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Conservation of the Eurasian Lynx (*Lynx lynx*) in a fragmented landscape – habitat models, dispersal and potential distribution

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Conservation of the Eurasian lynx (*Lynx lynx*) in a fragmented landscape – habitat models, dispersal and potential distribution

Lausanne, le 23 novembre 2004

pour Le Doyen
de la Faculté de Biologie et de Médecine
D. Haas
Prof. Dieter Haas

to Manuela
to my parents

‘No amount of clever modeling or detailed GIS habitat maps can circumvent our need for this natural history information’

Ruckelshaus *et al*., (1999)

M24 pictured by a camera-trap during the intensive session conducted in winter 2003-04 in the Simmental and Saanenland. This lynx has been captured in the year 1998 as juvenile and fitted with a radio-collar. We could follow his dispersal and home range establishment until March 2001 when the signal of his radio-collar got interrupted. Later on, he has frequently been pictured by means of camera traps in the study area.

Abstract

The expansion of a recovering population – whether re-introduced or spontaneously returning – is shaped by (i) biological (intrinsic) factors such as the land tenure system or dispersal, (ii) the distribution and availability of resources (e.g. prey), (iii) habitat and landscape features, and (iv) human attitudes and activities. In order to develop efficient conservation and recovery strategies, we need to understand all these factors and to predict the potential distribution and explore ways to reach it.

An increased number of lynx in the north-western Swiss Alps in the nineties lead to a new controversy about the return of this cat. When the large carnivores were given legal protection in many European countries, most organizations and individuals promoting their protection did not foresee the consequences. Management plans describing how to handle conflicts with large predators are needed to find a balance between “overabundance” and extinction. Wildlife and conservation biologists need to evaluate the various threats confronting populations so that adequate management decisions can be taken.

I developed a GIS probability model for the lynx, based on habitat information and radio-telemetry data from the Swiss Jura Mountains, in order to predict the potential distribution of the lynx in this mountain range, which is presently only partly occupied by lynx. Three of the 18 variables tested for each square kilometre describing land use, vegetation, and topography, qualified to predict the probability of lynx presence. The resulting map was evaluated with data from dispersing subadult lynx. Young lynx that were not able to establish home ranges in what was identified as good lynx habitat did not survive their first year of independence, whereas the only one that died in good lynx habitat was illegally killed.

Radio-telemetry fixes are often used as input data to calibrate habitat models. Radio-telemetry is the only way to gather accurate and unbiased data on habitat use of elusive larger terrestrial mammals. However, it is time consuming and expensive, and can therefore only be applied in limited areas. Habitat models extrapolated over large areas can in turn be problematic, as habitat characteristics and availability may change from one area to the other. I analysed the predictive power of Ecological Niche Factor Analysis (ENFA) in Switzerland with the lynx as focal species. According to my results, the optimal sampling strategy to predict species distribution in an Alpine area lacking available data would be to pool presence cells from contrasted regions (Jura Mountains, Alps), whereas in regions with a low ecological variance (Jura Mountains), only local presence cells should be used for the calibration of the model.

Dispersal influences the dynamics and persistence of populations, the distribution and abundance of species, and gives the communities and ecosystems their characteristic texture in space and time. Between 1988 and 2001, the spatio-temporal behaviour of subadult Eurasian lynx in two re-introduced populations in Switzerland was studied, based on 39 juvenile lynx of which 24 were radio-tagged to understand the factors influencing dispersal. Subadults become independent from their mothers at the age of 8-11 months. No sex bias neither in the dispersal rate nor in the distance moved was detected. Lynx are conservative dispersers, compared to bear and wolf, and settled within or close to known lynx occurrences. Dispersal distances reached in the high lynx density population – shorter than those reported in other Eurasian lynx studies – are limited by habitat restriction hindering connections with neighbouring metapopulations.

I postulated that high lynx density would lead to an expansion of the population and validated my predictions with data from the north-western Swiss Alps where about 1995 a strong increase in lynx abundance took place. The general hypothesis that high population density will foster the expansion of the population was not confirmed. This has consequences for the re-introduction and recovery of carnivores in a fragmented landscape. To establish a strong source population in one place might not be an optimal strategy. Rather, population nuclei should be founded in several neighbouring patches. Exchange between established neighbouring subpopulations will later on take place, as adult lynx show a higher propensity to cross barriers than subadults.

To estimate the potential population size of the lynx in the Jura Mountains and to assess possible corridors between this population and adjacent areas, I adapted a habitat probability model for lynx distribution in the Jura Mountains with new environmental data and extrapolated it over the entire mountain range. The model predicts a breeding population ranging from 74-101 individuals and from 51-79 individuals when continuous habitat patches < 50 km^2 are disregarded. The Jura Mountains

could once be part of a metapopulation, as potential corridors exist to the adjoining areas (Alps, Vosges Mountains, and Black Forest). Monitoring of the population size, spatial expansion, and the genetic surveillance in the Jura Mountains must be continued, as the status of the population is still critical.

ENFA was used to predict the potential distribution of lynx in the Alps. The resulting model divided the Alps into 37 suitable habitat patches ranging from 50 to 18,711 km^2, covering a total area of about 93,600 km^2. When using the range of lynx densities found in field studies in Switzerland, the Alps could host a population of 961 to 1,827 residents. The results of the cost-distance analysis revealed that all patches were within the reach of dispersing lynx, as the connection costs were in the range of dispersal cost of radio-tagged subadult lynx moving through unfavourable habitat. Thus, the whole Alps could once be considered as a metapopulation. But experience suggests that only few disperser will cross unsuitable areas and barriers. This low migration rate may seldom allow the spontaneous foundation of new populations in unsettled areas. As an alternative to natural dispersal, artificial transfer of individuals across the barriers should be considered.

Wildlife biologists can play a crucial role in developing adaptive management experiments to help managers learning by trial. The case of the lynx in Switzerland is a good example of a fruitful cooperation between wildlife biologists, managers, decision makers and politician in an adaptive management process. This cooperation resulted in a Lynx Management Plan which was implemented in 2000 and updated in 2004 to give the cantons directives on how to handle lynx-related problems. This plan was put into practice e.g. in regard to translocation of lynx into unsettled areas.

Résumé

L'expansion d'une population en phase de recolonisation, qu'elle soit issue de réintroductions ou d'un retour naturel dépend 1) de facteurs biologiques tels que le système social et le mode de dispersion, 2) de la distribution et la disponibilité des ressources (proies), 3) de l'habitat et des éléments du paysage, 4) de l'acceptation de l'espèce par la population locale et des activités humaines. Afin de pouvoir développer des stratégies efficaces de conservation et de favoriser la recolonisation, chacun de ces facteurs doit être pris en compte. En plus, la distribution potentielle de l'espèces doit pouvoir être déterminée et enfin, toutes les possibilités pour atteindre les objectifs, examinées.

La phase de haute densité que la population de lynx a connue dans les années nonante dans le nord-ouest des Alpes suisses a donné lieu à une controverse assez vive. La protection du lynx dans de nombreux pays européens, promue par différentes organisations, a entraîné des conséquences inattendues ; ces dernières montrent que tout plan de gestion doit impérativement indiquer des pistes quant à la manière de gérer les conflits, tout en trouvant un équilibre entre l'extinction et la surabondance de l'espèce. Les biologistes de la conservation et de la faune sauvage doivent pour cela évaluer les différents risques encourus par les populations de lynx, afin de pouvoir rapidement prendre les meilleures décisions de gestion.

Un modèle d'habitat pour le lynx, basé sur des caractéristiques de l'habitat et des données radio-télémétriques collectées dans la chaîne du Jura, a été élaboré afin de prédire la distribution potentielle dans cette région, qui n'est que partiellement occupée par l'espèce. Trois des 18 variables testées, décrivant pour chaque kilomètre carré l'utilisation du sol, la végétation ainsi que la topographie, ont été retenues pour déterminer la probabilité de présence du lynx. La carte qui en résulte a été comparée aux données télémétriques de lynx subadultes en phase de dispersion. Les jeunes qui n'ont pas pu établir leur domaine vital dans l'habitat favorable prédit par le modèle n'ont pas survécu leur première année d'indépendance alors que le seul individu qui est mort dans l'habitat favorable a été braconné.

Les données radio-télémétriques sont souvent utilisées pour l'étalonnage de modèles d'habitat. C'est un des seuls moyens à disposition qui permette de récolter des données non biaisées et précises sur l'occupation de l'habitat par des mammifères terrestres aux mœurs discrètes. Mais ces méthodes demandent un important investissement en moyens financiers et en temps et peuvent, de ce fait, n'être appliquées qu'à des zones limitées. Les modèles d'habitat sont ainsi souvent extrapolés à de grandes surfaces malgré le risque d'imprécision, qui résulte des variations des caractéristiques et de la disponibilité de l'habitat d'une zone à l'autre. Le pouvoir de prédiction de l'Analyse Ecologique de la Niche (AEN) dans les zones où les données de présence n'ont pas été prises en compte dans le calibrage du modèle a été analysée dans le cas du lynx en Suisse. D'après les résultats obtenus, la meilleure méthode pour prédire la distribution du lynx dans une zone alpine dépourvue d'indices de présence est de combiner des données provenant de régions contrastées (Alpes, Jura). Par contre, seules les données sur la présence locale de l'espèce doivent être utilisées pour les zones présentant une faible variance écologique tel que le Jura.

La dispersion influence la dynamique et la stabilité des populations, la distribution et l'abondance des espèces et détermine les caractéristiques spatiales et temporelles des communautés vivantes et des écosystèmes. Entre 1988 et 2001, le comportement spatio-temporel de lynx eurasiens subadultes de deux populations réintroduites en Suisse a été étudié, basé sur le suivi de 39 individus juvéniles dont 24 étaient munis d'un collier émetteur, afin de déterminer les facteurs qui influencent la dispersion. Les subadultes se sont séparés de leur mère à l'âge de 8 à 11 mois. Le sexe n'a pas eu d'influence sur le nombre d'individus ayant dispersés et la distance parcourue au cours de la dispersion. Comparé à l'ours et au loup, le lynx reste très modéré dans ses mouvements de dispersion. Tous les individus ayant dispersés se sont établis à proximité ou dans des zones déjà occupées par des lynx. Les distances parcourues lors de la dispersion ont été plus courtes pour la population en phase de haute densité que celles relevées par les autres études de dispersion du lynx eurasien. Les zones d'habitat peu favorables et les barrières qui interrompent la connectivité entre les populations sont les principales entraves aux déplacements, lors de la dispersion. Dans un premier temps, nous avons fait l'hypothèse que les phases de haute densité favorisaient l'expansion des populations. Mais cette hypothèse a été infirmée par les résultats issus du suivi des lynx réalisé dans le nord-ouest des Alpes, où la population connaissait une phase de haute densité depuis 1995. Ce constat est important pour la conservation d'une population de carnivores dans un habitat fragmenté. Ainsi, instaurer une forte population source à un seul endroit n'est pas forcément la stratégie la plus judicieuse. Il est préférable d'établir des noyaux de populations

dans des régions voisines où l'habitat est favorable. Des échanges entre des populations avoisinantes pourront avoir lieu par la suite car les lynx adultes sont plus enclins à franchir les barrières qui entravent leurs déplacements que les individus subadultes.

Afin d'estimer la taille de la population de lynx dans le Jura et de déterminer les corridors potentiels entre cette région et les zones avoisinantes, un modèle d'habitat a été utilisé, basé sur un nouveau jeu de variables environnementales et extrapolé à l'ensemble du Jura. Le modèle prédit une population reproductrice de 74 à 101 individus et de 51 à 79 individus lorsque les surfaces d'habitat d'un seul tenant de moins de 50 km^2 sont soustraites. Comme des corridors potentiels existent effectivement entre le Jura et les régions avoisinantes (Alpes, Vosges, et Forêt Noire), le Jura pourrait faire partie à l'avenir d'une métapopulation, lorsque les zones avoisinantes seront colonisées par l'espèce. La surveillance de la taille de la population, de son expansion spatiale et de sa structure génétique doit être maintenue car le statut de cette population est encore critique.

L'AEN a également été utilisée pour prédire l'habitat favorable du lynx dans les Alpes. Le modèle qui en résulte divise les Alpes en 37 sous-unités d'habitat favorable dont la surface varie de 50 à 18'711 km^2, pour une superficie totale de 93'600 km^2. En utilisant le spectre des densités observées dans les études radio-télémétriques effectuées en Suisse, les Alpes pourraient accueillir une population de lynx résidents variant de 961 à 1'827 individus. Les résultats des analyses de connectivité montrent que les sous-unités d'habitat favorable se situent à des distances telles que le coût de la dispersion pour l'espèce est admissible. L'ensemble des Alpes pourrait donc un jour former une métapopulation. Mais l'expérience montre que très peu d'individus traverseront des habitats peu favorables et des barrières au cours de leur dispersion. Ce faible taux de migration rendra difficile toute nouvelle implantation de populations dans des zones inoccupées. Une solution alternative existe cependant : transférer artificiellement des individus d'une zone à l'autre.

Les biologistes spécialistes de la faune sauvage peuvent jouer un rôle important et complémentaire pour les gestionnaires de la faune, en les aidant à mener des expériences de gestion par essai. Le cas du lynx en Suisse est un bel exemple d'une collaboration fructueuse entre biologistes de la faune sauvage, gestionnaires, organes décisionnaires et politiciens. Cette coopération a permis l'élaboration du *Concept Lynx Suisse* qui est entré en vigueur en 2000 et remis à jour en 2004. Ce plan donne des directives aux cantons pour appréhender la problématique du lynx. Il y a déjà eu des applications concrètes sur le terrain, notamment par des translocations d'individus dans des zones encore inoccupées.

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Contents

Chapter 1. Introduction

1.1. General introduction

The expansion of a recovering population – whether re-introduced or spontaneously returning – is shaped by (i) biological (intrinsic) factors such as the land tenure system or dispersal, (ii) the distribution and availability of resource (e.g. prey), (iii) habitat and landscape features, and (iv) human attitudes and activities. Habitat loss and excessive fragmentation is a well documented threat to wildlife (e.g. Andrén 1994; Hagen, Vander Haegen & McKinley 1996). As habitat is reduced, wildlife populations decrease in size and become more isolated. The extinction risks may be reduced by rescue effects due to dispersal between local populations (Hanski, Moilanen & Gyllenberg 1996). Connectivity between suitable habitat patches depends on the number of disperser available in the population, the distance between the source and the target populations, and the dispersal ability of the species under consideration (Wiens 1997). Dispersal is a key parameter in population dynamics, especially in threatened subpopulations within a metapopulation (Levin 1970; Hanski 1999). Dispersal alone can help a population to recover, if the reasons for the decline were demographic or genetic. Basically, removal of threat (habitat and prey restoration) can lead to a recovery through dispersal, if the connectivity to adjoining populations is granted and the dispersal rate sufficient. Removal of threats alone will not help to recover a (sub)population, if the connexion or the status of the source population are not adequate to allow for sufficient immigration. The ability to model, predict, and ultimately to manage theses eventualities thus depends, among others, on the knowledge of the process and parameters of dispersal, the species habitat requirements, as well as its live history parameters. All re-introduction recommendations have so far considered only the origin and translocation of individuals and the initial phase of the population foundation, but less attention was given to the long-term development and the spread of the population. All re-introduction guidelines currently assume that the local population pressure will be sufficient to lead to a spatial expansion, but this assumption is supported by few empirical data, particularly for felids in a cultivated landscape.

The large carnivores’ predatory behaviour and the frequent damage to livestock have always caused conflicts with humans. An increased number of lynx in the north-western Swiss Alps in 1996 lead to another grim controversy about the return of this cat between sheep breeders, hunters and conservationists (Breitenmoser *et al*. 1999). Hunters claimed that the roe deer populations were locally reduced, and sheep-breeders complained about increasing losses in their flocks due to lynx. Not only hunters and sheep-breeders, but also the local authorities demanded the lynx population in the area to be reduced. When the large carnivores were given legal protection in many European countries, most organisations and individuals promoting their protection did not foresee the consequences. Now, as the predator populations are increasing, problems are emerging, and the gap between law and reality needs to be filled with realistic concepts about the co-existence of people and predators (Breitenmoser 1998). Management plans describing how to handle conflicts with large predators are needed (Schröder & Promberger 1993). This challenging task needs a multidisciplinary approach involving scientists (wildlife biologists, conservation biologists, sociologists), policy makers, the local authorities, as well as representatives of the different interest groups (e.g. hunters, sheep breeders, and conservationists).

