on population development in the Harz Forest under different mortality scenarios. 8 females are fixed. Legend cf. Figure 18.

Table 12. Minimum number of females needed to establish a viable population under the mortality scenarios for the different source locations (Figure 10). Birth probability is 0.75 and the time horizon 50 years. I released the same amount of females and males in each patch. If a MRP is reached in a mortality scenario, the minimum number of females is given. The reached maximum carrying capacity of resident lynx and the patch size is shown as well. The number of occupied home ranges (HR) was measured for viable populations as the average number of home ranges after the first 20 years until the maximum time step of 50 years.

Location (patch no.)	patch size (km²)	occupied HR (SD) females	males	Mortality Scenario 1	2	3	4	5	6	7	8	9
Northern Black Forest (53)	1934	18 (3)	11 (2)	7	-	-	6	-	-	9	-	-
Bavarian-Bohemian Forest (49)	1849	18 (3)	11 (2)	6	30	-	7	-	-	7	-	-
*scenario 2**				✓	✓		✓			✓		
Palatine Forest (56)	5232**	13 (2)	8 (1)	8	-	-	9	-	-	9	-	-
Harz (20)	1566	15 (2)	9 (1)	7	-	-	8	-	-	7	-	-
North-eastern Forests (2)	1721	11 (2)***	7 (1)	17	-	-	-	-	-	-	-	-
Thuringian Forests (34)	1676	16 (2)	10 (1)	7	-	-	8	-	-	10	-	-

*   Here I released 15 females and 10 males in the Bavarian Forest and ran the simulations for 20 years to mimic the development of the current population. ✓ indicates mortality scenarios where the probability of extinction in 20 years was below 0.05.

**   Palatine and Vosges Mountains in France together. The size of the German part is 1354 km². Lynx emigrating into the Southern Vosges Mountains were deleted.

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

This shows that the dispersing (corresponding to a higher number of released that did not find a territory immediately) lynx have a buffer or rescue effect for the viability of the whole population, because vacant territories can be occupied quickly. The population in the north-eastern forests (2) could not spread because all the dispersers were killed on the highways. Thus, the extinction risk of the whole source patch was much higher and on average only 11 female occupied home ranges whereas at least 17 would have fitted inside.

b) Isolation or connectivity of the patches.— Generally, connectivity to other patches (i.e. that is at least one female reaching another patch in 50 years and 100 repeated simulation runs) occurs for each source patch (Appendix 2) and all the source patches are interconnected via target patches (Figure 10). The Thuringian Forest (34) would even be directly connected with the four source patches Harz Forest (20), Rothaar Mountains (27), Spessart (40) and Erz Mountains (29). However, sporadically arriving females do not guarantee colonisation.

The chances of an increasing population trend in the target patches are extremely low. With a probability $P_{col} \geq 50\%$ only the German-Czech border (49, 48, 41, 44, 39), Northern and Southern Black Forest (55, 53), Palatine Forest and the Vosges Mountains (56, 52) and Thuringian Forest and the Rhön (32, 34) could be colonised permanently within a time frame of 50 years. Connectivity of the patches mainly occurs for scenarios

with low resident mortality (scenario 1, 4, 7). Therefore, I can state that the ability of population spread is very restricted in Germany, though individual exchange is possible.

Scenario 2: Confirming the population model

When releasing 15 females and 10 males in the Bavarian/ Bohemian Forest the population did not go extinct after 20 years as long as resident mortality was low. This is in concordance with the findings along the German-Czech border. For mortality scenarios 1, 2, 4 and 7 the extinction probability is below 0.05, and even for a medium annual resident mortality of about 20% and medium dispersal mortality (mortality scenario 5) a low extinction probability of 0.06 was found. With a high resident and dispersal mortality (mortality scenario 9) the probability of extinction was 0.65, which is lower in comparison with the extinction probabilities of >0.96 when simulating the population development for 50 years.

A settlement of at least one female home range in the model was recorded along the German-Czech border in patches 39, 41, 44 and also 48, but only for low resident mortality scenarios (1, 4, 7). This leads to the conclusion that presumably in this region one of the mortality scenarios with low resident mortality is holding. It could also be possible that the birth rate is higher in this region, though I neither have evidence nor data to support this. Neglected here is the influence that further colonised suitable patches on the Czech side could have on population development.

Landscape scenarios

Scenario 3: Increase in dispersal habitat (forest)

An increase of 3% in dispersal habitat - which is double as high as it was in the last 50 years in Germany - does not increase the colonisation ability of a released population in the Thuringian Forest (34) to other patches (Figure 17, Appendix 2). Only a shift into the next higher probability class is observed. It is still only the Rhön (32) that is colonised with a very high probability ($P_{col} \geq 75\%$). Only the probability values did change when increasing dispersal habitat, that means that the patches 32 and 40 are colonised with higher probabilities in comparison to scenarios with the actual distribution of dispersal habitat. The Fichtelgebirge (37), which is connected with the German-Czech border, could then be colonised with a very low probability ($1\% \geq P_{col} < 5\%$). If I increase the amount of dispersal habitat to 10%, the patches 26, 38 and 41 connected are with a higher probability.

Table 13. Total annual mortality rates [%] of dispersers in the different source patches due to different road and highway densities under the different mortality scenarios. The parameters for crossing linear barriers have been adjusted for the Harz Forest.

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

*Only the roads on the German side could be considered

When I increase the amount of dispersal habitat to 20%, which corresponds with a total forest coverage of about 50% in Germany, I can have direct forest corridor linkages between the patches where there were fragmented forest patches before (Figure 17). This effect again increases the P_{col}-values from the Thuringian Forest to other patches, e.g. to the Erz Mountains (29) and the Oberpfälzer Forest (39) along the German-Czech border. Patches 32, 37, 38 and 40 could be colonised with a very high probability (P_{col} ≥75%).

Scenario 4: Reduction in highway mortality

Assuming that highways in Germany do not contribute to dispersal mortality, e.g. due to fencing and enough underpasses, green-bridges and viaducts, I obtain a very high colonisation probability of patches from the Thuringian Forest (34) with the actual distribution of dispersal habitat. Especially the German-Czech border (29, 37, 39) and the nucleus Odenwald-Spessart-Rhön (45, 40, 32) would be completely colonised. Even the Harz Forest (20) could be colonised, but only with a low probability (5%≥ P_{col} <25%).

Comparing the closest distances between the edge of the Thuringian Forest and these patches, I find differences in the probability of being colonised. The distance between the Thuringian Forest (34) and the Harz Mountains (20) (71 km) is about the same magnitude as between the Thuringian Forest (34) and the Kellerwald (25) (80 km) in the west or the Solling (18) (68 km). The distance to the Odenwald (45) is almost double as high (140 km; Figure 10). The Rothaar Mountains (27) or the Bavarian-Bohemian Forest (49) are about 120 km or 150 km away and were not colonised (P_{col} <1%). These examples show on the one hand, that small patches could serve as stepping stones for the expansion of a population, but in this case only when highway mortality is low. Patches 25 and 18 could have been sustained by patches 26 and 21, whereas small patches like that are missing on the direct way to the Harz Forest (20). On the other hand, stepping stones alone are not enough within a time horizon of 50 years. The Odenwald (45) was the only patch connected with the Thuringian Forest (34) via another source patch (Spessart (40)). Although in the same order of magnitude in distance, the Rothaar Mountains (27) or the Bavarian-Bohemian Forest (49) were not colonised. These findings are important when designing reserve networks (e.g. Biotop-verbundsysteme, Flora-Fauna-Habitat Directive in Germany). Comparing scenarios 3 and 4, another important finding concerning nature conservation is, that reducing mortality on highways has much more direct positive effects on enhancing colonisation ability of a lynx population than restoring dispersal habitat.

Discussion

PVA can be valuable supporting tools in practical conservation and can be used for the evaluation and design of management methods (Ebenhard 2000). The basic question of a PVA is "What are the minimum conditions for long-term persistence and adaptation of a species or population in a given place?" (Soulé 1987). A PVA is a declared field of research in conservation biology since the middle of the 1980s and has been conducted for a variety of species (e.g., Gaona *et al.* 1998; Wiegand 1998; Hansen *et al.* 1999; McKelvey, Buskirk & Krebs 1999; Ebenhard 2000; Kelly & Durant 2000; McCarthy & Lindenmayer 2000; McCarthy, Lindenmayer & Possingham 2000; Penn *et al.* 2000; Chapman *et al.* 2001). However, problems of PVA are associated with parameterising models resulting in unreliability of the results and uncertainty (Doak & Mills 1994; Ruckelshaus, Hartway & Kareiva 1997; Beissinger & Westphal 1998; Wiegand *et al.* 2002). Here, I presented a PVA for lynx in Germany assessing the viability of a population under present conditions and future landscape changes.