In order to develop efficient conservation and recovery strategies, wildlife and conservation biologists need to understand and evaluate the various threats confronting populations, and to predict the potential distribution and explore ways to reach it. The Geographic Information System (GIS) combined with habitat modelling has proved to be an important tool to assess the habitat suitability for a given species. It gives among others information about the spatial extent, arrangement and fragmentation of suitable habitat. This is a necessary prelude to estimate the potential population size (Mladenoff & Sickley 1998). The collection of dispersal data in a 1:1 experiment in the field should furthermore allow to get more insights in the expansion mechanism of a recovering population.

1.2. History

The Eurasian lynx (*Lynx lynx*) has been eradicated in central Europe at the beginning of the 20 century. Wherever human beings settled down, they persecuted the large carnivores because they represented a threat to livestock and were regarded as competitors for game species. Most administrations across Europe paid bounties for predators killed, and carnivores were trapped, shot, and poisoned. Direct persecution was the most obvious of several reasons for the fall of large carnivores (Breitenmoser 1998). Alteration of the ecosystem as a result of forest destruction and the expansion of cultivated areas were also substantial reasons for their reduction (Moore & Smith 1991). Roe deer and chamois, the staple prey of lynx, were excessively reduced by humans since the rise of agricultural societies (Ponting 1992). Cattle, sheep, horses, and goats were pastured in the forests, hindering the natural regeneration and ultimately turning forest into pastures (Küster 1995). The increasing stock of domestic animals destroyed forest and competed the wild ungulates out. Large predators were forced to kill livestock, thus provoking and facilitating their persecution. In Switzerland, the growing sensitivity of people for the protection of nature at the beginning of the 20 century, as well as the improvement of the legislation (e.g. the first Federal Forest Law was passed 1876; McShane & McShane-Caluzi 1996), helped to save the forests and to restore them for the game species (Baumann 1949). The wild ungulates progressively recolonized the Alps through spontaneous migration or translocations. The ecological recovery of the Alps was furthermore helped by industrialisation provoking a migration of people from the country side to the towns (Bätzing 1991). As consequence, the number of goats and sheep in the Swiss Alps declined drastically in the first half of the 20 century (Breitenmoser 1998). A similar process took place elsewhere in Europe.

The improvement of the ecological conditions was favourable for the return of large carnivores. Lynx were re-introduced in the Alps and adjacent regions (Jura and Dinaric Mountains) in the early 70s, when little experience and no guidelines were available for carnivore recovery programmes (Breitenmoser *et al*. 2001). These re-introductions were exceptionally poorly done when comparing them with the currently existing recommendations of the IUCN/SCC (1998). Most rules and recommendations were neglected at that time. The releases were not coordinated, and only a few individuals were released at different sites. Nevertheless, in both the Swiss Alps and the Jura Mountains, lynx populations have emerged (Breitenmoser & Baettig 1992; Breitenmoser, Breitenmoser-Würsten & Capt 1998; Vandel 2001), and spread over part of the range (Fig. 1.1).

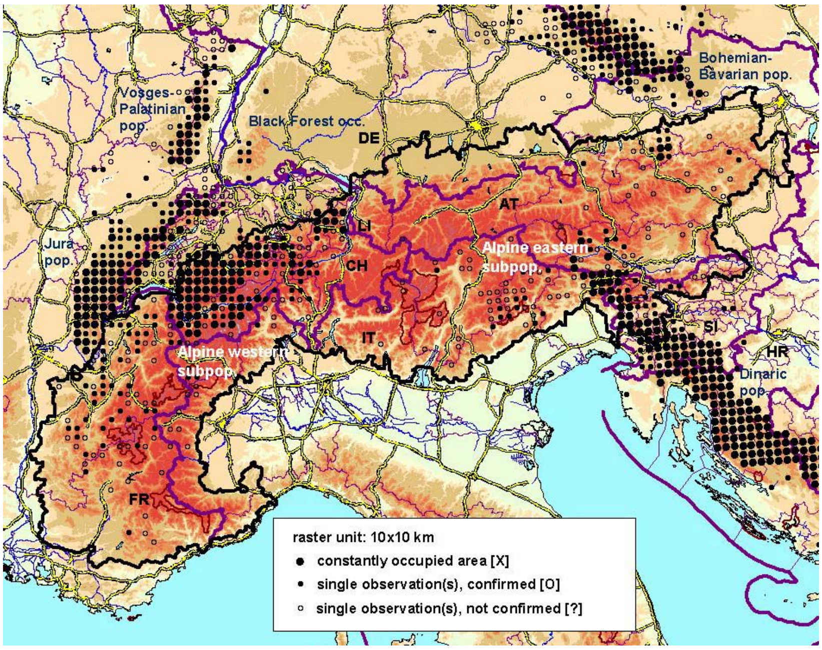


Figure 1.1. Distribution of the Eurasian lynx (*Lynx lynx*) in the Alps and the adjoining areas Jura, Vosges, Bohemian-Bavarian and the Dinaric Mountains in 2001. The black outline delimits the Alps according to the Alpine Convention. Reproduced after von Arx *et al*. (2004).

1.3. Habitat models

Powerful statistical techniques and GIS tools have allowed the development of predictive habitat distribution models in ecology in the past years. Such models relate the geographical distribution of species or communities to their present environment and are *de facto* static and probabilistic in nature. One must always bear in mind that a model is a simplification of the reality, and nature’s complexity and heterogeneity cannot be predicted accurately in every aspect of time and space from a single model. Ideally a model should have three desired proprieties: generality, reality and precision. Levins (1966) formulated the principle that only any two of the three can be improved simultaneously. It is often a trade-off between precision and generality (Guisan & Zimmermann 2000). A wide array of spectrums including biogeography, conservation biology, climate change research, and habitat or species management have been covered by different models. We can roughly distinguish between two categories of predictive habitat distribution models: (i) the empirically based models (see Guisan & Zimmerman 2000 for a review), and (ii) the so called expert-models. Empiric models relay on empiric data and statistical analysis (e.g. GLM: McCullagh & Nelder 1983; GAM: Yee & Mitchell 1991; ENFA: Hirzel *et al*. 2002) whereas expert information may consist of models based on the opinion of experts (e.g. Pereira & Duckstein 1993; Clevenger *et al*. 2002; Schadt *et al*. 2002; Doswald 2003; Doswald, Zimmermann & Breitenmoser subm.) or qualitative models based on the best information available from the literature (Boone & Hunter 1996). The later have largely been criticised mainly because of their arbitrary algorithms which makes any interpretation difficult. Among the empiric models, GLM are for example used to select the predictors (e.g. forest, distance to roads, elevation …) that best explained the presence/absence of the species of interest. In turn, expert-models are often used when data on species distribution are scarce and/or when time and money do not allow to collect such data in an efficient way. In this case, models are compiled with information available from the literature or from expert interviews or a combination of both. Expert-models are generally mathematical but they can also be descriptive. The currently used Habitat Evaluation Procedure (HEP) developed by the United States Fish and Wildlife Service (1980, 1981a,b) belongs to the mathematical expert-models. This procedure is comparable to the regression models and the habitat suitability (HS) is obtained by an equation in which each selected environmental predictor is multiplied by a coefficient but in this case the coefficient's weights are given by experts and do not result from a statistical analysis. Besides we can find more descriptive models governed by simple ecological rules that describe species habitat relationships in a simple and comprehensive manner. These rules can easily be implemented in the GIS to compute habitat suitability maps (e.g. Schadt *et al*. 2002).

Ecological Niche Factor Analyses (ENFA) and Generalized Linear Models (GLM) are presented more in details in the present section as they have been important tools in several chapters of my thesis. ENFA has only recently been implemented in the GIS (Hirzel, Hausser & Perrin 2001). It uses presence data only, and is appropriate in cases where absence data are difficult or impossible to collect efficiently. Suggested by Perrin (1984), this method was developed by Hausser (1995) and Hirzel *et al*. (2002). In this method, the ecogeographical predictors are first summarised into a few uncorrelated factors. The first factor extracted (marginality) is maximizing the ecological distance between the species optimum and the mean habitat within the reference area and the following factors (specialization) are maximizing the ratio Vg/Vd, where Vg is the variance of the ecological predictors computed on the whole grid, and Vd the variance computed on cells including presence records – a procedure not so different from the Discriminant Analysis. These factors define the space where the environmental envelope will be delineated. The frequency distribution and the median of the record sites are computed along each factor. Every grid cell can be compared to these distributions and the further the cell is from the medians, the less suitable it is.

Data are in the form of raster maps, which are grids of N isometric cells covering the whole study area. Each cell of a map contains the value of one variable. The eco-geographical maps contain continuous values, measured for each of the *V* standardised descriptive variables. Species maps contain Boolean values (0 or 1), a value of 1 meaning that the presence of the focal species was proved in this cell (presence cells). A value of zero simply means absence of proof. Alternatively, presence can be given a weight reflecting the amount of cell utilization by the focal species. Each cell can thus be represented by a point in the multidimensional space of the variables. If distributions are multi-normal, they will have the shape of a hyper-ellipsoid centred on the origin. The cells where the focal species was observed constitute a subset of the global distribution and define a smaller hyper-ellipsoid within the global one. The first factor, or *marginality* (*m-specialization* in Perrin 1984), corresponds to the straight line passing through the origin and the centroid of the presence cells. The *marginality* of the species is the distance between the origin and the centroid of the presence cells. The two ellipsoids are then projected onto a hyper plane perpendicular to the *marginality* factor. This ensures that subsequent factors will be uncorrelated to the first factor and removes one dimension from the environmental space. Successive independent *specialization* factors (*s-specialization* in Perrin 1984) are then obtained by computing the axes that maximize the ratio of global variance on species variance. The amount of *specialization* accounted for by a factor is necessarily lower than the one previously extracted. The few first *specialization* factors will thus generally contain most of the relevant information. The factors were retained as long as their eigenvalue is higher than predicted by a Mac-Arthur’s broken stick distribution. Their small number and independence make them easier to use than the original variables. From this process it follows that the ecological niche factors are relative to the reference area. The mathematical demonstration of this procedure has been developed by Hirzel *et al*. 2002. The species distribution according to these factors is used to compute a habitat suitability index ($0 \leq HS \leq 100$) for any set of descriptor values. The ENFA analyses have been performed with *Biomapper 2.1* (Hirzel, Hausser & Perrin 2002).

GLMs (Generalized Linear Models) are an extension of the classical multiple regression, allowing non-normal response variables to be modelled. As mathematical rationales can be found in statistical textbooks (McCullag & Nelder 1983), I describe these models only briefly.

In GLMs, the predictor variables X_j (j = 1, …, p) are combined to produce a linear predictor LP which is related to the expected value $\mu = E(Y)$ of the response variable Y through a link function $g()$, such as:

$$g(E(Y)) = g(\mu) = \alpha + X^T \beta = \mathrm{LP}$$

where α is a constant called the intercept, $X = (X_1, \ldots, X_p)$ is a vector of p predictor variables, $\beta = \{\beta_1, \ldots, \beta_p\}$ is the vector of p regression coefficients (one for each predictor). The above formula was written for generic variables X and Y; the corresponding terms for the ith observation in the sample is:

$$g(\mu_i) = \alpha + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_p x_{ip}$$

Unlike classical linear models, which presuppose a Gaussian (i.e. normal) distribution and an identity link, the distribution of Y in a GLM may be any of the exponential family distributions (e.g. Gaussian, Poisson or Binomial) and the link function may be a monotonic differentiable function (like logarithm or logit). For the generalized linear model, the variance of Y depends on $\mu = E(Y)$ through the variance function $V(\mu)$, giving $\mathrm{Var}(Y) = \phi V(\mu)$, where ϕ is a scale (also known as a dispersion) parameter. The logistic regressions are special cases of general linear model. To carry out a logistic regression the binomial family is declared which uses the *logit* link function defined by

$$g(p) = logit(p) = \log \frac{p}{1-p}$$

and the variance function defined by

$$\mathrm{var}(Y) = \phi \frac{p}{1-p}$$

where p is the probability of an event occurring. The parameter p corresponds to the mean response of a binary (0-1) variable. In my case I used GLMs to predict the presence or absence of lynx as a function of environmental predictors. The GLMs were fitted with S-PLUS (MatSoft), by specifying a binomial distribution and a *logit* link function.

More details on empirical models and their validation will be available in Chapters 2, 3, 7, and 8 of the thesis.

1.4. Dispersal

Movement is one of the most studied yet least understood concepts in ecology and evolutionary biology. It has been considered as a glue cementing sub-populations and allowing connections between usually isolated populations (Waser, Sorbeck & Paetkau 2001; Wiens 2001). Movements have consequences for individuals as well as for populations and communities, and their effects on inclusive fitness are ultimately the selecting forces for dispersal, migration, exploration, and other types of movement that affect the distribution, abundance, and dispersion of individuals (Clobert *et al.* 2001). Movement takes different forms (Dingle 1996), and means different things to different investigators and in different disciplines, as well as for different taxa (Clobert *et al.* 2001; Wiens 2001). For clarity we therefore need to define what we understand by movements. It is distinguished between **natal dispersal** i.e. the movement an individual makes from its birth site or previous breeding site to the place where it reproduces or would have reproduced if it had survived and found a mate, and **breeding dispersal** i.e. the subsequent movement between sites or groups. Dispersal followed by a successful breeding attempt is defined as **effective** or **genetic dispersal**. In this thesis particular attention was given to natal dispersal. Whether an individual leaves a location, for example, may depend on the mode of dispersal, genetic predisposition to disperse, local population density, habitat change, age, reproductive status, perturbation and other factors (Wiens 2001). Liddicker & Stenseth (1992) distinguish between ultimate (evolutionary) and proximate (triggering) factors. Ultimate mechanisms that most likely affect dispersal are environmental variations, kin structure (i.e. competition, altruism, inbreeding). The proximate mechanisms include competition, genetics, individual condition, and breeding habitat selection. The decision to stop dispersal may involve various elements of habitat selection or patch choice, such as conspecific attraction, habitat quality, or physiological factors (Wiens 2001). All these approaches considered dispersal in terms of movement from one location and the consequences of arriving at an other location. The movement between these locations was often regarded as a linear process in the past, on which the characteristics of intervening areas have little effect. Real environments however are heterogeneous and this heterogeneity can affect both the likelihood an individual will disperse and its movement path (Wiens 2001). The spatial pattern and texture of a landscape is given by the configuration of patches, corridors, ecotones, and patch boundaries. During dispersal, individuals are exposed to a range of cost and benefits that constantly change in space and time, and different individuals are exposed to different combinations of costs and benefits depending on when, where, and how far they disperse. In Chapters 4 and 5, I deal with the leaving and arrival phase of the dispersal process – the causes and consequences of dispersal, whereas in Chapters 2, 7 and 8 I address what happens along the way.

1.5. Ecological network

Different modelling approaches can be used to model the effect of habitat fragmentation on dispersal. It includes distance based models, diffusion-like models, and those based on the random walk concept (see Johnson *et al*. 1992 and Schippers *et al*. 1996 for a review).

In our case, dispersal was simulated with the help of the CostDistance extension from the GIS program ArcView (Esri 1996). These functions are similar to the Euclidian distance functions, but instead of calculating the actual distance from one point to another, they determine the shortest cost distance or accumulated travel cost from each cell to the nearest cell in the set of source cells. Furthermore, the cost-distance-functions apply distance not in geographic units but in cost units. These cost-distance-functions require a source-grid and a cost-grid. A source grid, for example the range map resulting from a habitat suitability analysis, can contain single or multiple zones. All cells that have a value (including 0) are processed as source cells. All non-source cells need to be assigned “No Data” on the source-grid. A cost-grid or so called friction map assigns an impedance in some uniform-unit measurement system that depicts the costs involved in moving through any particular cell. The value of each cell in the friction map is assumed to represent the cost-per-unit distance of passing through the cell, where a unit distance corresponds to the cell width.