Limitations of this PVA

Small populations in the wild can suffer increased risk because of inbreeding as shown by empirical studies (cf. Saccheri *et al.* 1998; Sobel *et al.* 1999; Ebenhard 2000). The long-term survival of a population is influenced by the genetic variation as a requisite for evolutionary adaptation to a changing environment, and the maintenance of population numbers and genetic variation should be a central theme of plans for long-term population management (Lande & Barrowclough 1987). Therefore, a likely limitation of the model is that it does not include the effects of inbreeding and genetic stochasticity (random genetic drift). If this is true for the Eurasian lynx, the model would underestimate the risk of extinction (but cf. Keane *et al.* 1994; Ballou 1997). It would be necessary to investigate how many initial individuals or how many immigrants per generation are needed to avoid genetic bottlenecks or inbreeding depression. The genetic structure and variability of the two reintroduced Swiss lynx populations (Alps and Jura Mountains) is presently investigated, and the results should be included in further assessments of suitable areas for reintroduction.

Another limitation is, that I did not consider catastrophic events in a scenario as a part of environmental stochasticity, which can sharply reduce population size in a short time. But severe environmental changes such as a sudden reduction of the main prey, roe deer, or breeding habitat or a severe disease are unlikely, and there is no historical information on their occurrence with the species (Ryser-Degiorgis 2001). There is now evidence of lynx losses due to infections with mange in the Swiss Alps. It seems improbable that mange will occur as an epidemic in lynx, but may have an impact on the population (Ryser-Degiorgis *et al.* 2002). Occasional death cases due to mange have been taken into account as "natural mortality" in the model.

Apart from that, the parameters are based on published field estimates or from other calibrated models (the dispersal part) and not directly from field data of the area of interest, which could skew the results. For this reason it would be important to update especially the dispersal part as soon as new data are available, as this could affect the estimates of colonisation success. One of the major uncertainties in the model is that I did not consider behavioural change of lynx. A probability would be that they learn to use underpasses or green-bridges, and that could reduce the mortality risk. In that case, the model results would underestimate the connectivity between the patches.

The future of a lynx population in Germany

Referring to the model results, a population in the Harz Forest under the current landscape situation is only viable when the mortality rates of the resident animals could be kept to a very low level. As known from other populations in Spain or Poland, such a mortality scenario is rather unrealistic. In Spain, the mortality rate of residents can be up to 30% in suitable habitat, but outside a protected area of a national park due to road casualties and poaching (Ferreras *et al.* 2001). Even in the protected area of Białowieża in Poland poaching contributes to 71% of the total mortality rate of the population of 37% and in Switzerland also 70% of the mortality causes of residents are due to road kills and poaching (Zimmermann 1998; Schmidt-Posthaus *et al.* 2002). It is not very probable that in Germany these human-induced mortality factors can be neglected. Thus, under expected mortality scenarios the probability of success of a lynx reintroduction into the Harz Forest is only about 50% for a time window of 50 years (Figure 18b).

The results have shown, that viable populations would also be possible in the other major patches like the Thuringian Forest, the Black Forest and Palatine Forest, but only under the precondition of low mortality for resident and dispersing lynx. A linkage in form of colonisation of other source patches is not given for the source patch Harz (20), not even with an increase in dispersal habitat. An exception is the Bavarian-Bohemian Forest that is connected along the German-Czech border with the Erz Mountains (29), a result that is also supported by field data (Wölfl *et al.* 2001). The Thuringian Forest (34) could also be linked with the patches along the German-Czech border and with the Rhön (32).

New highway construction, as planned and conducted between the Harz Forest (20) and the Thuringian Forest (34) and between the Erz Mountains (29) and the Bavarian Forest (49) will additionally worsen the colonisation success in new patches. Even short highway sections can play a significant role as barriers. In Slovenia, a 30 km long highway stretch contributed to 31% of the total mortality of bears in that area (Kaczensky 2000). That lynx are "bad colonisers" is presently shown in the Swiss Alps, where lynx had to be translocated from the Western to the Eastern population in the Alps. Barriers were

not only constituted by high and snow-capped mountain rifts, but especially by urbanised valleys, which additionally contain highways or waterways (KORA 1999).

The results of the landscape change scenarios have also shown, that restoring 3% of dispersal habitat of the total study area only had a weak influence on the colonisation ability of a population, whereas reducing mortality on highways had a much larger impact. An increase by 3% of dispersal habitat is already more than double the proportion as it was in the last 50 years, but I can expect that in certain areas set-aside land may increase to a greater extent, e.g. in Poland due to the signatory to the European Union (Schröder 1998). This may have further influence on a lynx population in Germany and shows how important conservation programmes across borders and international co-operation are (Kaczensky 2000).

But even with a high increase by 20% dispersal habitat can I conclude that the crucial factor would be reducing mortality rather than restoring habitat, a result which is supported by studies of the Iberian lynx in fragmented landscapes (Ferreras *et al.* 2001). Movement in fragmented landscapes has been included to a certain degree in using data of the Swiss Jura Mountains, but there were too few data to find out whether lynx actively avoid highways or if fences retain them crossing. If that would be the case, movement could be guided, and green-bridges or underpasses would reduce the mortality risk of dispersers. Experiences about the effectiveness of wildlife passages mainly stem from other species (Rodríguez, Crema & Delibes 1996; Rodríguez, Crema & Delibes 1997; Kaczensky *et al.* 1996; Clevenger & Waltho 2000; Clevenger, Chruszcz & Gunson 2001; Gloyne & Clevenger 2001). This implies testing methods to reduce traffic collisions, including measures to increase the attractiveness of existing bridges and underpasses for wildlife (Kaczensky 2000).

Recommendations for reintroductions

The results have shown, that about 10 females are needed for successfully establishing a minimum population, when the mortality rates are kept to a low level. I also showed that the success of a reintroduction can be influenced with the number of released lynx. This is in concordance with findings of critical population sizes of other large carnivores (e.g. Saether *et al.* 1998). If demographic parameters like the birth rate are unsure, it would be better to release more animals to be on the "safe side". This could also reduce inbreeding risk. In addition, more females than males can be released. However, a high mortality rate of residents can not be levelled with releasing many animals. Monitoring programmes should be launched that exceed the life span of the animals to assess reintroduction success (cf. IUCN/SSC 1995).

The study has only considered the demographic feasibility of reintroducing lynx to Germany, but additionally one must consider the desirability of a species within the wider social aspect. Special attention must be paid to the question whether lynx have a

positive or negative image for people in the destiny area, as this will greatly influence the survival rates of the lynx (Grandchamp & Tester 2001; Wotschikowsky *et al.* 2001). The genetic risk of a small population based on a few founder individuals should also be considered.

This study shows that simulation models are useful tools for establishing the comparative effectiveness of reintroduction plans aimed at increasing the viability of the species (van Appeldoorn *et al.* 1998). I recommend PVA and assessment of land change scenarios (Dale *et al.* 1994; White *et al.* 1997; Cooperrider *et al.* 1999; Pearson, Drake & Turner 1999; Urban 2000; Serneels & Lambin 2001) before releasing a species to focus efforts on the most promising and fruitful areas and hence to save money with releasing an appropriate number of animals that most probably leads to a successful reintroduction.

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Appendix 2

Probability P_{col} of showing an increasing trend in population dynamics in the target patches under the different mortality scenarios when the number of colonisation events in 50 years an 100 repetitions was higher than the number of extinction events (population scenario 1). Please note that I only consider a patch to be colonised when a female home range was established.

source patch	target patch	probability P_{col}	mortality scenario	no. of released females
Harz Forest (20)	18	≥1% and < 5%	1	≥6
		≥5% and < 25%	1	≥8
	21	≥1% and < 5%	1	≥5
		≥5% and < 25%	1	≥6
		≥25% and < 50%	1	≥15
	6, 9, 14, 17, 19, 23, 25, 26, 27, 34	< 1%	-	-
Bavarian Forest (49)	29	≥1% and < 5%	1	≥9
		≥5% and < 25%	1	≥13
		≥25% and < 50%	1	≥30
	37	≥1% and < 5%	1	≥13
		≥5% and < 25%	1	≥12
	39	≥1% and < 5%	1	≥2
		≥5% and < 25%	4	≥6
		≥25% and < 50%	1	≥3
			4	≥8
		≥50% and < 75%	**1**	**≥4**
			4	**≥30**
		≥75%	**1**	**≥7**
	41	≥1% and < 5%	1	≥5
		≥5% and < 25%	1	≥7
		≥25% and < 50%	1	≥11
		≥50% and < 75%	**1**	**≥25**
	44	≥1% and < 5%	2	≥11
			5	≥30
		≥5% and < 25%	1	≥2
			2	≥14
			5	≥25
			7	≥4
		≥25% and < 50%	1	≥3
			2	≥17
			4	≥3
			7	≥9
		≥50% and < 75%	**4**	**≥5**
			7	**≥10**
		≥75%	**1**	**≥4**
			4	**≥10**
	47	≥1% and < 5%	1	≥8
		≥5% and < 25%	1	≥25
	48***	≥1% and < 5%	8	≥10
	28, 34, 38, 46, 50	<1%	-	-
scenario 2*	**44**	**≥50% and < 75%**	**1**	**15**
		≥25% and < 50%	4	15

	48	**≥75%**	**1**	**15**
		≥50% and < 75%	**2**, 4, 7**	**15**
		≥25% and < 50%	5**	15
		≥5% and < 25%	8	15
		≥1% and < 5%	3**, 6**	15
	39, 41	<1%	-	15
Black Forest (53)	**55**	≥1% and < 5%	7	≥3
			2	≥16
		≥5% and < 25%	2	≥30
			4	≥3
			7	≥4
		≥25% and < 50%	1	≥3
			4	≥4
		≥50% and < 75%	**1**	**≥4**
			4	**≥5**
			7	**≥6**
		≥75%	**1**	**≥5**
			4	**≥6**
			7	**≥15**
	45, 56, 58	<1%	-	-
Palatine Forest (56)	42	≥1% and < 5%	1	≥9
		≥5% and < 25%	1	≥30
	52	≥1% and < 5%	3	≥20
			5	≥14
		≥5% and < 25%	1	≥3
			3	≥22
			4	≥3
			9	≥30
		≥25% and < 50%	8	≥22
		≥50% and < 75%	**1**	**≥4**
			4	≥4
			7	≥4
		≥75%	**1**	**≥5**
			4	≥6
			7	≥7
	31, 33, 35, 36, 43	<1%	-	-
north-eastern forests (2)	5	≥1% and < 5%	1	≥16
		≥5% and < 25%	1	≥30
	1, 5, 7, 8, 10, 12 15	<1%	-	-
Thuringian Forest (34)	**32**	≥1% and < 5%	4	≥6
			7	≥30
		≥5% and < 25%	4	≥12
		≥50% and < 75%	**1**	**≥4**
	40	≥1% and < 5%	1	≥15
		≥5% and < 25%	1	≥18
	18, 20, 21, 25, 26, 27, 29, 37, 38, 39, 41, 44, 45, 47	<1%	-	-
scenario 3**** increase by 3%	**32**	≥1% and < 5%	1	≥3
			2	≥25
			4	≥6
			7	≥9
		≥5% and < 25%	4	≥5
			7	≥16

		≥25% and < 50%	1	≥4
			4	≥11
		≥50% and < 75%	**1**	**≥6**
		≥75%	**1**	**≥13**
	37	≥1% and < 5%	1	≥8
		≥5% and < 25%	1	≥25
	40	≥1% and < 5%	1	≥15
		≥5% and < 25%	1	≥7
		≥25% and < 50%	1	≥10
	18, 20, 21, 25, 26, 27, 28, 29, 34, 35, 38, 39, 41, 44, 45, 46, 47	<1%	-	-
scenario 3** increase by 10%**	26	≥1% and < 5%	1	≥30
	32	≥1% and < 5%	1	≥3
			2	≥17
			3	≥30
			7	≥6
		≥5% and < 25%	2	≥22
			4	≥4
			7	≥5
		≥25% and < 50%	1	≥4
			2	≥30
			4	≥6
			7	≥13
		≥50% and < 75%	**1**	**≥5**
			4	**≥12**
		≥75%	**1**	**≥8**
	37	≥5% and < 25%	1	≥7
		≥25% and < 50%	1	≥8
	38	≥1% and < 5%	1	≥7
		≥5% and < 25%	1	≥9
	40	≥1% and < 5%	1	≥4
		≥5% and < 25%	1	≥5
		≥25% and < 50%	1	≥6
		≥50% and < 75%	**1**	**≥14**
	41	≥1% and < 5%	1	≥14
	17, 18, 20, 21, 25, 27, 28, 29, 35, 39, 44, 45, 46, 47, 48, 49, 50	<1%	-	-
scenario3 ** increase by 20%**	21	≥1% and < 5%	1	≥8
		≥5% and < 25%	1	≥11
		≥25% and < 50%	1	≥30
	26	≥1% and < 5%	1	≥5
		≥5% and < 25%	1	≥7
		≥25% and < 50%	1	≥12
	29	≥1% and < 5%	1	≥14
		≥5% and < 25%	1	≥20
		≥25% and < 50%	1	≥30
	32	≥1% and < 5%	5	≥22
			6	≥30
			8	≥25

		≥5% and < 25%	2	≥13
			4	≥4
			5	≥25
			7	≥5
		≥25% and < 50%	1	≥4
			2	≥17
			4	≥5
			7	≥6
		≥50% and < 75%	**1**	**≥5**
			4	**≥7**
			7	**≥8**
		≥75%	**1**	**≥7**
			4	**≥12**
	37	≥5% and < 25%	1	≥5
		≥25% and < 50%	1	≥8
		≥50% and < 75%	**1**	**≥14**
	38	≥1% and < 5%	1	≥4
			4	≥25
		≥5% and < 25%	1	≥6
		≥25% and < 50%	1	≥5
		≥50% and < 75%	**1**	**≥11**
	39	≥1% and < 5%	1	≥30
	40	≥1% and < 5%	4	≥9
		≥5% and < 25%	1	≥4
			4	≥8
		≥25% and < 50%	4	≥30
		≥50% and < 75%	**1**	**≥5**
		≥75%	**1**	**≥11**
	41	≥1% and < 5%	1	≥7
		≥5% and < 25%	1	≥9
		≥25% and < 50%	1	≥15
	17, 18, 20, 23, 25, 27, 28, 35, 44, 45, 46, 47, 48, 49, 50, 53	<1%	-	-
scenario 4***	18	≥1% and < 5%	1	≥7
		≥5% and < 25%	1	≥9
		≥25% and < 50%	1	≥15
	20	≥1% and < 5%	1	≥8
		≥5% and < 25%	1	≥15
	21	≥1% and < 5%	4	≥14
		≥5% and < 25%	1	≥3
		≥50% and < 75%	**1**	**≥4**
		≥75%	**1**	**≥9**
	25	≥1% and < 5%	1	≥7
		≥5% and < 25%	1	≥9
		≥25% and < 50%	1	≥12
	26	≥5% and < 25%	1	≥3
		≥25% and < 50%	1	≥4
		≥50% and < 75%	**1**	**≥5**
	29	≥1% and < 5%	1	≥3
		≥25% and < 50%	1	≥4
		≥50% and < 75%	**1**	**≥5**
		≥75%	**1**	**≥12**

32	≥1% and < 5%	2	≥12
		7	≥5
	≥5% and < 25%	2	≥13
		4	≥4
		7	≥6
	≥25% and < 50%	1	≥3
		2	≥20
		7	≥13
	≥50% and < 75%	**1**	**≥4**
		4	**≥5**
	≥75%	**1**	**≥7**
37	≥1% and < 5%	4	≥9
	≥5% and < 25%	1	≥3
		4	≥8
	≥25% and < 50%	1	≥4
	≥50% and < 75%	**1**	**≥5**
	≥75%	**1**	**≥17**
38	≥1% and < 5%	1	≥3
	≥5% and < 25%	1	≥5
	≥25% and < 50%	1	≥8
	≥50% and < 75%	**1**	**≥17**
39	≥1% and < 5%	1	≥5
	≥5% and < 25%	1	≥9
	≥25% and < 50%	1	≥12
	≥50% and < 75%	**1**	**≥22**
40	≥1% and < 5%	4	≥12
	≥5% and < 25%	1	≥2
		4	≥6
	≥25% and < 50%	1	≥3
	≥50% and < 75%	**1**	**≥4**
	≥75%	**1**	**≥5**
41	≥5% and < 25%	1	≥4
	≥25% and < 50%	1	≥6
	≥50% and < 75%	**1**	**≥5**
	≥75%	**1**	**≥5**
45	≥5% and < 25%	1	≥4
	≥25% and < 50%	1	≥7
	≥50% and < 75%	**1**	**≥8**
	≥75%	**1**	**≥17**
6, 9, 14, 17, 19, 23, 24, 27, 28, 33, 34, 35, 44, 46, 47, 48, 49, 50, 53, 56	<1%	-	-

*   Scenario 2 refers to the part-validation of the model with releasing 15 females and 10 males in the Bavarian/ Bohemian Forest (49) over a time horizon of 20 years.