The a.Grid.CostDistance request from the program ArcView (Esri 1996) creates an output grid in which each cell is assigned the accumulative cost to the closest source cell. The algorithm utilizes the node/link cell representation. In the node/link representation, each centre is considered a node, and each node is connected by links to its adjacent nodes (Fig.1.2). Every link has an impedance associated with it. The impedance is derived from the costs associated with the cells at each end of the link and from the direction of movement. Movements are in eight directions from any cell.

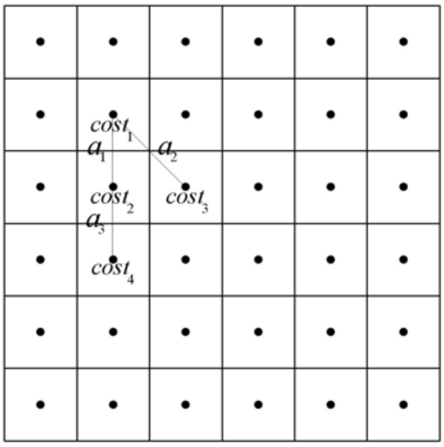


Figure 1.2. View of a grid through the graph theory showing the nodes (i.e. $cost_1$, $cost_2$, $cost_3$, $cost_4$) with examples of the calculation of the accumulative cost for three links (a_1, a_2, a_3).

When moving from a cell to one of its four directly connected neighbours, the costs to move across the links to the neighbouring node is:

$$a_1 = \frac{(cost_1 + cost_2)}{2}$$

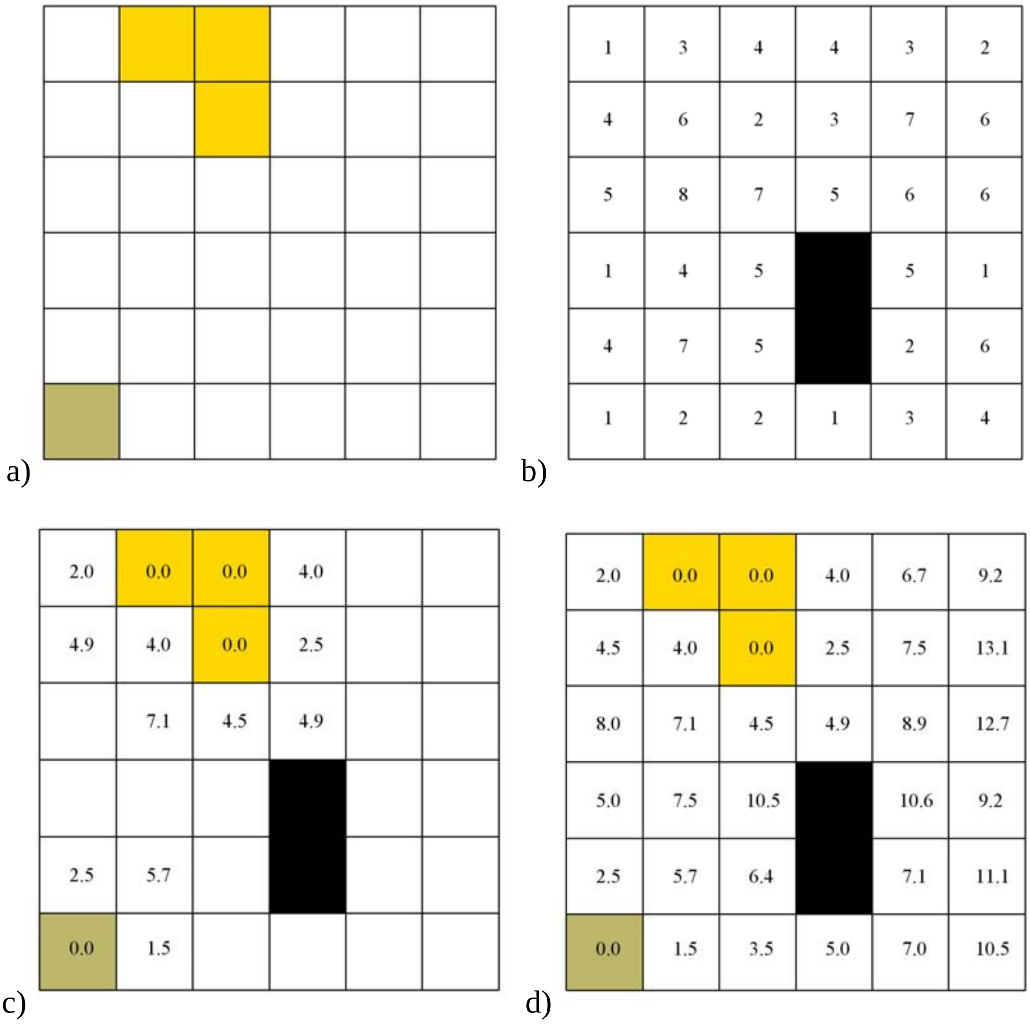
where $cost_1$ is the cost of cell 1, $cost_2$ the cost of cell 2 and a_1 is the length of the link from nod of cell 1 to nod of cell 2. If the movement is diagonal, the cost to travel over the link is $\sqrt{2}$ times the cost of cell 1 plus the cost off cell 2 divided by 2 (Fig. 1.2).

$$a_2 = \sqrt{2} \times \frac{(cost_1 + cost_3)}{2}$$

The accumulative cost (*accumulation*) is determined by the following formula:

$$accumulation = a_1 + \frac{(cost_2 + cost_4)}{2}$$

Creating an accumulative cost-distance Grid using graph theory can be viewed as an attempt to identify the lowest cost cell and adding it to an output list. It is an iterative process that begins with the source cells (Fig. 1.3a).



a)

b)

1	3	4	4	3	2
4	6	2	3	7	6
5	8	7	5	6	6
1	4	5	■	5	1
4	7	5	■	2	6
1	2	2	1	3	4

c)

2.0	0.0	0.0	4.0		
4.9	4.0	0.0	2.5		
	7.1	4.5	4.9		
			■		
2.5	5.7		■		
0.0	1.5				

d)

2.0	0.0	0.0	4.0	6.7	9.2
4.5	4.0	0.0	2.5	7.5	13.1
8.0	7.1	4.5	4.9	8.9	12.7
5.0	7.5	10.5	■	10.6	9.2
2.5	5.7	6.4	■	7.1	11.1
0.0	1.5	3.5	5.0	7.0	10.5

Figure 1.3. Calculation of the accumulative cost-distance Grid using the graph theory in a = source grid, b = cost grid, c = first iteration of the accumulative cost-distance Grid calculation, d = cost distance output grid. In black the cells for which the costs are not known (No Data).

In the first iteration, the source cells are identified and assigned to zero since there is no accumulative cost to return to themselves. Next, all source cell's neighbours are activated and a cost is assigned to the links between the source cell nodes and neighbourhood cell's nodes using the above accumulative cost formulas and the values of the friction map (Fig. 1.3b, 1.3c). Each of these neighbourhood cells can now reach a source, consequently, they can be chosen or assigned to the output accumulative cost Grid. To be assigned to the output Grid, a cell must have the next least-cost path to a source. The accumulative cost values are arranged in a list from the lowest accumulative cost to the highest. The lowest cell is chosen from the active cost list and the value for that cell location is assigned to the output cost-distance Grid. The list of active cells is now expanded to include the neighbours of the chosen cell, because those cells now have a way to reach a source. Only those cells that can possibly reach a source can be active in the list. The cost to move into these cells is calculated using the accumulative cost formulas. Again, the active cell on the list with the lowest cost is chosen, the neighbourhood is expanded, the new costs are calculated and these new cost cell are added to the active list. Source cells do not have to be connected. All disconnected sources contribute equally to the active list. Only the cell with the lowest accumulative cost is chosen and expanded, regardless of the source to which it will be allocated. Furthermore, cells on the active list are updated if a new, cheaper route is created by the addition of new cell locations to the output Grid. When all cells have been chosen from the active list, the result is the accumulative-cost or weighted-distance Grid (Fig. 1.3d). More details on habitat connectivity, fragmentation and potential distribution can be found in Chapters 7 and 8.

1.6. Aims, objectives and thesis contents

The thesis is organized in seven main chapters with Chapters 2-3 dealing with habitat modelling, Chapters 4-5 with dispersal, Chapter 6 with monitoring, and Chapters 7-8 with habitat connectivity analyses. GLM analyses were performed in Chapter 2 to determine if easily available spatial data in the GIS can successfully describe lynx habitat in the Jura Mountains and contribute to a predictive spatial model. In Chapter 3 I analysed the predictive power of the Ecological Niche Factor Analyses (ENFA) in Switzerland in areas not used to build the model and defined a sampling strategy for future analyses. The ultimate and proximate causes of lynx dispersal are described in Chapters 4 and 5. Two hypothesis were specifically tested: (1) dispersal in lynx is male biased as predicted for a polygynous species, (2) subadults in crowded areas with prey depletion should leave the maternal home range earlier, move further and longer (trophic resource competition hypothesis) which would lead to an expansion of the population. Data on dispersal allowed furthermore to assess the connectivity between suitable habitat patches in Chapters 7 and 8 to predict the potential lynx distribution. Habitat modelling was used in Chapter 6 as monitoring-tool in order (1) to reveal suitable areas that are not yet occupied by the species, and (2) to estimate the actual number as well as the potential number of lynx in each of the large carnivore management units in Switzerland. In Chapter 7 I recalibrated the predictive spatial model from Chapter 2 with new environmental variables that were available at a broader scale, and extrapolated it over the whole Jura Mountains to predict the potential size of the lynx population based on knowledge of the land tenure system of the resident lynx. The connectivity to the adjoining areas Vosges, Black Forest, Chartreuses and the French Alps were furthermore investigated. In Chapter 8 the habitat suitability and connectivity for the lynx in the Alps was analysed by means of GIS-based models in order to reveal (1) the suitable habitat patches, (2) the potential size of the sub-population, and (3) the connectivity between the sub-populations. Each Chapter of the present thesis represents an independent scientific paper:

2) Zimmermann, F. & Breitenmoser, U. (2002) A distribution model for the Eurasian lynx in the Jura Mountains, Switzerland. *Predicting Species Occurrences: Issues of Accuracy and Scale* (eds J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall & F.B. Samson), pp. 653–659. Island Press, Covelo, CA.

3) Zimmermann, F., Hausser, J. & Breitenmoser, U. (to be submitted) How well can ENFA predict Animal’s distribution? The case of the Eurasian Lynx (*Lynx lynx*) in Switzerland. *Journal of Applied Ecology*.

4) Zimmermann, F., Breitenmoser, Ch. & Breitenmoser, U. (submitted) Natal dispersal of Eurasian lynx (*Lynx lynx*) in the north-western Swiss Alps and the Jura Mountains. *Journal of Zoology (London)*.

5) Zimmermann, F., Breitenmoser, Ch. & Breitenmoser, U. (submitted). Importance of dispersal for the expansion of an Eurasian lynx (*Lynx lynx*) population in a fragmented landscape. *Biological Conservation*.

6) Molinari-Jobin, A., Zimmermann, F., Breitenmoser-Würsten, Ch. & Breitenmoser, U. (2001). Present status and distribution of the lynx in the Swiss Alps. *Hystrix*, **12**, 21-31.

7) Zimmermann, F. & Breitenmoser, U. (submitted) Potential distribution and population size of the Eurasian lynx (*Lynx lynx*) in the Jura Mountains and possible corridors to adjacent ranges. *Wildlife Biology*.

8) Zimmermann, F. (to be submitted). Potential distribution and population size of the Eurasian lynx (*Lynx lynx*) in the Alps and patch connectivity.

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Chapter 2. A Distribution Model for the Eurasian Lynx *(Lynx lynx)* in the Jura Mountains, Switzerland

2.1. Abstract

The Eurasian lynx (*Lynx lynx*), once widespread throughout Europe, disappeared from most parts of the continent during the 18th and 19th centuries. Lynx were re-introduced since the 1970s into different mountain ranges in western and central Europe. Up to the present, all re-introduced populations have remained small and isolated. The return of the lynx – which preys upon small ungulates and occasionally kills sheep – is matter of controversy, and hence, management conflicts exist. We developed a GIS probability model for the lynx, based on habitat information and radio-telemetry data from the Swiss Jura Mountains, in order to predict the potential distribution of the lynx in this mountain range, which is only partly occupied by lynx. We tested 18 variables for each square kilometer, describing land use, vegetation, and topography in a logistic regression analysis for their capacity to predict lynx presence. The sample unit was a 1x1-km quadrat. We used three sets of response variables to build the model: presence/absence data (i) for both sexes pooled, (ii) for females, and (iii) for males. Three of 18 predictors tested qualified to predict the probability of the species and of female lynx presence, whereas four predictors were necessary to predict the probability of male presence. We then extrapolated the model over the entire Swiss Jura Mountains and evaluated the resulting maps using data from dispersing subadult lynx. When dispersing, subadult lynx traveled along the zones where the model predicted a high probability of lynx presence. Young lynx that were not able to establish home ranges in the good lynx habitat did not survive their first year of independence, whereas the only one that died in good lynx habitat was illegally killed. The model makes it possible to predict lynx distribution in the Jura Mountains and to estimate the population size. This information is needed in order to design a conservation and management plan for the lynx in the area. Such strategies are needed for the conservation of large carnivores in areas of conflicts with human activities.

2.2. Introduction

The lynx populations of western and southern Europe disappeared during the eighteenth and the nineteenth centuries, as a consequence of direct persecution, alteration of the ecosystem (forest destruction and expansion of cultivated land), and the excessive reduction of wild ungulates (Breitenmoser 1998). Since the end of the nineteenth century, forests have regenerated in many mountainous region of Europe, and the wild ungulate populations have recovered quickly. This improvement in the ecological conditions also inspired the idea to bring back large predators. Lynx were re-introduced to the Swiss Alps and the Swiss Jura Mountains in the 1970s (Breitenmoser, Breitenmoser-Würsten & Capt 1998). Although the Swiss re-introductions are considered to be rare examples of successful translocations of large predators (Yalden 1993), these small populations cannot yet be regarded as viable. In the Swiss Jura Mountains, only the southern half of the range is permanently occupied by lynx. The reasons for the lack of vitality are not known; they may include ecological, anthropogenic, and intrinsic (genetic) factors. However, habitat suitability analyses were never carried out for the Jura Mountains, although such a tool is recognized to be important for re-introduction programs.

The purpose of this study is to assess small-scale habitat variables and their importance to lynx recolonisation of the whole Jura Mountains, and to estimate available lynx habitat throughout the mountain range. We used a geographic information system (GIS) to determine if easily available spatial data can successfully describe lynx habitat and contribute to a predictive spatial model (see Guisan & Zimmermann (2000) for a review). The model was built using data from adult, resident lynx that were followed by means of radio-telemetry in the southern part of the Swiss Jura Mountains We then extrapolated the model over the entire Swiss Jura Mountains and evaluated the reliability of the resulting maps using radio-fixes from dispersing subadult lynx. Such a spatial model permits prediction of the future distribution and the potential size of the lynx population in the Jura Mountains, and could be of use in drafting a lynx conservation plan for this mountain range.

2.3. Study Area

The study was performed in the Jura Mountains, a secondary limestone mountain chain forming the northwestern border of Switzerland with France (Fig. 2.1). The altitude varies from about 500 meters to 1,679 meters (Mont Tendre). The main study area (680 square kilometer) was confined to the northern part of the canton of Vaud (VD). Lynx were also followed into the adjoining areas of the canton of Neuchâtel (NE) and into France, this total area is approximately 3,000 square kilometers. Deciduous forests along slopes and coniferous forests on the ridges cover 53 percent of the highlands. Cultivated areas are typically pastures. The human population reaches a density of 120 per square kilometer in most parts of the Jura Mountains, and people living on the Swiss Plateau use the highlands intensively for recreation. The center of the study area is crossed by two railways, a highway, and some additional roads with dense traffic. As in the Swiss Alps (Breitenmoser & Haller, 1987; Haller 1992), roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) are the main prey of lynx in the Jura Mountains (Jobin, Molinari & Breitenmoser 2000).

2.4. Material and method

2.4.1. Data set

From April 1988 to June 1998, a total of twenty-nine lynx were surveyed by means of radio-telemetry in the Jura Mountains (Breitenmoser *et al*. 1993; Swiss Lynx Project, unpublished data). Some of the radio-tagged lynx roamed into the French part of the mountain range. All analyses for this study were done using the radio fixes from the Swiss part of the study area, because environmental data for France were unavailable.