**   The number of extinction events was greater than the number of colonisation events.

*** P_{col} for patch 48 was ≥ 75% for all scenarios, but the number of extinction events was greater than the colonisation events, indicating that this patch could only be colonised due to a constant stream of immigrants from the source patch.

****   Scenario 3 increases the amount of dispersal habitat by 3, 10 and 20% additionally to the given dispersal habitat in the study area (cf. also to Figure 17).

***** In scenario 4 I did not consider mortality on highways.

KAPITEL V

Diskussion und Zusammenfassung

In der vorliegenden Arbeit wurde eine Reihe von Methoden der ökologischen Modellierung angewandt und weiterentwickelt, um Fragen des praktischen Naturschutzes zu bearbeiten. Eine ganze Reihe drängender Probleme lassen sich nur mit Hilfe von Modellen bearbeiten, insbesondere wenn die Raum- und Zeitskalen den Rahmen von Feldexperimenten sprengen und wenn - wie bei Populationsgefährdungsanalysen (PVA) - Risikoabschätzungen und Wahrscheinlichkeitsaussagen gefordert sind (Wiegand 1998). In einem Modellierungsansatz müssen das verfügbare Wissen strukturiert, unbekannte Größen (Parameter) abgeschätzt und Hypothesen über unbekannte Mechanismen bzw. Verhaltensweisen aufgestellt werden. Das kann durchaus als Vorteil aufgefaßt werden, denn so entdecken Modelle Lücken in der Forschung, und sie können zur Anregung weiterer Feldexperimente dienen (Schippers *et al.* 1996). Die systematische Analyse von Szenarien in Modellen ist ein Werkzeug, um mögliche zukünftige Ereignisse untersuchen zu können. Sie können also als ein Mittel der Vorhersage dienen, um die möglichen Konsequenzen von Maßnahmen und Entscheidungen abzuwägen (Gaona, Ferreras & Delibes 1998; van Appeldoorn *et al.* 1998).

Das Habitatmodell

Besonders für Tierarten mit großen Raumansprüchen in fragmentierten Landschaften ist dies ein wichtiger Punkt, denn Habitatfragmentierung und der Verlust von Lebensraum sind derzeit die größte Bedrohung für die Überlebensfähigkeit vieler Arten. Die Rückkehr des Luchses in die anthropogen überformte Landschaft Deutschlands steht exemplarisch für das Schicksal einer Art, die sich unter neuen Lebensbedingungen behaupten muss. Effektiver Naturschutz erfordert ein Verständnis davon, wie Arten auf die Zerschneidung von Lebensräumen reagieren. Grundlegende Fragestellungen, die das Management und den Schutz von Großraubtieren wie dem Luchs betreffen, sind immer noch unbeantwortet, beispielsweise wie die minimalen Habitatanforderungen unter den jetzigen Landschaftsbedingungen aussehen, und ob es sich bei der Rückkehr der Großräuber lediglich um ein lokal begrenztes Phänomen handelt oder ob sie auf dichter besiedelte Bereiche erweitert werden kann.

Aufbau des Modells und Methodik

Um diese Fragen zu beantworten und die Art-Habitat-Beziehung zu analysieren, wurde ein statistisches Habitatmodell (Kapitel II) entworfen. Ein genereller Überblick über Habitatmodelle wurde bereits in Kapitel I gegeben. Zur Auswertung der Präsenz-Absenz-Daten aus dem Schweizer Jura wurde die Methode der logistischen Regression verwendet, deren Prinzip auf der Kontrastierung von genutzten Einheiten gegen ungenutzte beruht. Aufgrund der sehr begrenzten Datenmenge von nur vier sich nicht überlappenden Luchs-Streifgebieten war es nicht möglich, einzelne Streifgebiete als Einheit für die statistische Auswertung zu verwenden. Zudem sollte das Habitatmodell als Grundlage für das Populationssimulationsmodell dienen und mußte dazu im Rasterformat vorliegen. Deshalb wurde über die Landschaft des Schweizer Jura ein Gitter von 1 km x 1 km gelegt. Pro Rasterzelle wurden Landschaftsvariablen entnommen, die die intensive bzw. extensive Nutzung der Landschaft durch den Menschen beschreiben. Beispielsweise zählen hierzu der Waldbedeckungsgrad und die Straßendichte. Wie erreicht man aber nun eine Beschreibung des für den Luchs wichtigen großräumigen Zusammenhangs der Landschaft, die über diese sehr lokale Einheit einer Rasterzelle von 1 km² hinausgeht? Dazu wurden zwei Landschaftsindizes errechnet, die für jede Rasterzelle die relative Häufigkeit von extensiv genutzten Flächen in verschieden großen zirkularen Nachbarschaften angeben[2]. Ist der Wert des Indexes hoch, befinden sich in der Nähe der Zelle viele ander Zellen mit extensiver Landnutzung, d.h. in der Umgebung der Zelle ist die Fragmentation extensiv genutzter Flächen gering.

Die Indizes wurden für verschiedene Radien berechnet und als zusätzliche Landschaftsvariablen genutzt. Die Landschaftsvariablen aus Zellen der vom Luchs besiedelten Gebiete wurden dann in einer logistischen Regression mit Landschaftsvariablen ungenutzter Gebiete verglichen. Die Methode der logistischen Regression bietet gegenüber anderen Verfahren wie beispielsweise der Diskriminanzanalyse den Vorteil, daß die Variablenwerte nicht normalverteilt vorliegen müssen (Kleyer *et al.* 2000). Allerdings ist Vorsicht geboten bei der blinden Anwendung einer logistischen Regression als Prognosewerkzeug, denn oft werden sämtliche Variablen verwendet, die aus Karten abgeleitet werden können, ohne sie auf ihre biologische Plausibilität zu untersuchen (vgl. Woolf *et al.* 2002). Daher liefern diese Modelle wenig Einsicht in die Ökologie der betreffenden Art. Um diesem Problem zu begegnen, wurden eine Reihe statistischer Analysen durchgeführt. Beispielsweise wurde die biologische Relevanz einer Variable in einem Streifgebiet mit einem Kruskal-Wallis-Test überprüft, der auf signifikante Unterschiede im Vorkommen von Landschaftsvariablen aus Streifgebieten und Nicht-Streifgebieten prüft. Streifgebiete von Luchsen, die wie üblich mit der "minimum convex polygon"-Methode abgegrenzt werden, stellen Artefakte dar und können oft Landnutzungen enthalten, die von Luchsen nicht genutzt werden.

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[2] Der Begriff der „extensiv genutzten Flächen" ist ein anthropozentrischer Begriff und nicht die Perspektive des Luchses. Aus allem, was über die Biologie des Luchses bekannt ist, kann man aber davon ausgehen, daß zwischen extensiver Nutzung und den Ansprüchen des Luchses ein Zusammenhang besteht.

Räumliche Autokorrelation, die durch Rasterung der Grundlagenkarte entstanden ist, wurde weitgehend ausgeschlossen, indem ein räumlicher Korrelationsindex für verschiedene Skalen errechnet wurde. Es wurden nur die Raster übernommen, die keine oder nur eine geringe räumliche Korrelation zueinander aufwiesen. Starke räumliche Korrelation der abhängigen Variable würde zu Überparameterisierung eines Modells führen, und damit wäre es nicht mehr auf andere Gebiete übertragbar. Akaikes Informations-Kriterium (AIC) wurde für die Auswahl des besten Modells verwendet, und die statistische Signifikanz dieses Modells mit der Methode der ROC-Kurven ("receiver-operator-characteristics") bewertet.

Das beste Modell besteht nur aus einer Variable und beschreibt den Zusammenhang extensiv genutzter Flächen auf einer Skala von ca. 80 km². Ausschlaggebend waren also nicht feinskalige Landschaftsvariablen, wie sie oft in Habitatmodellen benutzt werden, sondern eine regionale Landschaftsvariable. Daher ist davon auszugehen, daß ein solches Habitatmodell auch auf andere Gegenden übertragbar ist, ohne daß feine Strukturen wie die Zusammensetzung des Waldes oder die Beuteverteilung berücksichtigt werden müssen. Feinskalige Strukturen sind vermutlich eher auf der intraterritorialen Ebene von Bedeutung. Das Modellergebnis hat außerdem eine klare biologische Bedeutung, da die Variable den Zusammenhang von extensiv genutzten Gebieten auf ungefähr der Fläche eines Territoriums eines weiblichen Luchses beschreibt.

Ein weiterer wichtiger Punkt in der Habitatmodellierung ist die Validierung der Modelle. Dazu wurden Daten aus Slowenien und aus dem deutsch-tschechischen Grenzgebirge verwendet. Die hohe Übereinstimmung von prognostizierter Habitateignung und tatsächlicher Habitatnutzung läßt darauf schließen, daß das Modell auch auf andere Gebiete in Mitteleuropa übertragen werden kann.

Anwendung im Naturschutz

Außer für die Weiterentwicklung der Methoden der Habitatmodellierung haben die Ergebnisse praktische Relevanz für den Naturschutz, indem nun in Deutschland die Lebensräume ermittelt werden können, die groß genug für eine Luchspopulation wären. Die ungefähre Anzahl an residenten Luchsen wurde errechnet, in dem die im Habitatmodell ermittelten Gebiete durch die durchschnittliche exklusiv genutzte Territoriengröße von Männchen und Weibchen dividiert wurde. Geeignete Gebiete für eine Luchspopulation, die mindestens 50 bis 100 Tiere umfassen sollte (Franklin 1980), sind demnach die Wälder in Brandenburg und Mecklenburg-Vorpommern, der Pfälzer Wald mit den Vogesen, der Schwarzwald und der deutsch-tschechische Grenzgebirgsbogen, der sich zwischen Bayerischem Wald und Elbsandsteingebirge spannt, wobei bei letzterem noch der Anschluß an Österreich und das polnisch-tschechische Grenzgebirge zu berücksichtigen wäre.

Ein Habitatmodell in der hier vorgestellten Form kann allerdings nur einen groben Anhaltspunkt über maximale Luchskapazitäten liefern, da es statischer Natur ist. Umweltschwankungen bzw. hohe Mortalitätsraten, wie sie z.B. durch eine hohe Verkehrsdichte bewirkt werden, können die Eignung eines Lebensraumes stark einschränken. Dazu ist aber eine Populationsgefährdungsanalyse notwendig, wie sie im Gesamtmodell in Kapitel IV durchgeführt wurde. Das Habitatmodell bildet jedoch die Basis für die räumlich-expliziten Simulationsmodelle der Abwanderung und Populationsdynamik, und bietet einen ersten Anhaltspunkt zur Ermittlung der potentiell geeigneten Luchs-Gebiete in Deutschland.

Das Ausbreitungsmodell

Eine ganz andere Frage stellt sich, wenn man die geeigneten Lebensräume hinsichtlich ihrer Verbindung zu anderen Lebensräumen bewertet. Kleine isolierte Populationen sind anfälliger gegenüber demographischen Schwankungen und sogenanntem „Umweltrauschen" sowie Inzuchtdepressionen. Genetisch betrachtet dürfen auch Populationen, die ca. 50 Tiere umfassen können wie z.B. die im Schwarzwald mögliche Population, als klein und isoliert angesehen werden. Der Individuen-Austausch zwischen diesen Lebensräumen ist ein Schlüsselfaktor in der Beurteilung der Lebensfähigkeit einer Population, wobei der Abwanderungsprozeß (Dispersal) von Individuen in anthropogen überformten, heterogenen und fragmentierten Landschaften schwierig zu untersuchen ist (Lima & Zollner 1996; Fahrig 1997). Ein Verständnis davon, wie eine bestimmte Landschaftsstruktur ein abwanderndes Individuum beeinflußt, ist aber eine Grundvoraussetzung, um die Populationsdynamik in heterogenen Landschaften beschreiben zu können (Johnson *et al.* 1992; Wiens, Stenseth & Ims 1993; Ims 1995; Turchin 1998). Das Dispersal wird damit zu einem Schlüsselprozeß in der landschaftsökologischen Forschung (Wiens 1995). Die Frage, ob die im vorliegenden Habitatmodell ermittelten Lebensräume vernetzt sind, spielt somit eine entscheidende Rolle für die Frage des langfristigen Überlebens einer Luchspopulation in Deutschland. Es ist unmöglich, dieses Überleben mit Feldexperimenten abzuschätzen.

Aufbau des Modells und Methodik

Im zweiten Teil der Dissertation wurde dieser Frage mit einem Ausbreitungsmodell nachgegangen (Kapitel III). Dazu wurden wiederum die Telemetriedaten von sechs abwandernden Jungluchsen im Schweizer Jura herangezogen und analysiert, um zu verstehen, welche mechanistischen Regeln der Abwanderung zugrunde liegen. Da die Daten allerdings nur in maximal täglichen Abständen aufgenommen wurden, liefern die Analysen lediglich "Fingerabdrücke" mit verschlüsselten Informationen über Parameter und Prozesse des Systems "Abwanderung". Solche Fingerabdrücke können beispielsweise die Verteilung der täglichen Wanderdistanzen sein, aber auch die Häufigkeit einer

bestimmten Habitatnutzung. Die eigentliche Wanderbewegung der Luchse und damit die Reaktion auf die Landschaftsstruktur erfolgte zwischen den Telemetrieaufnahmen.

Die Regeln für das Abwanderungsmodell wurden daher mit Hilfe von Literaturanalysen und Expertengesprächen entworfen und mit Hilfe der „Fingerabdrücke" kalibriert. Wegweisend für die Kalibrierung des Ausbreitungsmodells war der musterorientierte Modellier-Ansatz ("pattern-oriented modelling approach", Grimm *et al.* 1996; Wiegand, Revilla & Knauer 2002), der die Modellparameter und -regeln an den gegebenen "Fingerabdrücken" orientiert. Die Modellierung der Abwanderung war ein iterativer Prozeß zwischen Aufstellung von Modellregeln und deren Überprüfung an den vorhandenen Mustern. Dieser Modellieransatz bot weiterhin die Möglichkeit, reale Muster, die nicht zur Formulierung der Regeln benutzt wurden, mit ensprechenden vom Modell erzeugten Mustern zu vergleichen und damit Parameterwerte und Modellprozesse abzugleichen (vgl. Wiegand 1998; Jeltsch, Milton & Moloney 1999). Dies war beispielsweise der Fall, um die maximalen Distanzen abzuschätzen, die ein Luchs in ungeeignetem Gelände zurücklegt. Somit haben Entwurf und Kalibrierung des Ausbreitungsmodells auch Einsicht in die Prozesse geliefert, die der Abwanderung der Luchse zugrunde liegen. Das Abwanderungsmodell geht damit über den Rahmen eines prediktiven "black-box"-Modells hinaus, das die Abwanderung zwar beschreiben, aber nicht erklären kann.

Aber eine bloße Übereinstimmung der realen mit erzeugten Mustern muß nicht unbedingt bedeuten, daß die richtigen Parameter bzw. Prozesse gefunden sind. Daher ist eine Konsistenz- und Plausibilitätsuntersuchung der Ergebnisse sowie eine umfangreiche Untersuchung der vom Modell produzierten Muster nötig. Es sollte zum einen sichergestellt werden, daß die den realen nahekommenden simulierten Muster (z.B. Verteilung der Wanderdistanzen, Habitatnutzung) weder singulär sind, d.h. nur durch eine Parameterkombinationen erzeugt werden können. Zum anderen sollten sie nicht auf beliebige Weise erzeugt werden können, da das Muster in diesem Falle keine zusätzliche Information, die nicht schon berücksichtigt wäre, enthalten würde (Wiegand 1998). Im vorliegenden Abwanderungsmodell wurden etwa 82% aller Parameterkombinationen herausgefiltert, da sie nicht die Dynamik des Abwanderungsprozesses im Schweizer Jura zeigten, d.h. nicht mit den realen Mustern übereinstimmten. Wie bereits beim Habitatmodell hat sich auch hier gezeigt, daß trotz einer geringen Menge an Felddaten der immanente Informationsgehalt ausreicht, ein Modell zu entwerfen, das dem derzeitigen Wissensstand entspricht und die Feldbeobachtungen reproduzieren kann und daher als plausibel gelten kann.