We used a total of 6,282 radio fixes of eleven resident lynx followed from 1988 to 1998 to generate the models on the assumption that these adult, territorial individuals (Breitenmoser *et al.* 1993) would occupy the best habitat. The sample unit was a 1x1-kilometer quadrat. The sampling area was restricted to all the quadrats intercepted by the minimum convex polygone (MCP), including all the fixes of the resident lynx. Quadrats falling within France were disregarded. A total of 1,085 quadrats remained for the analyses (Fig. 2.1). We split the data in two subsets. One was used for calibration of the model, and the other was used to evaluate the model predictions (*split sample approach*; see Guisan & Zimmermann 2000).

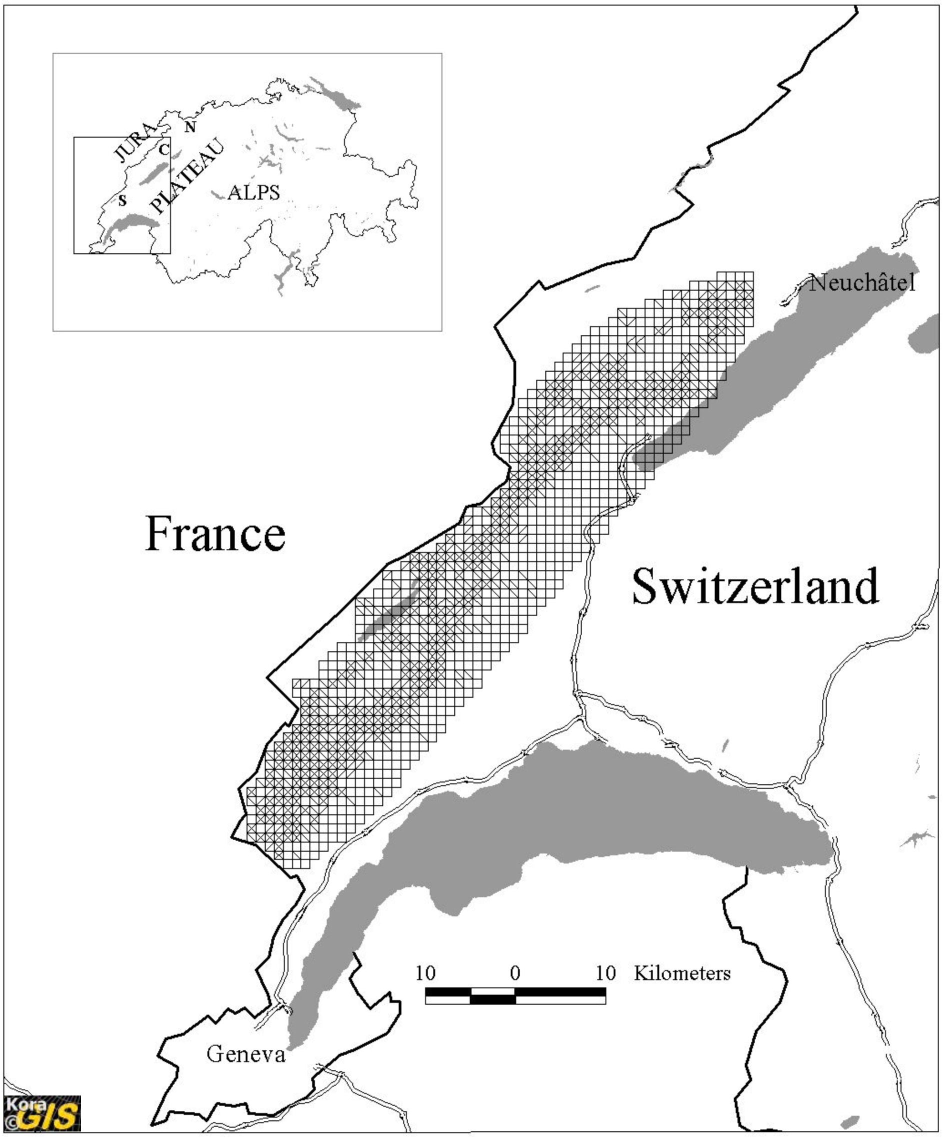

Figure 2.1. Situation of the study area in the Jura Mountains of Switzerland (small map) and France. The grid (large map) shows the 1,085 quadrats where the predictor and response variables have been sampled. Cells are hatched as follows: \ = cells visited by female lynx; / = visited by male lynx; X = visited by both sexes. In addition, S = southern, C = central, and N = northern part of the Swiss Jura Mountains (small map).

We compared the results from different sample sizes ranging from two hundred to one thousand quadrats for the calibration of the model in order to test the consistency (stability) of our model. Since all samples greater than three hundred quadrats produced the same parameters, we decided on a sample of four hundred quadrats to calibrate our model. The quadrats were chosen randomly, with a distance constraint between them in order to reduce spatial autocorrelation. The remaining 685 quadrats were then used to evaluate the model.

The response variable is the presence/absence of lynx in each quadrat. Lynx were considered to be present in each quadrat containing one or more telemetry fixes. Every quadrat without any radio-fixes was considered as absence, as lynx were radio-tracked intensively over ten years in the main study area. From this set of quadrats three sets were prepared (Fig. 2.1), using radio fixes of (1) all lynx (females and males); (2) females only; and (3) males only.

The eighteen predictor variables (Table 2.1) were selected from among all statistical parameters available according to our empirical knowledge of the lynx's ecological requirements, but also with respect to their availability in digital form.

A previous study of lynx recolonization of the Jura Mountains (Breitenmoser & Baettig 1992), based on random observations, had shown that the lynx distribution was *a priori* determined by the extension of the forest and human activity. Each of these factors can be described in terms of many concurrent environmental predictors and can be correlated to the lynx distribution. The environmental predictors came from the database of the Swiss Federal Statistical Office and from the database of the Federal Office of Topography. Both databases had an accuracy of 1 hectare and were in digital form and ready to be analyzed using GIS ArcView software (ESRI 1996a,b,c). From the hectare information, we then computed a summary statistics to each square-kilometer quadrat: (1) the proportion of the different land use predictors, and (2) the mean value in the case of the quantitative predictors: fringe length, elevation, declivity, human population density, exposure of the slope (predictors 1-18 in Table 2.1).

Table 2.1. Source of the eighteen predictors used in the logistic regression analysis. Sources: GEOSTAT database of the Swiss Federal Statistical Office and FOT = Vector 200 database of the Federal Office of Topography. Predictors had an accuracy of 1 hectare.

Predictor	Units	Sources
1. Forest areas	ha/km^2	GEOSTAT
2. Other wooded areas	ha/km^2	GEOSTAT
3. Fringe length	meter	FOT
4. Horticulture, viticulture	ha/km^2	GEOSTAT
5. Arable land, meadows	ha/km^2	GEOSTAT
6. Pastures	ha/km^2	GEOSTAT
7. Pastures in mountain areas	ha/km^2	GEOSTAT
8. Lakes and rivers	ha/km^2	GEOSTAT
9. Non-productive vegetation	ha/km^2	GEOSTAT
10. Areas without vegetation	ha/km^2	GEOSTAT
11. Built-up areas	ha/km^2	GEOSTAT
12. Rest areas, parks	ha/km^2	GEOSTAT
13. Roads and railways	ha/km^2	GEOSTAT
14. Elevation	meter	GEOSTAT
15. Slope	degree	GEOSTAT
16. Eastness	(cosinus)	GEOSTAT
17. Northness	(sinus)	GEOSTAT
18. Human population density	ind./ha	GEOSTAT

2.4.2. Methods

Generalized linear models (GLM; McCullagh & Nelder 1989; see Nicholls 1989) were used to select those predictors that best explained the presence/absence of lynx. All the analyses were computed in S-PLUS (MathSoft) according to the method described in Guisan, Weiss & Weiss (1999). To facilitate the final ecological discussion of the model, we did not orthogonalize the predictors (e.g., through principal component analysis) prior to the model calibration. Predictors were only selected when they significantly contributed to the deviance reduction, as attested by a $\chi 2$-test (p-value $\leq$ 0.05). In addition, we did not retain the predictors that explained less than one percent of the total deviance, to avoid having predictors with few or no biological meaning appearing in the final model.

We used the Receiver Operating Characteristic (ROC; see Fielding 2001), a threshold-independent measure of accuracy, to evaluate our models. An ROC plot is obtained by plotting the true positive proportion on the *y*-axis against the false positive proportion on the *x*-axis. The area under the ROC function (AUC) is usually taken as the index of performance because it provides a single measure of overall accuracy independent of any particular threshold in the training data (Fielding 2001). Final GLMs were fitted and evaluated using custom S-Plus functions (written by A. Guisan).

We compared the three lynx distribution maps by subtracting the computed probabilities of lynx presence for each quadrat in the GIS: (i) total (both sexes combined) minus female, (ii) total minus male, and (iii) female minus male. Values close to –1 or +1 indicate a high discrepancy between corresponding grid cells, whereas values close to 0 indicate a high conformity.

We extrapolated the resulting model over the entire Swiss Jura Mountains in the GIS. GLM models are readily implemented in a GIS by building a single formula in which each coefficient multiplies its related predictor variable (Guisan *et al.* 1999). The results of the calculations are obtained to the scale of the linear predictor so that the inverse logistic transformation is then necessary to obtain probability values between 0 and 1 at every quadrat of the grid. Finally, we evaluated the resulting models with the spatial behavior of dispersing subadult lynx.

2.5. Results

The proportion of deviance significantly explained (adj-D^2) in the models ranged from 0.39 to 0.44, corresponding to a medium fit of the models (both sexes pooled, females, males). The AUC at calibration and evaluation ranged between 0.84 and 0.90 (Table 2.2).

Three out of eighteen predictors were selected in the final model when presence/absence data of both sexes were used. They were: elevation (second-order polynomial; 20 percent of the deviance explained), slope (20.5 percent) and forest (3.4 percent). The same predictors were retained when presence/absence data from female lynx were used to build the model (elevation second-order polynomial 16.3 percent, slope 19.9 percent, and forest 3.4 percent, respectively). Four predictors were selected when we used presence/absence data from males.

Here, elevation explained 17.4 percent, slope 20.2 percent, forest 4.2 percent and roads 1.4 percent of the deviance.

The comparison of the resulting probabilities showed a high conformity between the three distribution maps. The subtractions of the probability values of most grid cells gave results close to zero. The differences between the probabilities of the 1,085 grid cells from the female versus the male distribution ranged from –0.34 to 0.33. More than 90 percent (978 cells), however, had values between –0.2 and 0.2. When subtracting the female lynx distribution probability map from the total map, all grid cells had a positive value less than 0.12. The differences for the male versus total map comparison ranged from –0.31 to +0.45, with 68 percent (735 cells) falling into the class from –0.2 to 0.2.

Table 2.2. Results of the GLM analyses with the three different sets of response variables. AUC = area under the Receiver Operating Characteristic function.

	Calibration			**Evaluation**
Response variables	**GLM formulas**	**Proportion of explained variance**	**AUC**	**AUC**
P/A of lynx	$elev^2$ + slo + forest	0.435	0.89	0.88
P/A of females	$elev^2$ + slo + forest	0.386	0.87	0.84
P/A of males	elev + slo + forest + roads	0.423	0.90	0.89

We then extrapolated the outcome of the three distribution probabilities over the entire Swiss Jura Mountains (Fig. 2.2). The map of the potential distribution for males shows the most restrictive potential distribution, whereas the map for the females and for both sexes combined showed larger areas in the higher probability classes.

Maps of potential lynx distribution were based on the telemetry locations of resident lynx only. As a supplementary evaluation of the models, we investigated the survival of young, dispersing lynx according to their habitat use. The lynx is a solitary, territorial species, and subadult lynx have to leave the parental home range at the age of about ten months (Breitenmoser *et al.* 1993).

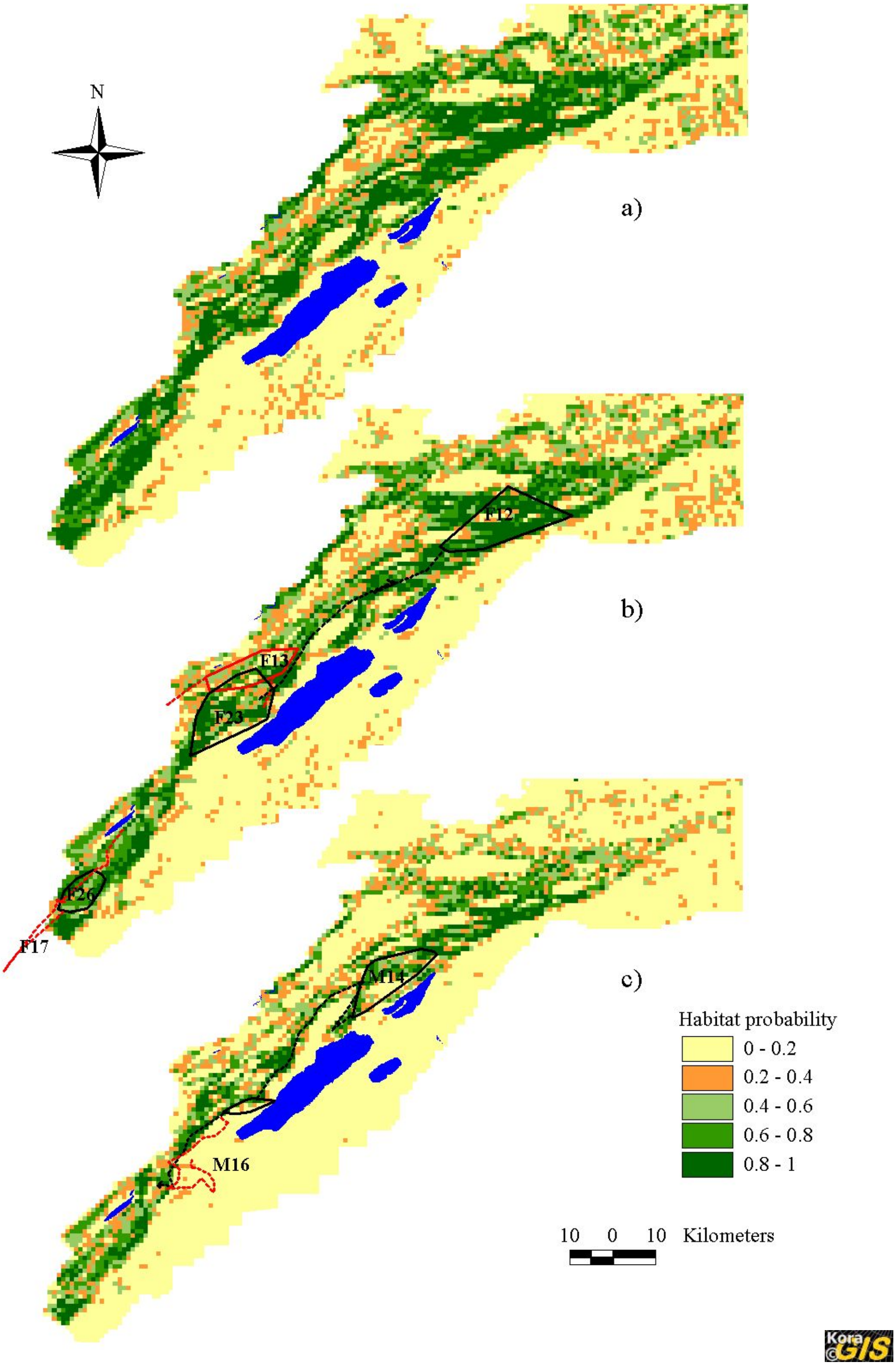

Figure 2.2. Potential distribution of the lynx in the Swiss Jura Mountains according to the model derived from the three sets of response variables (a = both sexes combined, b = females alone, and c = males alone). Lines represent the dispersal route of subadult lynx (F = females, M = males); polygons represent transient or definitive home ranges. Subadult lynx that survived the first year of independence are shown in black, and those that died are shown in red.