Um das Modell anwenden zu können, wurden durch einen indirekten Parameterabgleich Mortalitätswerte kalibriert. Mortalitätsraten wurden dabei an Werte angelehnt, die aus der Literatur stammen. Die Mortalitätswahrscheinlichkeit orientierte sich dabei auch an Barrieren in der Landschaft. D.h. die Möglichkeit zu sterben war nicht beliebig, sondern von größerer Wahrscheinlichkeit an bestimmten Orten, insbesondere bei Überquerung

von Hauptstraßen, Autobahnen und Flüssen. Verschiedene Mortalitätsszenarien wurden getestet; diese Szenarien umfaßten beispielsweise unterschiedliche Zeitrahmen für die Abwanderung sowie unterschiedliche Wahrscheinlichkeiten der natürlichen Mortalität und der Mortalität bei Überquerung linearer Barrieren.

Anwendung im Naturschutz

Auch das Ausbreitungsmodell hat praktische Relevanz für den Naturschutz. Es wurde auf Deutschland übertragen, und es wurde damit die Proportion der Luchse ermittelt, die in den Zielhabitaten ankommen. Damit kann der Einfluß von Verkehrswegen und der Landschaftsstruktur auf die Verbindung zwischen geeigneten Lebensräumen abgeschätzt werden. In einem Szenario ohne Mortalität kann beispielsweise ermittelt werden, wie sich die gegeben Verteilung von Ausbreitungshabitat auf die Verbindung zweier Lebensräume auswirkt. Durch Hinzunahme von Straßenmortalität wird dann deren zusätzlicher Einfluß sichtbar. Auch kann unter Annahme eines realistischen Mortalitätsszenarios der Isolationsgrad einzelner Lebensräume bestimmt werden.

Für das Luchsmanagement haben sich zwei Ergebnisse als sehr wichtig erwiesen. Zum einen hat sich unter der Annahme realistischer Mortalitätsszenarien, in die das Verkehrsnetz einbezogen ist, herausgestellt, daß sämtliche Lebensräume, die groß genug für eine Luchspopulation wären, voneinander isoliert sind. Ohne Verkehrsmortalität wären diese Lebensräume z.T. gut verbunden. Eine Ausnahme bildet hierbei der aus mehreren Populationsarealen zusammenhängende deutsch-tschechische Grenzgebirgsbogen, der nur von wenigen Verkehrswegen zerschnitten ist. Zum anderen hat sich auch für Deutschland bestätigt, was von einer fragmentierten Pardelluchspopulation aus Spanien bekannt ist: Eine Erhöhung der Tragfähigkeit eines Populationsareals durch Habitatrestaurierung hat weniger Erfolg als die Reduktion von Straßenmortalität, wenn es um die Verringerung des Aussterberisikos einer Population geht. Bei der planerischen Abwägung zwischen Reduktion von Straßenmortalität und Restauration von Lebensraum sollten also die finanziellen Mittel zur Verringerung der Mortalität eingesetzt werden (Ferreras *et al.* 2001). Das Beispiel des Ausbreitungsmodells zeigt, daß solche Ansätze ein wichtiges Hilfsmittel darstellen können, wenn es um die Wiedereinbürgerung von Tierarten geht (Cramer & Portier 2001).

Für die Naturschutzbiologie ergeben sich noch weitere Konsequenzen. In Metapopulationsmodellen wird der Raum zwischen einzelnen Populationen immer als homogen angenommen. Es hat sich aber herausgestellt, daß die Heterogenität der Landschaft besonders auf kurzen Distanzen ein uneinheitliches Bild der Austauschwahrscheinlichkeit bewirkt, d.h. die Austauschwahrscheinlichkeit ist nicht nur durch die Entfernung zweier Lebensräume bestimmt. In vielen Modellen wird die Austauschrate von Individuen lediglich als eine Funktion der Distanz und Habitatgröße angenommen (Ricketts 2001; Verboom *et al.* 2001). Die Heterogenität der Landschaft zwischen den Habitaten (bzw. die Heterogenität der "Matrix" zwischen den Lokalpopulationen, in der Terminologie

der Metapopulationstheorie) hat aber, wie sich ergab, einen bedeutenden Einfluß auf den Individuenaustausch zwischen geeigneten Lebensräumen. Dies kann erhebliche Auswirkungen auf Diskussionen im Naturschutz nach sich ziehen, beispielsweise in der Diskussion um nationale Biotopverbundysteme auf der Basis des Metapopulationskonzepts. Die Anwendung des letzteren hat einen Aufschwung im Wildtiermanagement erfahren (Storch & Schröder 1996); Metapopulationsmodelle berücksichtigen die Struktur des Raumes zwischen geeigneten Lebensräumen jedoch nicht. Neuere Ansätze in der Metapopulationstheorie versuchen daher, mehr räumliche Details mit einzubeziehen (Moilanen & Hanski 1998).

Das Populationsmodell

Es gibt eine ganze Reihe an Fragen, die das Ausbreitungsmodell nicht beantworten kann. Beispielsweise hängt die Frage, ob eine lokale Population lebensfähig ist, nicht nur vom Individuenaustausch ab, durch den "genetische Flaschenhälse" vermieden werden, sondern auch ganz entscheidend von Aussterbe-und Wiederbesiedelungsereignissen kleiner, aber verbundener Lebensräume. Diese könnten, wenn sie besiedelt werden, zwar die Abwanderung zunächst verzögern, stellen dann aber eine weitere Quelle an abwandernden Jungtieren bereit, so daß große Lebensräume möglicherweise doch erreicht und besiedelt werden könnten.

Aufbau des Modells und Methodik

Die Populationsdynamik wurde daher in einem Gesamtmodell (Kapitel IV) betrachtet, das neben dem Ausbreitungsmodul (Kapitel III) auch demographische Prozesse wie Reproduktion, Altern und Besetzung von Territorien enthält, und die Überlebensfähigkeit einer Population in den im Habitatmodell ermittelten Lebensräumen (Kapitel II) über einen Zeithorizont von 50 Jahren vorausschätzt. Zwei Aspekte waren hierbei von besonderer Wichtigkeit, und zwar die Reaktion einer Population einerseits auf verschiedene Mortalitätsszenarien, und andererseits auf Szenarien, die Veränderungen der Landschaftsstruktur enthielten. Die demographischen Parameter entstammen der Literatur über Luchspopulationen in der Schweiz, Polen und Spanien. Daneben wurden mit der Modellierung wichtige Fragen des Wildtier-Managements angesprochen, die besonders für die Verbesserung von Wiedereinbürgerungsmaßnahmen relevant sind. Beispielsweise war von Interesse, wie groß eine Initialpopulation mindestens sein muß, um Erfolg bei einer Wiederansiedelung zu gewährleisten.

Die untersuchten Mortalitätsszenarien nahmen jeweils für abwandernde Jungtiere und residente Adulte eine geringe, mittlere und hohe jährliche Mortalitätsrate an. Die Szenarien wurden dann in den für Wiederansiedelungen wichtigsten Lebensräumen getestet (Schwarzwald, Pfälzer Wald, die Wälder im Nordosten Deutschlands, Bayerischer

Wald, Harz und Thüringer Wald). Damit war es möglich, neben dem Einfluß der Straßen und anderer Elemente der Landschaft auch die Auswirkungen beispielsweise der Wilderei auf eine Luchspopulation abzuschätzen. Diese Prozesse betreffen residente Adulte und Jungtiere gleichermaßen. Illegale Abschüße machen beispielsweise in Białowieża in Polen mit 70% den größten Anteil an der Gesamtmortalität der Population aus (Jedrzejewski *et al.* 1996). Auch in der Böhmerwald-Population war Wilderei in den 1990er Jahren die weitaus wichtigste Todesursache. Von 45 tot aufgefundenen Luchsen im Verbreitungsgebiet der Böhmerwald-Population waren 35 gewildert worden (Wölfl *et al.* 2001).

Andererseits könnte sich der in Deutschland anhaltende Trend der Flächenstillegung und Aufforstung positiv auf die Populationsentwicklung und Verbindung der Lebensräume auswirken. Dies wurde untersucht, indem eine Zunahme von ca. 3%, 10% und 20% Waldanteil bezogen auf die Fläche Deutschlands angenommen wurde, wobei bereits bestehende Waldflächen ausgeweitet wurden. Zusätzlich wurde der Einfluß von Grünbrücken und Unterführungen getestet, indem im Modell die Mortalität auf Autobahnen weggelassen wurde. Dies setzt die Annahme voraus, daß Luchse davon abgehalten werden, Autobahnen zu überqueren, und daß sie an ihnen entlang wandern, bis sie eine Querungsmöglichkeit gefunden haben. In den Mittelgebirgsgebieten können Autobahnen auch sehr durchlässig sein, da sie häufig über Talbrücken geführt werden. Für die Annahme über die Verhaltensweise des Luchses, Autobahnen zu meiden, gibt es allerdings noch keine Felddaten. Von Bären in Slowenien ist bekannt, daß die Mortalität auf Autobahnen 31% an der gesamten jährlichen Mortalität ausmacht. Unterführungen bzw. Brücken, die zwar nicht für Wildtierpassagen angelegt waren, waren zwar vorhanden und wurden auch z.T. genutzt, hielt die Bären aber nicht davon ab, trotzdem die Autobahn zu queren. Diese wurde somit zu einem eindeutigen Ausbreitungshindernis für Bären, wenn auch nicht zu einem absoluten (Kaczensky 2000). Aus Spanien ist allerdings bekannt, daß gezäunte Autobahnen Wildtiere erfolgreich von Überquerungen abhalten (Rodríguez, Crema & Delibes 1996 und 1997).

Anwendung im Naturschutz

In den Szenarien hat sich ergeben, daß es unabhängig von der Größe des jeweiligen Lebensraumes ungefähr 10 weiblicher und 5 männlicher Luchse bedarf, damit sich eine Luchspopulation etablieren kann. Ähnliche Größen für Initialpopulationen wurden als Faustregeln für Wiedereinbürgerungen bereits von Experten gefordert (Simon Capt, zitiert in Thor & Pegel 1992) und in der vorliegenden Arbeit bestätigt. Jedoch ist es in jedem Fall sinnvoll, noch mehr Individuen auszusetzen. Sollte beispielsweise die Geburtswahrscheinlichkeit geringer sein als angenommen, so kann das Aussterberisiko durch eine höhere Anzahl an ausgesetzten Tieren abgepuffert werden. Programme zur Überwachung des Wiederansiedelungserfolges sollten über einen längeren Zeitraum geführt werden. Selbst in Szenarien mit sehr hoher Aussterbewahrscheinlichkeit ent-

sprach die durchschnittliche Dauer der Anwesenheit einer Population in etwa der Lebensspanne eines Individuums.

Wie bereits das Zwischenergebnis des Ausbreitungsmodells gezeigt hat, werden viele Lebensräume von abwandernden Jungtieren zwar erreicht, und in einigen Fällen kommt es zu einer sporadischen Wiederbesiedelung, d.h., nach einigen Jahren werden kleinere Lebensräume besiedelt und es findet Reproduktion in ihnen statt. Aber es handelt sich bei den besiedelten Flächen um kleine Lebensräume, die keine dauerhafte Population beherbergen können. Als Trittsteine zur Besiedelung größerer Flächen können sie - zumindest über einen Zeitraum von 50 Jahren und mit Straßenmortalität wie in unserem Modell angenommen - nicht gesehen werden. Diese Flächen hängen von ständig einwandernden Individuen ab, und Aussterbeereignisse treten dort häufig auf. Die für dauerhafte Wiederansiedelungen in Frage kommenden großen Lebensräume bleiben isoliert, d.h. können nicht von Quellpopulationen aus besiedelt werden. Weitere Straßenbaumaßnahmen, beispielsweise die in Planung begriffene Autobahn zwischen Harz und Thüringer Wald und die Trasse, die nördlich des Oberpfälzer Waldes Deutschland mit Tschechien verbinden soll, werden die Isolation der Lebensräume natürlich weiter verstärken.

Daß der Luchs eine wenig ausbreitungsfähige Art ist, zeigt auch das Beispiel der Schweizer Alpenpopulation. Obwohl der Populationsdruck im Nordwestalpenraum sehr hoch ist und geeigneter Lebensraum im Süden, Osten und Westen des besiedelten Gebietes zur Verfügung stünde, erfolgt eine weitere Ausdehnung der Population nicht oder höchstens sehr zögernd. Einer weiteren Ausbreitung stellen sich hier einerseits Hindernisse in Form hoher Bergkämme entgegen, andererseits stark besiedelte und von Gewässern und Verkehrsachsen durchschnittene Täler (KORA 1999). Barrieren wie dichte Siedlungs- und Verkehrsbänder, im ungünstigsten Fall noch in Kombination mit Flüssen wie z.B. am Rhein, schränken insbesondere in Deutschland die Ausbreitungsfähigkeit einer Luchspopulation stark ein. Bisher besteht lediglich entlang des deutsch-tschechischen Grenzgebirgsbogens die Chance einer Ausbreitung und Wiederbesiedelung beispielsweise des Erzgebirges vom Bayerischen Wald bzw. Böhmerwald aus.

Betrachtet man lediglich die Überlebensfähigkeit in den isolierten potentiellen Lebensräumen Harz, Thüringer Wald, Schwarzwald und Pfälzer Wald, so hat sich die Mortalitätsrate der residenten Luchse, also derjenigen, die zur Reproduktion beitragen, als der wichtigste Faktor erwiesen. Landschaftsveränderung im positiven Sinne für den Luchs, beispielsweise durch Aufforstungen (Zunahme von 3% Waldfläche auf die gesamte Fläche Deutschlands bezogen), wirken sich den Modellergebnissen nach nicht wesentlich auf ihre Kapazität aus, weitere Lebensräume zu besiedeln. Einige Lebensräume werden von abwandernden Jungtieren zwar erreicht, dabei handelt es sich aber um Einzelfälle. Bei einer Zunahme der Waldfläche um 20%, wodurch fast alle Lebensräume durch Waldkorridore verbunden wären, wäre der Thüringer Wald mit einer sehr hohen Wahrscheinlichkeit mit dem deutsch-tschechischen Grenzgebirge und der Rhön ver-

bunden, aber nicht mit dem Harz. Im Vergleich dazu zeigte ein Szenario mit Reduktion der Mortalität auf Autobahnen einen höheren Erfolg bezogen auf die Wiederbesiedelungswahrscheinlichkeit anderer Lebensräume.

Die Reduktion der Mortalität allgemein sollte daher Priorität eines Luchsmanagements in Deutschland sein, sei es durch Maßnahmen an Straßen wie Wildzäunen oder Querungshilfen, vor allem aber durch die Verbesserung der Akzeptanz des Luchses in den Teilen der Bevölkerung, die sich betroffen fühlen, um illegale Tötungen zu verhindern (Grandchamp & Tester 2001). Letzteres ist eines der größten Probleme, mit denen Luchspopulationen auch in anderen Ländern, beispielsweise der Schweiz, Tschechien und Schweden, zu kämpfen haben (Wotschikowsky, Kaczensky & Knauer 2001).

Schlußbemerkung

Hat der Luchs in Deutschland also eine Zukunft? Diese Frage ist schwer mit einem klaren Ja oder Nein zu beantworten. Wenn man davon ausgehen kann, daß Mortalitätsursachen weitgehend reduziert werden, so sind lebensfähige Populationen in den meisten großen Lebensräumen, nämlich Harz, Schwarzwald, Pfälzer Wald und Thüringer Wald, durchaus möglich. Man muß sich aber darüber im Klaren sein, daß es sich voraussichtlich um isolierte Populationen handeln wird, mit Ausnahme des - bisher noch von Autobahnen unzerschnittenen - deutsch-tschechischen Grenzgebirgsbogens. D.h. Wiederbesiedelung von Gebieten durch eine Population in einem benachbarten Lebensraum, z.B. des Harzes vom Thüringer Wald aus, und des letzteren durch die Population im Bayerisch-Böhmischen Wald, kann den Modellergebnissen nach weitgehend ausgeschlossen werden. Nur mit sehr geringer Wahrscheinlichkeit könnten einzelne Individuen die Lebensräume erreichen.