One can predict that subadult lynx can only establish a permanent home range if they find free space; otherwise, they would be driven into sub-optimal habitat. Each subadult lynx revealed an individual fate, although the tendency observed was consistent with our habitat model: Two subadult lynx (M14, F12 in Fig. 2.2) dispersed north from our study area into the still-unoccupied part of the Jura Mountains (Breitenmoser & Baettig 1992; Capt, Breitenmoser & Breitenmoser-Würsten 1998). They traveled along the corridors predicted from the habitat model (Fig. 2.2), and both settled in good-quality habitat (Table 2.3).

Table 2.3. Survival of subadult lynx (F = females, M = males) according to their habitat use. The percentage of radio fixes of the subadults during their first year of independence falling into the different lynx habitat probability categories is shown for each response variable set. Highest percentages are in bold. Probability class: 1: 0-0.2; 2: 0.2-0.4; 3: 0.4-0.6; 4: 0.6-0.8; 5: 0.8-1.

		Probability class					
Model	**Lynx**	**1**	**2**	**3**	**4**	**5**	**Destiny**
Both sexes pooled	F12	0.0	4.4	2.2	3.3	**90.1**	Survived
	M14	13.3	3.5	12.1	12.1	**59.0**	Survived
	F23	12.1	4.1	19.7	7.6	**56.5**	Survived
	F26	0.0	1.8	21.4	25.0	**51.8**	Survived
	F13	0.0	17.1	17.2	28.6	**37.1**	Died
	F17	0.0	0.0	11.1	**66.7**	22.2	Died
	M16	**66.8**	4.8	11.9	2.3	14.2	Died
Females	F12	0.0	2.3	4.3	6.6	**86.8**	Survived
	M14	8.1	6.9	6.9	14.5	**63.6**	Survived
	F23	3.6	5.8	10.3	8.5	**71.8**	Survived
	F26	0.0	2.4	7.8	38.0	**51.8**	Survived
	F13	8.6	5.7	20.0	**37.1**	28.6	Died
	F17	0.0	22.2	**44.4**	33.3	0.0	Died
	M16	**61.9**	7.1	16.7	2.4	11.9	Died
Males	F12	4.4	3.3	6.6	6.6	**79.1**	Survived
	M14	14.5	9.8	13.3	16.2	**46.2**	Survived
	F23	21.1	8.5	1.8	20.6	**48.0**	Survived
	F26	2.4	6.0	19.6	**44.0**	28.0	Survived
	F13	8.6	17.1	**34.3**	11.4	28.7	Died
	F17	11.2	22.2	**44.4**	22.2	0.0	Died
	M16	**69.1**	19.0	0.0	4.8	7.1	Died

F12 was poached one year after independence. Two other young lynx (F23, F26) were able to establish home ranges in good-quality habitat inside the study area (Table 2.3). Both had taken over the home ranges of their mothers, after the deaths of the latter. The subadult female (F17) was killed by a car during her dispersal. Finally, the locations of F13 and M16 showed a high share of sub-optimal habitat (Table 1.3). Both lynx died from a natural death during the dispersal – F13 after she had left a temporary home range in marginal habitat (Fig. 2.2).

2.6. Discussion

Our models do not identify single variables but rather the combination of variables limiting lynx distribution. Different combinations of variables can result in the same probability of presence. Slope and elevation were the most powerful variables predicting lynx presence/absence in the three models. This is not so much typical for the lynx, which lives in a large part of its distribution area in lowland forests, but was for our study area, where forested areas are correlated with elevation and slope as a result of human activities. This observation underlines the local nature of our models and shows that the selected variables do not necessarily have a biological value for the species in question, as discussed by Guisan & Zimmermann (2000). Consequently, such models should only be applied to regions similar to those where the basic data were originally gathered. The human impact on carnivores is extremely difficult to evaluate, although today this is the main factor limiting their distribution (Boitani & Cuicci 1993; Mladenoff *et al*. 1995, Corsi, Sinibaldi & Boitani 1998). It is not a simple variable, nor can its distribution be easily mapped. In our model, we suppose that the human impact is included in other variables such as road density, human population density, or land use. Even in areas of generally good habitat, roads, which have a limited spatial extension and seem not to reduce the habitat quality considerably, can be a risk factor, as demonstrated by the fate of F17 (Fig. 2.2). Failure to incorporate such spot-like or linear, but critical habitat features or ecological factors such as prey availability, competition, predation (Pearce *et al.* 2001) and the like can lead to prediction errors. Data on number and distribution of roe deer and chamois, the main prey of lynx in the study area (Jobin *et al*. 2000), are presently not available in adequate form or precision to be incorporated into a habitat model. However, as ungulate distribution is habitat dependent, too, we can assume that the presence/absence approach of lynx at least partly reflects prey availability.

Most classifiers assume that class membership is known without errors (Fielding 2001). Lynx were not located in all favorable lynx zones within the study area, because peripheral spots of good habitat (1) might not be connected to the lynx zone, (2) might be occupied by neighboring lynx, or (3) surveillance density might have been insufficient. It is a shortcoming of our method that the defined categories (presence/absence) are not exclusive. Assuming absence of a species where it was actually present is a type II error that could be corrected with adequate sample size and monitoring duration to increase the power of the statistical evaluation (Morrison, Marcot & Mannan 1998). To minimize this error, we restricted our sample area to the southern portion of Swiss Jura Mountains, where lynx were followed most intensively by telemetry.

The model provides a tool for the conservation and the management of the lynx in the Jura Mountains An early study by Breitenmoser & Baettig (1992), based on random observations of lynx gathered from 1972 to 1987, revealed the discontinuous distribution of the lynx in the Jura Mountains and a lack of observations in the central part of the range (Figs. 2.1, 2.2). Our model confirms that the central part especially for males, seems to be a sub-optimal habitat (Fig. 2.2). So far, the AUC values from the evaluation as well as the anecdotal observations of dispersing subadult lynx seem to confirm the validity of the model for the Jura Mountains None of the subadults settled in the central part of the Jura Mountains but continued on to adjacent areas (Figs. 2.1, 2.2). All subadult lynx dispersed through corridors predicted by the model. The final test for our model, however, will be the future spread of the lynx population through the northern part of the Swiss Jura Mountains The model can predict the potential distribution of the lynx in the Jura Mountains and, when based on knowledge of the land tenure system of the resident lynx (Breitenmoser *et al.* 1993), allows estimation of the possible population size. Such knowledge will be crucial for the conservation and management of this large carnivore species living in such close proximity to intensive human activities. Since large-carnivore populations are difficult to census over vast areas, a modeling approach based on high-quality, local data from telemetry may be more efficient. Decisions will have to be made in regard to the choice of the model and the threshold value. We prefer the model built from presence/absence data of both sexes, because this had the best fit (Table 2.2) and represents best the need of the population as a whole.

In conservation-oriented models, the overestimation of false-positive locations (the model predicts presence of a species when in fact it is absent) versus the overestimation of false negative locations includes different conservation risks (see also Fielding 2001). The balance between false positives and false negatives is defined through the threshold value and must be set according to the question to be answered. The lower the threshold value, the higher the percentage of all quadrats containing lynx fixes included, but also the higher the share of quadrats without any locations.

Another practical use of the model will be the evaluation of potential connections of the Jura population with neighboring lynx populations in the Alps or in the Vosges Mountains For this purpose, however, we will have to expand our model into France and test its capability to predict corridors or barriers.

2.7. References

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Chapter 3. How well can ENFA predict species' distribution? The case of the Eurasian lynx (*Lynx lynx*) in Switzerland

3.1. Abstract

Radio-telemetry fixes are often used as input data to calibrate habitat models. Radio-telemetry is the only way to gather accurate and unbiased data on habitat use of elusive larger terrestrial mammals in a landscape. However it is time consuming and expensive, and can therefore only be applied in limited areas. Habitat models extrapolated over large areas can in turn be problematic, as habitat characteristics and availability may change from one area to the other. We analysed the predictive power of Ecological Niche Factor Analysis (ENFA) in Switzerland with the lynx as focal species. Lynx were re-introduced since the 1970s into different mountain ranges in western and central Europe. Up to now, all re-introduced populations remained small and isolated. Predicting the further expansion of the population is important as the return of this large cat – which preys upon small ungulates and occasionally kills sheep – is still a matter of controversy, leading to management conflicts.

ENFA differs from the classical multivariate analyses in so far that it requires only presence data. Fourteen environmental variables describing land use and human "disturbances" were used to compute the models. The response data set was divided into three sets according to the geographic regions of Switzerland (Jura Mountains, Prealps, Alps). A total of six different set combinations were used for model calibration. Each model was validated with its own calibration set through Jack-knife cross-validation, but also with the response variable of the remaining regions, in order to (i) test which data set combination would produce the best prediction for each region and (ii) to see if model prediction were reliable in areas not used to build the model.

According to our results, the optimal sampling strategy to predict species distribution in an Alpine area lacking available data would be to pool presence cells from contrasted regions (e.g. Jura Mountains and Prealps), whereas in regions with a low ecological variance, like the Jura Mountains, only local presence cells should be used for the calibration of the model. ENFA analyses were particularly robust regarding the quality of the input data to predict the distribution of the species in regions not used in the calibration phase.

Lynx were essentially linked to forest areas with high values of fringe length and high levels of extensive agricultural areas – mainly pastures – in mountain regions. On the other hand they tended to avoid zones of permanent human activities (settlements, intensive agricultural areas). However, distance to roads – which reflect the impact of humans in remote areas – did not come out in our models, suggesting that lynx, when ranging in good habitats, are adapted to human presence.

Our models allow among others to predict the extension, distribution and fragmentation of suitable lynx habitat. When combined with knowledge on the land tenure system of resident lynx, they can be useful to estimate the potential size of the lynx populations, and therefore provide a tool for the conservation and management of the lynx.

3.2. Introduction

Most empirical habitat suitability models share similar principles: they need to be calibrated with presence/absence data. This is for instance the case for the General Linear Models (GLM; McCullagh & Nelder 1983; see Nicholls 1989) and the Discriminant Function Analysis (DFA; Verbyla & Litvaitis 1989; Dubuc *et al*. 1990; Livingston *et al*. 1990). Presence and – more important - absence data must be gathered according to a rigorous protocol to grant an accurate analysis; lack of observation does not per se mean absence of the studied species. Data collection ranges from collection of signs of presence (Jaberg & Guisan 2001; Hirzel & Arlettaz 2003; Reutter *et al*. 2003) over snow-tracking (Wabakken *et al*. 2001; Andrén *et al*. 2002) and photo-trapping (Karanth & Nichols 1998; Moruzzi *et al*. 2002) to radio-telemetry studies (Mladenoff *et al*. 1995; Zimmermann & Breitenmoser 2002). The only year-round method allowing to observe an elusive (mammal) species such as a large carnivore unbiased from human activities is radio-telemetry. But this method is expensive and time consuming, and can therefore generally not be used for large areas and over a long-term period. Consequently, radio-telemetry can only be applied in reference areas representing a fraction of the distribution area of the species. Another flaw of radio-telemetry is the impossibility to create an unbiased sample of unused sites, because there is an infinite number of points in the landscape, many of them likely to be used by the species without being recorded (Boyce *et al*. 2002).

The Ecological Niche Factor Analysis (ENFA, Hirzel *et al*. 2002) uses presence data only. This approach is recommended when absence data are not available (most data banks, radio-telemetry), unreliable (most cryptic and rare species) or meaningless (invaders) (Hirzel, Helfer & Metral 2001). The ENFA computes a habitat suitability model by comparing the environmental niche of the species to the environmental characteristics of the entire study area.

Habitat models, on the other hand, are used not only to predict habitat suitability in the reference area (where the basic data were collected) but also to forecast habitat suitability in areas devoid of data. This process has for instance been applied in reintroduction programs (Mladenoff *et al*. 1997; Breitenmoser *et al*. 2000) or feasibility studies (Schadt *et al*. 2002). Such extrapolations frequently give rise to some problems, as habitat characteristics may be different in the new area, what will usually lead to a change in the model coefficients.

The aim of our study was to see how ENFA performs in areas from which no data have been used to build the model, in order to test the predictive power of such analyses. As radio-telemetry data from several long-term studies in different regions of Switzerland were available, Eurasian lynx (*Lynx lynx*) was chosen as focal species. Lynx was re-introduced in the Swiss Alps and the Jura Mountains in the 1970s (Breitenmoser, Breitenmoser-Würsten & Capt 1998). There are actually two established lynx populations in Switzerland, one in the Jura Mountains, the other in the north-western Swiss Alps. Up to 2001, the species occupied only moderately the central and south-western Swiss Alps, but had not yet settled in the eastern and southern Alps of Switzerland. To counteract the uneven distribution of this species in Switzerland, six individuals (three males and three females) were translocated from the north-western Alps to the north-eastern Prealps of Switzerland in Spring 2001 and three more (one male and two females) from the Jura Mountains in Spring 2003. This gave us the opportunity to test which data set would best predict the habitat use of the translocated animals. To evaluate the predictive power of ENFA, we split our response data sets according to the geographical delimitation of Switzerland (Fig. 3.1; Jura, Prealps and Alps). Telemetry data from the translocated lynx were not included in the calibration of the model, but used for its validation. The results of these analyses allow us to test the model predictions for new areas, as well as to define a sampling strategy for future analyses.

3.3. Study area

Switzerland was divided in five regions (Fig 3.1; Jura Mountains, Plateau; Prealps, Alps, southern Alps) according to the forest zones of Switzerland (Brändli & Strobel 1988). This classification is based on the different wood productivities prevailing in each region (Ott 1972).

The Jura Mountains are a series of parallel secondary limestone mountain chains forming the north-western border of Switzerland with France. The altitude ranges from about 500 m to 1,679 m (Mont Tendre). Deciduous forest along slopes and coniferous forest on the ridges cover 48% of this mountain range. Cultivated areas are typically pastures. The human population reaches a density of 153/km^2 in most parts of the Swiss Jura Mountains. The Plateau (= flat country) lies between the Jura Mountains and the Prealps, about 395 m above sea level in average elevation and some 50 km wide; it extends from Lake Geneva in the extreme southwest to the Lake of Constance in the extreme northeast of the country.

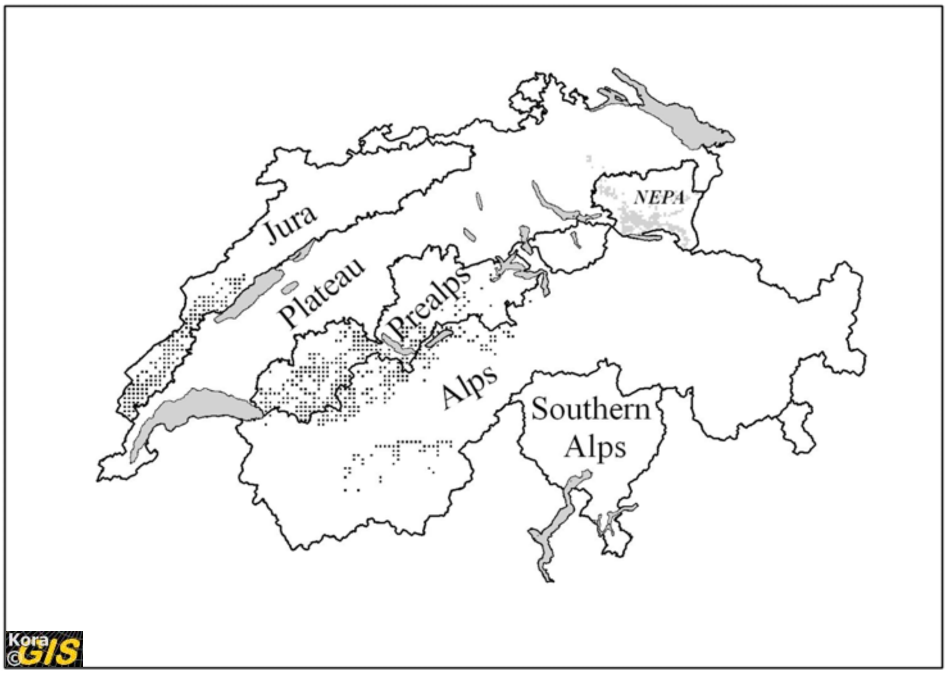

Figure 3.1. Geographic regions of Switzerland (Jura, Plateau, Prealps, Alps and southern Alps) and study areas of the *Swiss Lynx Project*. The dark 1x1-km raster in the south part of the Jura Mountains, in the Prealps and the Alps, represent the square kilometre cells with lynx radio fixes and/or kill sites that have been used to build and validate the models. The light 1x1-km raster in the north-eastern Prealps (*NEPA*) were only used for the validation of the models.

Contrary to its name, the Plateau is rather hilly. Intensive agriculture is the predominant landscape feature covering more than 50% of the area. Most of the Swiss population is concentrated on the Plateau, reaching a density of 460/km^2. The Alps in the broad sense encompass the Prealps, the Alps and the southern Alps and cover more than 70% of the Swiss area. Rocks, glacier and perpetual snow make up to 24% of this mountain range. Forests extend along steep slopes up to timberline at 1,800-2,200 m, forming ribbons along the mountain slopes and covering less than 35% of the Alps. Lower ridges and slopes have been deforested a long time ago and provide summer pastures for cattle. The valley bottoms have been deforested as well and are densely populated. The human population is less clustered compared to the Jura Mountains and reaches a density of 58/km^2 in most parts of the mountain range.

3.4. Material and method

The ENFA analyses have been performed with *Biomapper 2.1* (Hirzel, Hausser & Perrin 2002; see Chapter 1 for details). The whole of Switzerland was chosen as reference area, and modelled as a raster map based on the Swiss Coordinate System (plane projection), comprising 39,028 squares of 1 km. The environmental predictors came from the database of the Swiss Federal Statistical Office (SFSO) and from the Federal Office of Topography (FOT). Both data sets were in digital form and ready to be used in the Geographic Information System (GIS) ArcView (ESRI 1996a,b,c) and IDRISI 2.0 (Eastman 1997). The twenty-four main land-use classes of the SFSO have first been pooled into nine categories according to similarities between classes and to our knowledge of lynx biology (Breitenmoser-Würsten *et al*. 2001; Zimmermann & Breitenmoser 2002; Table 3.1). From this hectare information a summary statistics was then computed to each square-kilometre: (i) the length in the case of the fringe (forest edge); (ii) the frequency of the different land use predictors and southern aspects in each square kilometre (eco-geographical variables 2-9 in Table 3.2); (iii) the mean value in the case of quantitative eco-geographical variables like elevation, slope, distance to freeway, distance to major roads, distance to minor roads, distance to town and human population density (eco-geographical variables 10-16 in Table 3.2). Prior to the analyses the environmental predictors have been normalized as much as possible using the Box-Cox transformation (Box & Cox 1964). Slope and elevation were highly correlated with the remaining variables and have therefore been removed in the final analyses.

Data from five radio-telemetry studies were used: (1) from the north-western and central Alps (Haller & Breitenmoser 1986, Breitenmoser & Haller 1987); (2) from the southern Alps (Haller 1992); (3) from the north-western Alps (Breitenmoser-Würsten *et al.* 2001; unpublished data); (4) from the Jura Mountains (Breitenmoser *et al*. 1993; unpublished data); and (5) from the north-eastern Swiss Alps (Ryser *et al*. 2004). A total of 8,227 radio fixes accurate to the square kilometre and 1,480 kill site locations of 71 resident lynx followed from 1983 to 2002 were used to generate and/or to validate the models. The response variable was the presence of lynx in each kilometre square. Lynx was considered to be present in each square containing one or more telemetry fix/kill site. This response variable was then sampled according to a regular sampling, also called grid-sampling design (Hirzel & Guisan

2002). In our case, we paid attention to leave out at least one presence cell between every second in order to reduce spatial autocorrelation (Fig. 3.1).

Table 3.1. Land-use categories used in the analyses. The twenty-four land-use categories of the Swiss Federal Statistical Office (SFSO) have been combined in nine categories according to similarities between categories and our knowledge of lynx biology.

24 land-use categories of the SFSO	SFSO land-use categories used for the analyses
Closed forest	**Closed forest**
Open forest	**Open forest**
Bushes Small woods	**Other wooden areas**
Vineyards Fruit-growing areas Horticultural areas Agricultural areas Green urban areas	**Intensive agricultural areas**
Home pastures Hey production areas Pastures in the Jura Mts. and the Alps Unproductive vegetation	**Extensive agricultural areas**
Water bodies Water course	**Water**
Areas without vegetation	**Areas without vegetation**
Building area Industrial area Industrial buildings Industrial swing Special settlements	**Urban areas**
Road network Railway network Airports	**Roads and railways**

Table 3.2. Source of the sixteen predictors used in the ENFA analysis. Sources: GEOSTAT database of the Swiss Federal Statistical Office and FOT = Vector 200 database of the Federal Office of Topography. Predictors had an accuracy of 1 hectare.

Predictor	Code	Units	Sources
1. Fringe length	Frl	meter	GEOSTAT
2. Close forest	Cfor	ha/km^2	GEOSTAT
3. Open forest	Ofor	ha/km^2	GEOSTAT
4. Other wooden areas	Owa	ha/km^2	GEOSTAT
5. Extensive agricultural areas	Extaa	ha/km^2	GEOSTAT
6. Intensive agricultural areas	Intaa	ha/km^2	GEOSTAT
7. Urban areas	Urba	ha/km^2	GEOSTAT
8. Roads and railways	Rr	ha/km^2	GEOSTAT
9. Southern aspect	Sa	ha/km^2	GEOSTAT
10. Mean elevation	Malt	meter	GEOSTAT
11. Mean slope	Mslo	degree	GEOSTAT
12. Mean distance to minor roads	Mdmir	meter	FOT
13. Mean distance to main roads	Mdmar	meter	FOT
14. Mean distance to freeway	Mdf	meter	FOT
15. Mean distance to settlements	Mds	meter	FOT
16. Human population density	Hpd	ind./ha	GEOSTAT

From this set of species cells seven subsets were compiled, using presence cells laying (1) in the Prealps, Alps and in the Jura Mountains (*ALL*); (2) in the Jura Mountains and the Prealps (*J-PA*); (3) in the Jura Mountains and the Alps (*J-A*), (4) in the Prealps and the Alps (*PA-A*); (5) in the Jura Mountains (*J*); (6) in the Prealps (*PA*); and (7) in the Alps (*A*). Each set has been used in turn to calibrate the models using ENFA. This procedure allowed to test how models perform in regions from where no presence data have been included in the analyses and which combination of response data sets would produce the best model predictions for each area. The response data set from the north-eastern Prealps (*NEPA*) has only been used to validate the models.

The lack of absence data makes predictive power assessment of a presence-only based model difficult. One possibility is to count the proportion of evaluation points occurring in the predicted core habitat (HS>50). However, according to this "absolute validation index" method, a model predicting a value > 50 for every cell would be absurdly seen as perfect as it would have 100% of the evaluation points above 50. To overcome this problem when comparing algorithms, a "contrast validation index" (Hirzel & Arlettaz 2003) was computed by comparing the above index to the value that could be expected by chance: let *Av* be the proportion of validation points being in the core habitat and *Ag* be the proportion of cells > 50 for the whole study area. The contrast *C* value is then given by :

$$C = Av - Ag$$

This contrast index ranges from 0 to (1–*Ag*), a value of 0 meaning that there is no difference between the model predictions, what would have been achieved by a random model. The higher the index the better the model (both more accurate and more "contrasted"). The accuracy of these models was evaluated through jack-knife cross-validation (Fielding & Bell 1997). Huberty's rule of thumb was used to determine the model training to testing ratio:

$$t = \frac{1}{1 + \sqrt{(p-1)}}$$

where *t* and *p* are the proportion for the test data and the number of environmental predictors, respectively. A testing ratio of 22% was determined and a k-fold partition of five groups considered. Using cross-validation procedures, we trained our model iteratively on four of the five data sets using ENFA analyses. Validation was based on the remaining testing set. The resulting k-fold suitability maps of each model were also validated with the remaining testing set of each subset (*J, PA, A, NEPA*) in order to see which models produce the best predictions in each area.

The resulting seven habitat suitability maps (*J, PA, A, J-PA, J-A, PA-A, ALL*) have subsequently been compared in the GIS by computing a correlation coefficient matrix between them.

3.5. Results

By applying the ENFA method to the calibrations sets (Table 3.3) of each region (*J, PA, A, J-PA, J-A, PA-A, ALL*) we got an overall *marginality* of *M* ranging from 0.722 to 1 and an overall *specialization* value of *S* ranging from 1.26 to 1.79, i.e. a *tolerance* of *T* (1/*S*) ranging from 0.56 to 0.792, indicating that lynx' habitat differs from the average condition in Switzerland, and that lynx are not very restrictive in the range of conditions they withstand. According to the Mac-Arthur's Broken-Stick distribution two factors (*M, S1*) have been retained in all models except the one built with only presence data from the Alps where three factors (*M, S1, S2*) have been retained.

Table 3.3. Results of the ENFA analyses with seven different sets of response variables. The response variable is the presence of lynx in each square kilometre. Radio fixes (n = 8227) and locations of lynx kills (n = 1480) were used to generate and validate the models. Positive values on the marginality factor mean that lynx prefers locations with higher values on the corresponding ecogeographical variable (EGV) than the Swiss average. Factors: *M = Marginality*, *S1* and *S2 = Specialization*. Bold = ecogeographical variables (EGV) with an absolute score ≥ 0.2. The amount of the specialization accounted for is given in each column heading. The definition of the variables' code is given in Table 3.2.

Models	**Results**	**Code**	***M***	***S1***	***S2***
	% of the total *S* explained		**32.5%**	**30.6%**	
J	Sample size N=140 Number of factor: 2 Explained variance: 0.816 Marginality: 0.73 Tolerance: 0.56	**Cfor**	**+0.717**	0.005	
		Frl	**+0.390**	0.091	
		Ofor	**+0.280**	0.172	
		Mds	+0.062	**0.373**	
		Mdf	+0.038	**0.870**	
		Owa	+0.020	0.010	
		Sa	+0.017	**0.232**	
		Extaa	+0.001	0.023	
		Rr	-0.057	0.030	
		Intaa	-0.185	0.025	
		Mdmir	-0.192	0.099	
		Urba	**-0.210**	0.001	
		Hpd	**-0.254**	0.015	
		Mdmar	**-0.257**	0.022	
	% of the total *S* explained		**23.6%**	**20.7%**	
PA	Sample size N=212 Number of factor: 2 Explained variance: 0.722 Marginality: 0.928 Tolerance: 0.7	**Frl**	**+0.467**	0.104	
		Ofor	**+0.405**	0.031	
		Extaa	**+0.381**	0.063	
		Cfor	**+0.378**	0.077	
		Owa	**+0.244**	**0.434**	
		Mdmir	+0.173	0.006	
		Mdf	+0.094	**0.314**	
		Mds	+0.078	**0.798**	
		Mdmar	+0.002	0.035	
		Sa	-0.022	0.068	
		Rr	-0.146	0.019	
		Urba	**-0.247**	0.136	
		Hpd	**-0.247**	0.089	
		Intaa	**-0.285**	0.147	
	% of the total *S* explained		**22.8%**	**20.9%**	**13.2%**
A	Sample size N=190 Number of factor: 3 Explained variance: 0.716 Marginality: 1.0 Tolerance: 0.745	**Ofor**	**+0.525**	0.160	0.130
		Frl	**+0.421**	0.164	**0.331**
		Owa	**+0.338**	**0.204**	0.158
		Cfor	**+0.329**	0.153	**0.497**
		Mdf	**+0.303**	0.184	0.101
		Extaa	**+0.258**	0.001	**0.665**
		Mdmar	+0.121	0.139	0.171
		Mdmir	+0.102	0.098	0.166
		Mds	+0.034	**0.820**	0.162
		Sa	-0.114	0.084	0.063
		Rr	-0.146	0.018	0.015
		Urba	-0.170	**0.329**	0.129
		Hpd	-0.188	0.092	0.014
		Intaa	**-0.202**	0.151	**0.213**

	% of the total *S* explained		**20.5%**	**23.8%**
J-PA	Sample size N=352 Number of factor: 2 Explained variance: 0.722 Marginality: 0.794 Tolerance: 0.756	**Cfor**	**+0.528**	0.021
		Frl	**+0.471**	0.012
		Ofor	**+0.388**	0.086
		Extaa	**+0.268**	0.197
		Owa	+0.179	**0.312**
		Mdf	+0.080	**0.386**
		Mds	+0.077	**0.801**
		Mdmir	+0.052	0.076
		Sa	-0.009	0.137
		Mdmar	-0.093	0.041
		Rr	-0.124	0.011
		Urba	**-0.250**	0.193
		Hpd	**-0.267**	0.033
		Intaa	**-0.268**	0.001
	% of the total *S* explained		**21.9%**	**23.7%**
J-A	Sample size N=330 Number of factor: 2 Explained variance: 0.728 Marginality: 0.815 Tolerance: 0.792	**Cfor**	**+0.507**	0.041
		Ofor	**+0.480**	0.181
		Frl	**+0.448**	0.135
		Owa	**+0.248**	**0.206**
		Mdf	**+0.230**	**0.322**
		Extaa	+0.184	0.114
		Mds	+0.048	**0.801**
		Mdmir	0.000	0.030
		Mdmar	-0.012	0.050
		Sa	-0.074	0.136
		Rr	-0.125	0.035
		Urba	**-0.201**	**0.317**
		Intaa	**-0.214**	0.123
		Hpd	**-0.231**	0.085
	% of the total *S* explained		**24.4%**	**20.6%**
PA-A	Sample size N=402 Number of factor: 2 Explained variance: 0.725 Marginality: 0.95 Tolerance: 0.752	**Ofor**	**+0.472**	0.093
		Frl	**+0.452**	**0.218**
		Cfor	**+0.360**	0.016
		Extaa	**+0.326**	0.083
		Owa	**+0.295**	**0.280**
		Mdf	**+0.201**	**0.235**
		Mdmir	+0.141	0.096
		Mdmar	+0.061	0.119
		Mds	+0.057	**0.838**
		Sa	-0.068	0.068
		Rr	-0.148	0.036
		Urba	**-0.213**	**0.249**
		Hpd	**-0.222**	0.065
		Intaa	**-0.248**	0.069
	% of the total *S* explained		**22.5%**	**22.5%**
ALL	Sample size N=542 Number of factor: 2 Explained variance: 0.725 Marginality: 0.846 Tolerance: 0.787	**Frl**	**+0.463**	0.126
		Cfor	**+0.459**	0.001
		Ofor	**+0.456**	0.118
		Extaa	**+0.271**	0.086
		Owa	**+0.250**	**0.270**
		Mdf	+0.175	**0.305**
		Mdmir	+0.074	0.014
		Mds	+0.061	**0.833**
		Mdmar	-0.006	0.048
		Sa	-0.053	0.110
		Rr	-0.136	0.030
		Urba	**-0.224**	**0.275**
		Hpd	**-0.241**	0.072
		Intaa	**-0.248**	0.079

3.5.1. Jura Mountains (*J*)

Marginality coefficient of the ENFA method applied to calibration data from the *J* (Table 3.3) accounts for 32.5% of the total *specialization* and showed that in this area, lynx were essentially linked to closed forest and open forest areas with high values of fringe length (bold values in Table 3.3). On the other hand, they tended to avoid areas with high human population densities and urban areas (bold values in Table 3.3). In this region lynx were closer to main roads than the Swiss average. Southern aspect as well as mean distance to freeway, mean distance to settlements, other wooden areas, extensive agricultural areas, roads and railways, mean distance to minor roads, and intensive agricultural areas contributed only marginally to this factor. The second factor (*S1*: 30.6% of the *specialization*) accounted for more *specialization*, in particular mean distance to freeway, mean distance to settlements and southern aspect.

3.5.2. Prealps (*PA*)

Marginality coefficient explained 23.6% of the total *specialization*. Lynx were linked to the same variables as in the *J*, and additionally to extensive agricultural areas and other wooden areas (bold values in Table 3.3). Compared to the *J*, they furthermore avoided areas of intensive agricultural areas (bold values in Table 3.3). All other categories had only marginal effects. The second factor (*S1*: 20.7% of the *specialization*) accounted for more *specialization*, in particular other wooden areas, mean distance to freeway, and mean distance to settlements.