Daran schließt sich natürlich die Frage an, ob eine Wiedereinbürgerung in Deutschland "sinnvoll" ist. Damit wäre man wieder beim Ausgangspunkt angekommen: diese Frage kann nämlich die vorliegende Arbeit nicht beantworten. Allerdings kann sie, sollte über diese Frage diskutiert werden, einige fundierte Resultate liefern und Handlungshinweise geben, die die Diskussionen in eine sachliche Richtung beeinflussen können.

Es darf aber nicht vergessen werden, daß die biologisch-technische Seite der Durchführbarkeit einer Wiedereinbürgerung nur eine unter denen ist, die überprüft werden muß. Wiedereinbürgerungen speziell von Großräubern sind langwierige und kostspielige Prozesse. Eine gute Öffentlichkeitsarbeit, um die breite Unterstützung der Bevölkerung zu gewinnen, vor allem aber der direkt Betroffenen bzw. derer, die auf den Wiedereinbürgerungsprozeß Einfluß nehmen können, sind weitere Grundvoraussetzungen. Schließlich und endlich darf auch die organisatorische Seite nicht vernachlässigt werden, denn durch die großen Raumansprüche von Arten wie dem Luchs ist eine

internationale Zusammenarbeit unerlässlich (Breitenmoser *et al.* 2000; Breitenmoser *et al.* 2001; Schröder 1998).

Grundsätzlich weist die Untersuchung in zwei Richtungen zukünftiger Arbeit. Zum einen können Fragestellungen der theoretischen Ökologie näher beleuchtet werden, wie z.B. der Zusammenhang zwischen Lebensraumgröße, Distanz zu anderen Lebensräumen, Konfiguration des Ausbreitungshabitats und Kolonisierungserfolg. In den Ergebnissen des Gesamtmodells hat sich ja bereits angedeutet, daß es eine Mindestgröße an Lebensraum geben muß, wo die Mortalität gering ist. Das Beispiel der Wälder in Brandenburg und Mecklenburg-Vorpommern, die von einer Autobahn zerschnitten sind, hat gezeigt, daß große zusammenhängende Waldflächen allein nicht ausschlaggebend dafür sind, daß sich eine Population dauerhaft ansiedeln kann. Die Ergebnisse aus weiteren Untersuchungen würden generelle Diskussionen über die Gestaltung von Schutzgebieten, Biotopverbundsystemen und die Erhaltung von Arten anstoßen (vgl. Cabeza & Moilanen 2001).

Zum anderen gibt es Einsatzmöglichkeiten in der angewandten Ökologie, denn mit diesem Modell können detailliertere Teilfragen behandelt werden, sollte es zu konkreten Planungen kommen. Untersuchungen über die Nutzung von Wildtierpassagen sollten ausgeweitet und die Ergebnisse in das Modell einfließen.

Die vorliegende Arbeit zeigt, daß der Modelltypus der räumlich-expliziten Populationssimulation nicht nur bei der Untersuchung angewandter Fragestellungen in spezifischen Situationen sinnvoll sein kann (z.B. Mindestindividuenzahlen für eine bestimmtelebensfähige Population) sondern auch bei der Analyse genereller Themen hilfreich ist (z. B. Einfluß der Landschaftsstruktur auf die Populationsentwicklung im allgemeinen). Damit ist dieser Ansatz geeignet, theoretische Ökologie, empirische Untersuchungen und angewandte Naturschutzbiologie miteinander zu verknüpfen (Wiegand 1998).

Die Probleme, die ein solcher Ansatz mit sich bringen kann, liegen auf der Hand. Zu hohe Komplexität, hoher Datenbedarf und hohe Unsicherheit bei der Parameterisierung werden immer noch als Kritikpunkte angeführt (Doak & Mills 1994; Ruckelshaus, Hartway & Kareiva 1997; Beissinger & Westphal 1998). diese Einwände konnten aber teilweise durch die konsequente Anwendung der musterorientierten Modellierung, durch Sensitivitätsanalysen und Teil-Validierung der Modellergebnisse ausgeräumt werden. Gerade dieser Modellansatz ist im Spannungsfeld zwischen zu starker Vereinfachung und zu hoher Komplexität angesiedelt. Bei jeder Reduktion, wie sie Modellannahmen darstellen, können sich Fehler einschleichen, beispielsweise bei der Zusammenfassung des Raumes in wenige Kategorien der Landnutzung und durch die Rasterung der Landschaft. Feine Strukturen wie Waldstreifen entlang von Flußläufen gehen damit verloren, können aber wichtige Ausbreitungsmedien für wandernde Tierarten darstellen (Boone & Hunter 1996). Offene Landschaften könnten dadurch weniger als Barrieren wirken als es die Modelluntersuchung ergibt, was wiederum Einfluß auf

die Individuenaustauschrate hätte. Eine noch feinere Auflösung der Landschaft ist allerdings auf dem Maßstab Deutschlands nicht möglich. Eine kontinuierliche Überprüfung der Modellregeln anhand neuer Daten aus Feldbeobachtungen ist daher unerlässlich, zumal das Habitatmodell die Grundlage weiterer Modellierungsansätze ist. Daher ist es sinnvoll, sich nicht nur auf ein Habitatmodell als Basis zu verlassen. Das zeigt der Vergleich mit einem weiteren Habitatmodell: In einem vorangegangenen Habitatmodell, das sich nicht auf Felddaten und statistische Analysen stützte (Schadt *et al.* in Druck), wurde der Fragmentierung der Landschaft nicht genügend Rechnung getragen, so daß die Ergebnisse geeigneten Lebensraum in Deutschland überschätzt haben könnten.

Auch das Ausbreitungsmodell muß, wie jedes Modell, Vereinfachungen beinhalten, da die Datengrundlage sehr dünn war und möglicherweise wichtige Prozesse fehlen können. Zum Beispiel könnten neuere Daten Aufschluß darüber geben, ob Luchse Autobahnen gar nicht erst zu queren versuchen und an ihnen entlang wandern, oder ob sie sie - unter bestimmten, bisher unbekannten Voraussetzungen - direkt überqueren. Dies hätte natürlich Einfluß auf die Wanderrichtung und damit auf den Einwanderungserfolg in andere Gebiete. Andererseits verlieren Modelle durch zunehmende Komplexität ihre Transparenz und Überschaubarkeit, was ja gerade der Vorteil einer Modellierung ist. Im Modell nicht beachtet wurden mögliche genetische Veränderungen oder modifikatorische Veränderungen der Lebensweise, die natürlich ebenso einen erheblichen Einfluß auf die langfristige Lebensfähigkeit einer Luchspopulation haben könnten. Solche Veränderungen können verschiedene Auswirkungen haben, beispielsweise Degeneration oder Verlust der Scheu. Unter neuen Modellannahmen würden sich auch neue potentielle Lebensräume ergeben. Ergebnisse aus Untersuchungen von eingebürgerten Luchspopulationen liegen dazu allerdings noch nicht vor. Aus anderen Untersuchungen ist aber jetzt schon klar abzulesen, daß die einzelnen Lebensräume in Deutschland an der unteren Grenze der Toleranz dessen liegen werden, was genetische Gesichtspunkte anbetrifft, d.h. Inzuchtdepression und Allelverlust (Reed & Bryant 2000).

Naturschutzbiologie wird oft als "Krisendisziplin" bezeichnet, da sie in dem Spannungsfeld lebt, dringende Aufgaben des Naturschutz möglichst schnell und effizient bearbeiten zu müssen, die Erhebung von Daten als Grundlage aber sehr lange dauert (Soulé 1986; Doak & Mills 1994). Die Schlüsselfrage in der Naturschutzbiologie ist, ob die Forschung zu einem adäquaten Management des Problems führen wird (z.B. Krebs 1994). Die vorliegende Arbeit hat den Bogen zwischen Wissenschaft und Praxis gespannt und gezeigt, wie man mit relativ wenigen Daten und der Weiterentwicklung der Methoden in der Modellierung zu konkreten Handlungsanweisungen für ein effektives Luchsmanagement in Deutschland kommen kann. Es darf jedoch nicht vergessen werden, daß Modelle nicht die "Wahrheit" vorhersagen, sondern allenfalls das derzeit beste Wissen über die Wirkungsweise von Prozessen und Faktoren eines Systems quantitativ repräsentieren (Starfield 1997).

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