3.5.3. Alps (*A*)

Marginality coefficient explained 22.8% of the total *specialization*. Lynx showed a preference for the same variables as in the *PA*, and additionally, to mean distance to freeway (bold values in Table 3.3). Lynx tended to avoid areas with intensive agricultural areas (bold values in Table 3.3). The second factor (*S1*: 20.9% of the *specialization*) and the third factor (*S2*: 13.2% of the *specialization*) account for more *specialization*, in particular fringe length, other wooden areas, close forest, extensive agricultural areas, mean distance to settlements, urban areas, and intensive agricultural areas.

3.5.4. Jura Mountains-Prealps (*J-PA*)

Marginality coefficient (Table 3.3) accounted for 20.5% of the total *specialization* and showed that in this area, lynx showed a preference for the same variables as in the *J*, and additionally to extensive agricultural areas (bold values in Table 3.3). Contrarily, they tended to avoid the same variables as in the *PA* (bold values in Table 3.3). The second factor (*S1*: 23.8% of the *specialization*) accounted for more *specialization*, in particular other wooden areas, as well as mean distance to freeway and mean distance to settlements.

3.5.5. Jura Mountains-Alps (*J-A*)

Marginality coefficient (Table 3.3) accounted for 21.9% of the total *specialization* and showed that in this area, lynx were essentially linked to the same variables as in the *J*, and additionally to other wooden areas and mean distance to freeway (bold values in Table 3.3). On the other hand, they tended to avoid the same variables as in the *PA* (bold values in Table 3.3). The second factor (*S1*: 23.7% of the *specialization*) accounted for more *specialization*, in particular other wooden areas, mean distance to freeway, mean distance to settlements, and urban areas.

3.5.6. Prealps-Alps (*PA-A*)

Marginality coefficient (Table 3.3) accounted for 24.4% of the total *specialization* and showed that in this area, lynx were essentially linked to the same variables as in the *A* (bold values in Table 3.3). On the other hand, they tended to avoid the same variables as in the *PA* (bold values in Table 3.3). The second factor (*S1*: 20.6% of the *specialization*) accounted for more *specialization*, mostly regarding fringe length, other wooden areas, mean distance to freeway, mean distance to settlements, and urban areas.

3.5.7. All data sets combined (*ALL*)

Marginality coefficient applied to the combined dataset *ALL* explained 22.5% of the *specialization* and showed that in these areas, lynx preferred and avoided the same variables as in the *PA* (bold values in Table 3.3). The next factors accounting for more *specialization*, in particular other wooden areas, mean distance to freeway, mean distance to settlements, and urban areas for the second factor (*S1*: accounted for 22.5% of the *specialization*).

3.5.8. Validation and conformity of the habitat suitability maps

Suitability maps (Fig. 3.2) were built from the first two factors except the model built with calibration data from the Alps (*A*) where three factors have been used (see above). For each cross validation group the distribution of the Habitat Suitability values (HS) of the global distribution was compared with the k-fold validation set originating from the same area as the calibration set but also with independents set stemming from the remaining areas (*J, PA, A, NEPA*; Fig. 3.3). In the Jura Mountains (*J*) model predictions were better with the model built with presence data from the Jura Mountains only, whereas in the Prealps, the Alps, and in the north-eastern Prealps of Switzerland, the combination *J-PA*, *J-A* and *ALL* gave the best results (Fig. 3.3). Species' distribution predictions in regions of which no presence cells have been used to calibrate the model were improved when presence cells from contrasted regions were combined (e.g. Jura/Prealps, Jura/Alps). Combining presence cells from less contrasted regions like the Prealps and the Alps did not improve model predictions. The proportion of validation points being in the core habitat *Av* and the contrast index *C* were positively correlated (Spearman $r=0.935$, $N=140$, $p<0.05$; Fig. 3.4), showing that both indexes are closely linked.

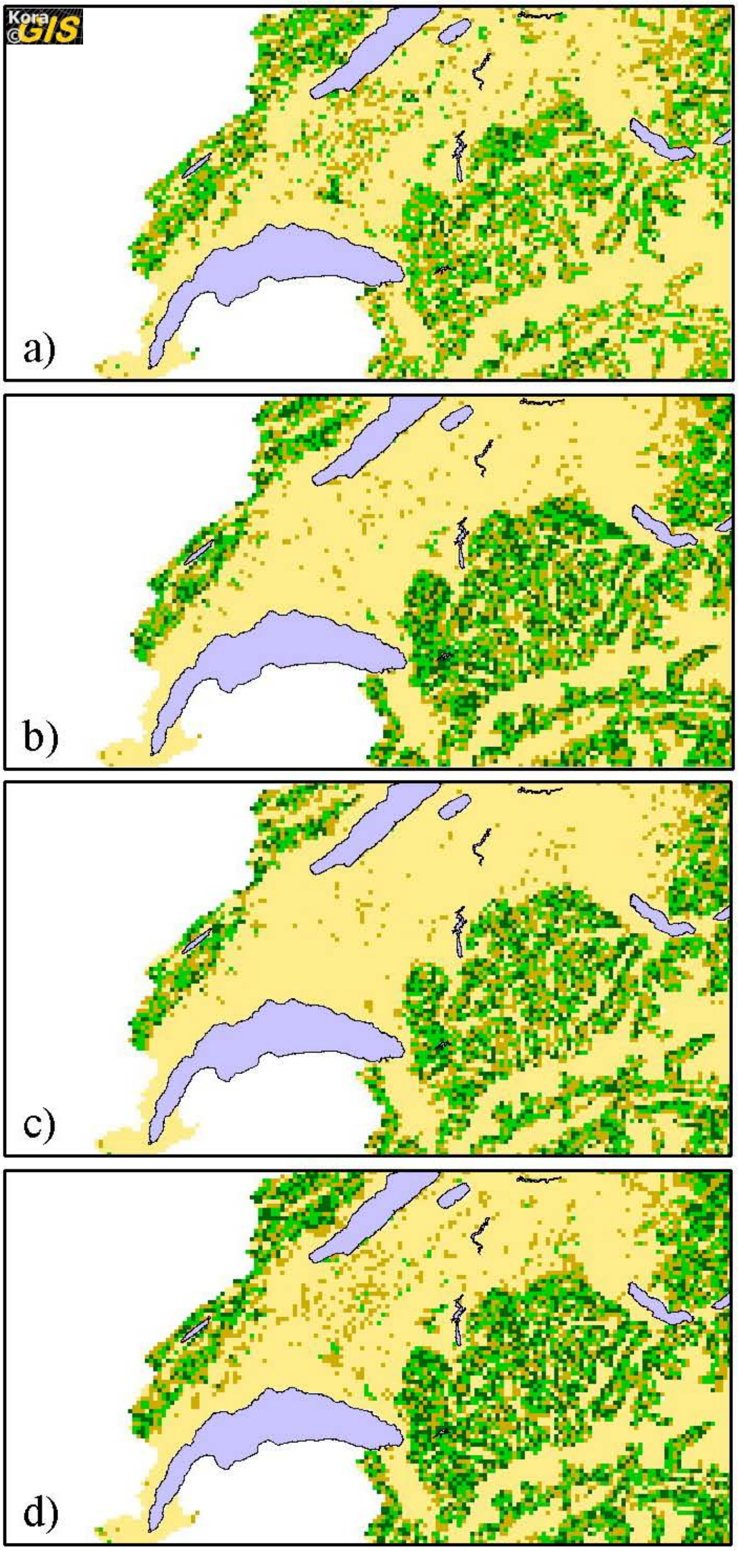

Figure 3.2. Habitat suitability maps for the lynx according to the models derived from four sets of response variables (a=Jura Mountains, b=Prealps, c=Alps, and d=Jura Mountains and Prealps combined).

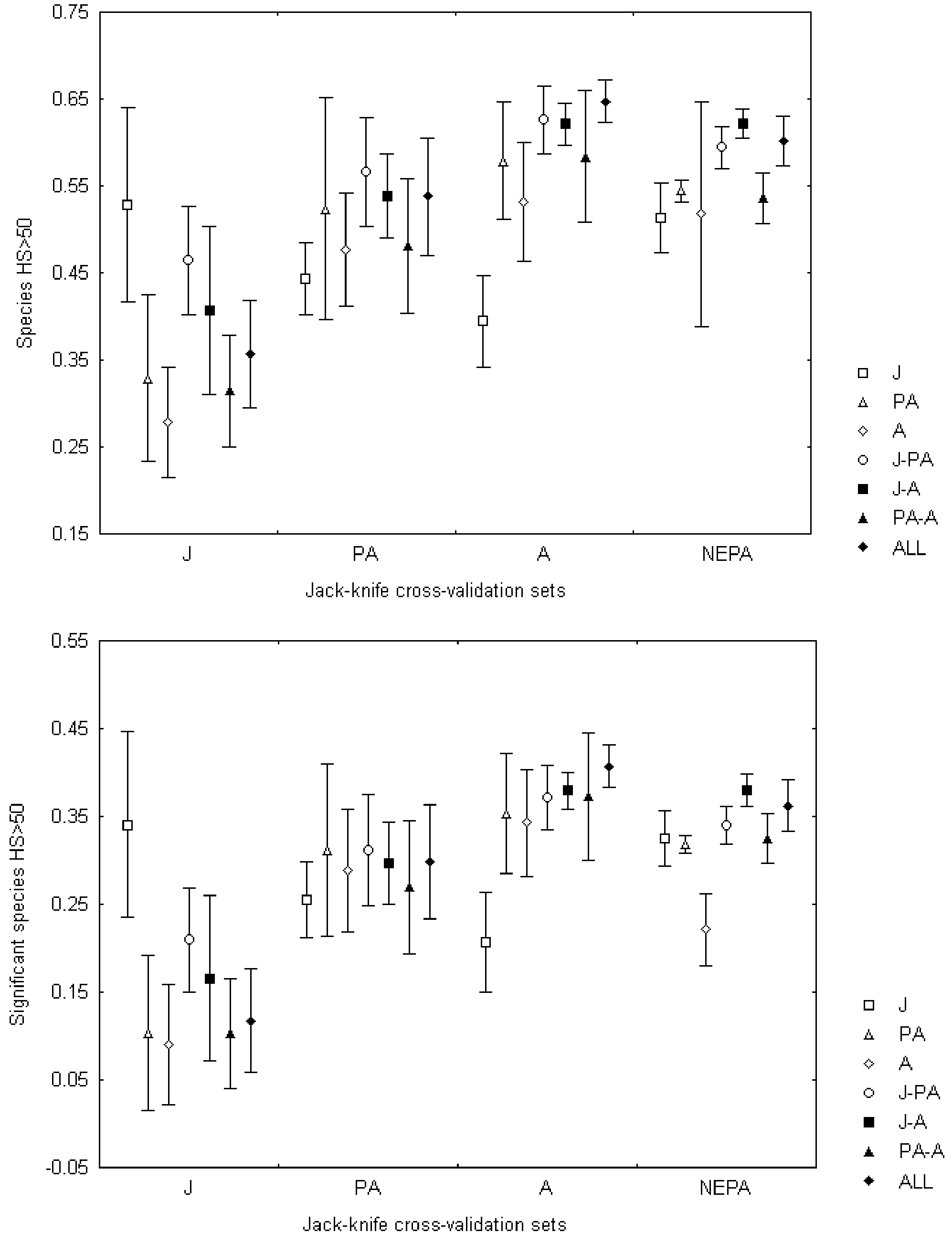

Figure 3.3. The proportion of presence cells from the different validation sets (*J*=Jura, *PA*=Prealps, *A*=Alps, *NEPA*=north-eastern Prealps) being in the core habitat *Av* (upper graph) and the contrast *C* (lower graph) value for each model (*J*=Jura Mountains, *PA*=Prealps, *A*=Alps, *J-PA*=Jura Mountains and Prealps, *J-A*=Jura and Alps, *ALL*=Jura Mountains, Prealps and Alps). The mean and standard deviation (SD) are indicated for each cross-validation set.

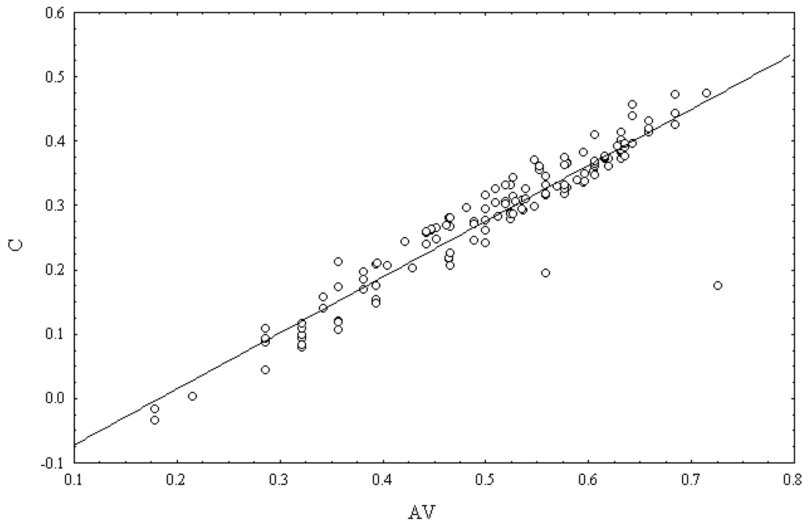

Figure 3.4. Correlation between the proportion of validation points being in the core habitat *Av* and the contrast *C* value.

The HS maps were highly correlated (r: 0.85-0.98; Table 3.4) except the one built with presence data from the Jura Mountains where correlation coefficients ranged from 0.58 to 0.76.

Table 3.4. Correlations between the different HS maps (*J* = Jura; *PA* = Prealps; *A* = Alps; *J-PA* = Jura and Prealps; *J-A* = Jura and Alps; *PA-A* = Prealps and Alps; *ALL* = Jura, Prealps and Alps).

	J	***PA***	***A***	***J-PA***	***J-A***	***PA-A***	***ALL***
J	1	-	-	-	-	-	-
PA	0.60	1	-	-	-	-	-
A	0.58	0.92	1	-	-	-	-
J-PA	0.76	0.93	0.85	1	-	-	-
J-A	0.75	0.89	0.88	0.96	1	-	-
PA-A	0.60	0.97	0.97	0.92	0.91	1	-
ALL	0.70	0.95	0.91	0.98	0.98	0.97	1

3.6. Discussion

3.6.1. Lynx habitat preferences

Lynx are linked to forest areas with high values for fringe length (forest edge). This is not surprising for a species whose range in Europe overlaps more or less with the distribution of forests (Breitenmoser *et al*. 2000). A high score of fringe length could be correlated with the presence of roe deer, lynx' main prey (Breitenmoser & Haller 1987; Haller 1992; Jobin, Molinari & Breitenmoser 2000; Molinari-Jobin *et al*. 2002). Studies analysing the habitat selection of ungulates (Chang, Verbyla & Yeo 1995) showed that deer home ranges had higher old-growth/clear-cut edge densities than expected by chance. In our study, the first factor, called *marginality*, is positively correlated to the frequency of extensive agricultural areas, in mountains areas mainly represented by pastures. Recent telemetry studies in the Swiss Alps (Breitenmoser-Würsten *et al*. 2001) have shown that lynx – re-introduced some 30 years ago from highly forested Carpathian Mountain – have adapted to open areas compared to the time of the first telemetry studies in the early 1970s (Haller & Breitenmoser 1986). Breitenmoser-Würsten *et al.* (2001) observed an individual variability in the habitat selection. Some individuals stayed above the timberline or in open forest, whereas others ranged more frequently in close forest. The presence of lynx was negatively correlated to the frequency of intensive agricultural areas and urban areas. This suggests that lynx tend to avoid areas of high human activities. However, areas occupied by lynx are by no means free of human presence. The whole Alps are populated, and the highest peak of human activity is observed during weekends and holidays, when people use these areas for skiing or hiking. The variable human population density mostly highlights areas permanently occupied by man like settlements; they differ from areas in the mountains where human presence fluctuate over time. Human "disturbance" is not a single variable nor can its distribution be mapped easily. Nevertheless, it is often believed to be the main factor limiting the distribution of large mammalian predators, which are generally not habitat-specific (Mladenoff *et al*. 1995; Corsi, Duprè & Boitani 1998). Compared to wolf and brown bear, lynx is certainly the one with the most specific demands regarding habitat and prey base (Breitenmoser 1997). In our models we assume that disturbances are included in other variables like for example habitat use, distance to freeways, main roads and minor roads. The later one should reflect the access and hence the impact of humans in remote areas. The fact that distance to roads (main roads, minor roads) did not come out in most of our models or were even negatively correlated (J) to the presence of lynx shows that lynx, when ranging in good habitat, are adapted to human presence.

3.6.2. ENFA predictive power and sampling design

Our results suggest that, when using indirect indicators (see Guisan & Zimmermann 2000) like for example habitat type or human disturbances, a model can only be applied within a limited geographical extent without significant errors. It would not make sense to build a habitat suitability model for the Alps with a calibration set originating only from the Jura Mountains and vice versa (Fig. 3.3). Validation sets fit well with habitat suitability maps (HS) built from calibration sets stemming from the same regions. This is not a surprising finding, since in the jack-knife cross-validation the calibration and the validation set are closely linked. The combination of geomorphologically contrasted regions (e.g. Prealps/Jura; Alps/Jura) improves species' distribution predictions in regions from which no data have been used to calibrate the model (e.g. Alps, north-eastern Switzerland). The combination of less contrasted regions (e.g. Prealps/Alps) did not improve model predictions at all. Combined data sets gave also better results in regions where presence cells have been used to calibrate the model, except for the Jura Mountains where the best results were obtained by only taking presence cells from the Jura Mountains. This may be explained by the higher habitat diversity (more habitat types) of the Prealps and the Alps, and by the fact that lynx actually use a broader habitat range in these regions than in the Jura Mountains (Breitenmoser-Würsten *et al.* 2001; this study). Pooling presence cells from the Alps or the Prealps with cells from the Jura Mountains shifts the localisation of the latter farther away from the modal value on the selected niche factors. Consequently, the computed habitat suitability for the Jura Mountains is lower. The reciprocal is less marked as presence cells from the Prealps and the Alps show both a higher heterogeneity and a larger sample size than the Jura's ones. According to our results, the optimal sampling strategy to predict species distribution in a new area without available data would be to pool presence cells from contrasted regions. Model predictions in new areas (e.g. *NEPA*) were quite good. These findings confirm the results of a previous work by Hirzel, Helfer & Metral (2001), showing that ENFA analyses are particularly robust to the quality and the quantity of the input data, thus making them particularly suitable for a spreading species. However ENFA did not perform as well in new areas with a low ecological variance (e.g. Jura Mountains). In such situations new presence data should be gathered in the field. The comparison of the predictions derived from different data sets – all together in a relatively small area – however discloses the limits of such models. Using input data from distinct landscapes or habitats can considerably influence the results. Consequently, building reliable models to predict a species' distribution requires a high quality information on the habitat use of the specimens in the same or a very similar area.

3.6.3. Management implications

Our models provide a tool for the conservation and management of the lynx in the Alps and the Jura Mountains. They predict the distribution, the extent, and the fragmentation of favorable lynx habitat in Switzerland. When combined with knowledge of the land tenure system of the resident lynx (Breitenmoser *et al.* 1993) they can be used to estimate the potential size of the lynx populations (Molinari-Jobin *et al.* 2001; Schadt *et al.* 2002; Chapter 7) and hence support developing management and conservation strategies. Another practical use of the model will be the planning of future translocations (e.g. Breitenmoser *et al.* 1999). When combined with a spatially structured dispersal model (Schippers *et al.* 1996; Brooker, Brooker & Cale 1999), it will further allow us to predict the potential spread of the lynx throughout the Alps.

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Chapter 4. Natal dispersal of Eurasian lynx (*Lynx lynx*) in the north-western Swiss Alps and the Jura Mountains

4.1. Abstract

Dispersal influences the dynamics and persistence of populations, the distribution and abundance of species, and gives the communities and ecosystems their characteristic texture in space and time. The Eurasian lynx is a medium sized solitary carnivore that has been re-introduced in central Europe and currently occurs in rather small metapopulations, where dispersal is believed to play a prominent role for the recolonisation of unsettled areas and persistence of subpopulations. Between 1988 and 2001 we studied the spatio-temporal behaviour of subadult Eurasian lynx in two re-introduced populations in Switzerland, based on 39 juvenile lynx of which 24 were radio-tagged to understand the factors influencing dispersal. Age at independence ranged from 8.1-10.7 months and did not differ between populations. Juvenile separated from their mother from January to the beginning of May with a peak in April. After separation, subadults in the high density population stayed longer in the maternal home range. Direct aggression of resident lynx towards juveniles and subadults was never observed and seems not to cause separation or dispersal. Age at dispersal was affected by population but not by gender, condition or the presence of a new progeny by itself. Dispersers of both sexes established transient home ranges although only one male did it in the saturated population. Subadults are conservative disperser and settled within or close to known lynx occurrences. Although only two females took over the maternal home range there was no significant sex bias in the proportion of individual that dispersed in both populations. About three quarters of the dispersers successfully settled in a territory at distances that differed between populations, but not between gender or body condition for itself. Dispersal distances reached in the high lynx density population – shorter than those reported in other Eurasian lynx studies but comparable to those observed in an Iberian lynx population – are limited by habitat restriction hindering connections with neighbouring metapopulations.

4.2. Introduction

Dispersal influences the dynamic and persistence of populations, the distribution and abundance of species, and the community structure. Howard’s (1960) definition of dispersal as the movements of an animal from its point of origin to another area where it might reproduce was used for the purpose of this article. Subadults generally disperse in higher proportion, roam longer distances than adults, and are assumed to gain advantages by dispersing, as they would otherwise be competing with their parents for resources (Waser & Jones 1983). Dispersal in mammals is often male biased whereas it is female biased in birds (Greenwood 1980). Three major hypotheses have been proposed to explain the ultimate cause of dispersal and sex biased dispersal: avoidance of close inbreeding (Wolff 1993; 1994), competition for mates (Dobson 1982), and competition for resources (Greenwood 1980; 1983).

An animal remaining philopatric is at risk of inbreeding with close relatives, more specifically of mating with its opposite-sex parent. Inbreeding is most costly for the sex that contributes more to the parental investment. Waser, Austad & Keane (1986) suggest that females should be the dispersing sex in a polygynous mating system, because their threshold for accepting inbreeding is lower. Since the opposite is usually observed in such mating systems Waser *et al*. (1986) concluded that inbreeding plays only a marginal role in dispersal. This argument may actually be reversed if females have the ability to choose their partner according to his dispersal status (see Perrin & Mazalov 1999).

Philopatry induces competition for mates among kin, which leads to both indirect and direct fitness cost (Hamilton 1972). The sex with the higher reproductive potential should suffer more from competition, and thus disperse more. In most mammals females are the limiting sex and will profit more than males from familiarity with food resources and denning sites (Pusey 1987). Males should benefit from moving to areas where there a large numbers of potential mates (Greenwood 1980; Pusey 1987).

Philopatry is beneficial in terms of the ability to exploit local resources according to the resource-competition (e.g. food and/or denning sites; Greenwood 1980; 1983) hypothesis. In polygynous species, such benefits are more valuable for females, as they are mainly responsible for defending the breeding territory and rearing young. Females are therefore under a stronger selective pressure than males to remain philopatric. This hypothesis predicts a male-biased dispersal in polygynous species.

Potential causes are too often considered as alternative rather than interacting factors (Perrin & Goudet 2001). Plasticity in the presence and direction of sex-biased dispersal within taxa revealed by new studies argue against a single factor accounting for the interspecific patterns in dispersal (Lambin, Aars & Piertney 2001).

Most studies on natal dispersal come from birds (e.g. Greenwood & Harvey 1982; Adriaensen, Verwimp & Dhondt 1998; Keller 1998; Kenward, Walls & Hodder 2001) and small mammals (e.g. Anderson 1989; Ims 1990; Lambin 1994; Koporowski 1996; Favre *et al*. 1997). In carnivores there have mainly been studies on social living species (e.g. fox *Vulpes sp.*: Zimen 1984; Harris & Trewhella 1988; Allen & Sergeant 1993; Koopman, Cypher & Scrivner 2000; lions *Panthera leo*: Hanby & Bygott 1987; badger *Meles meles*: Woodroffe, Macdonald & da Silva 1993; jackal: *Canis sp.* Loveridge & MacDonald 2001). Few studies have focused on solitary felids and most of them dealt with large cats (e.g. tiger *Panthera tigris*: Smith 1993; puma *Puma concolor*: Beier 1995; Sweanor, Logan & Hornocker 2000; Maehr *et al*. 2002). Only four studies are known within the genus *Lynx* (Poole 1997; Schmidt 1998; Sunde *et al*. 2000; Ferreras *et al*. 2004). A representative set of species should be considered to have a complete picture of the mechanisms and function of dispersal.

We studied the dispersal characteristics of the Eurasian lynx (*Lynx lynx*), a solitary medium sized felid with a moderate polygynous mating system in two populations, one in the Jura Mountains and one in the north-western Swiss Alps. Up to now there was only a moderate presence of the species outside the north-western Swiss Alps, in the central and south-western Alps and no or hardly any lynx were found in the eastern and southern Alps of Switzerland, although suitable habitats are available (Molinari-Jobin *et al*. 2001). This uneven distribution is a consequence of the eradication of the lynx in western Europe in the 19th century and the subsequent re-introduction of the species in the Swiss Alps and in the Jura Mountains in the early 1970s (Breitenmoser, Breitenmoser-Würsten & Capt 1998). The Alps and the Jura Mountains differ in their physiographic characteristics. The first have a reduced and more fragmented forest cover, steeper slopes, higher elevation, and their ridgelines have no predominant orientation compared to the latter. We can assume that these differences must have consequences for the dispersal of a mainly forest living species.

Comparing the spatio-temporal behaviour of subadult lynx in the two mountain ranges may consequently help understanding the mechanism of dispersal. Our objectives are to describe the dispersal pattern of subadult lynx, the characteristics of transient and definitive home ranges as well as subadult lynx’ diet, and to give an answer to questions such as when and how far they disperse. Two predictions are specifically tested: (i) dispersal in lynx, both rate and distance, is male biased, as predicted for a polygynous species with female-defence (Greenwood 1980, Dobson 1982; Greenwood 1983; Clark, Saether & Roskaft 1997); (ii) subadults in crowded areas with low prey density leave the maternal home range earlier, move farther and longer (trophic resource competition hypothesis). Understanding lynx dispersal is important in regard to the conservation and management of the species in a human-dominated landscape.

4.3 Study areas

The dispersal patterns of subadult lynx were examined in two study sites in the Swiss Alps and the Jura Mountains. The north-western Swiss Alps (NWSA), is a 2,800 km^2 patch limited in the north-east by the valley of the Aare River with the lakes of Brienz and Thun, in the north-west by the Swiss Plateau, in the west by the Rhone valley with the Lake of Geneva, and in the south by the Bernese Alps rising to 4,000 m (Fig. 4.1). The valley bottoms have been deforested and are densely populated. The human population reaches a density of 140/km^2 in most parts of the study area and people living in the lowlands use the Alps intensively for recreation (skiing, hiking). Forests cover 30% of the study area but are highly fragmented. They extend along steep slopes up to the timberline at 1,800-2,200 m. Lower ridges and gentle slopes were deforested a long time ago and provide summer pastures for cattle and sheep. From late spring to autumn, domestic sheep graze unguarded on remote mountain meadows. Lynx’s main prey in the study area are roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) (Breitenmoser & Haller 1987) which were locally depressed during a peak of the lynx density at the end of the nineties. On rare occasions lynx prey upon sheep. In 1999, the year with the highest loss, 157 sheep were killed that is 0.4% of the 39,000 sheep aestivated in the study area (Angst, Olsson & Breitenmoser 2000). The overall lynx density in the NWSA based on the distribution of radio-collared animals and information on additional, not tagged individuals from photo-trapping and from reports by game wardens was rather high and estimated at 1.4–1.5 resident lynx/100 km^2 during the study period (Breitenmoser-Würsten *et al*. 2001; Molinari-Jobin *et al*. 2001).

The Jura Mountains (JM), a secondary limestone mountain chain forming the north-western border of Switzerland with France (Fig. 4.1), are more homogeneous than the Alps, forming basically a block of contiguous suitable habitat of 6,670 km^2 (Chapter 7). The altitude ranges from about 500 m to 1,718 m (Crêt de la Neige). Deciduous forests along slopes and coniferous forests on the ridges cover 53% of the study area. Agricultural areas are typically pastures. The human population reaches a density of 120/km^2 in most parts of the JM but is more clustered than in the Alps. People living on the Swiss Plateau use the highlands intensively for recreation. As in the Swiss Alps, roe deer and chamois are the main prey of lynx (Jobin, Molinari & Breitenmoser 2000; Molinari-Jobin *et al.* 2002). Prey base was not a limiting factor during the study time (Molinari-Jobin, Molinari & Breitenmoser subm.). The overall lynx density in the main study area remained fairly constant over the whole study period (Breitenmoser-Würsten *et al.* subm.) and was estimated at 0.7–0.8 resident lynx/100 km^2 (Breitenmoser *et al.* 1993, Molinari-Jobin *et al.* 2002, Breitenmoser-Würsten *et al.* subm.).

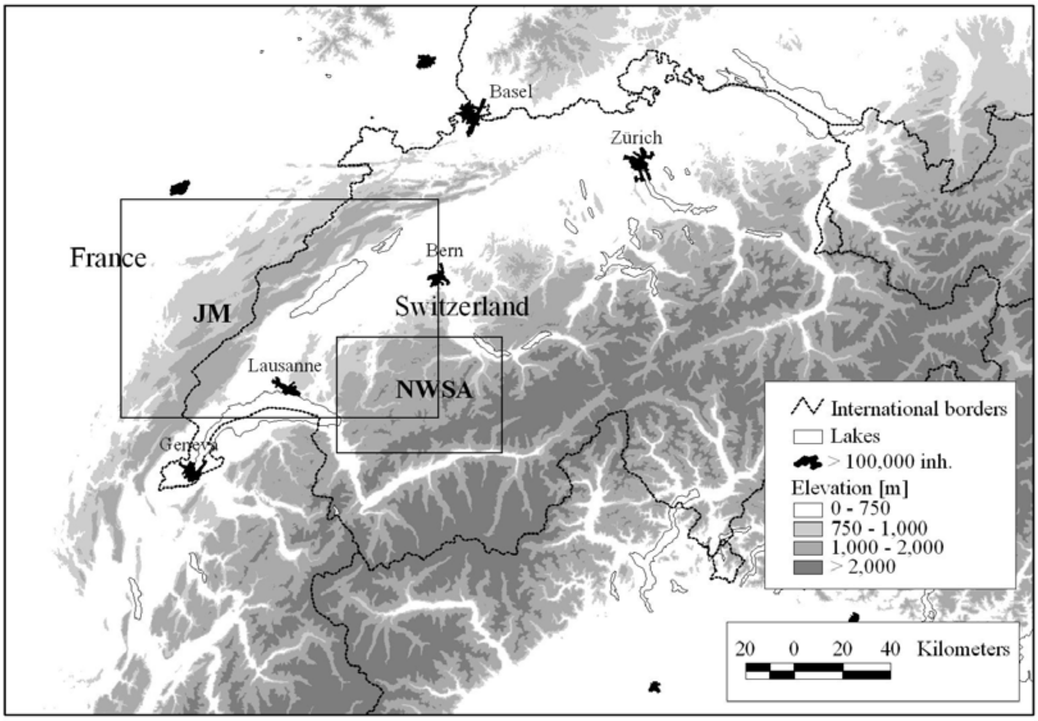

Figure 4.1. Study areas in the Jura Mountains (JM) and the north-western Swiss Alps (NWSA). The inserted frames correspond to the maximal range of lynx dispersal trajectories and home range establishments shown in Fig. 4.4 and 4.5.

4.4. Material and method

4.4.1. Field Study

Subadult lynx were captured with foot snares at fresh kills from January to April 1988−2001, just before they separated from their mother. At this time they have the adequate size to be radio-collared. Lynx were immobilized with 0.1-0.15 mg/kg medetomidin (Domitor®, Farmos, Finland) and 0.8-1 mg/kg ketaminum (Ketasol®, Graeub, Switzerland) and fitted with radio-collars (200 g; K. Wagener, Germany). As an antagonist we used 0.5-0.75 mg/kg atipamezol (Antisedan®, Farmos, Finland). Dispersal characteristics were obtained for 22 and 17 lynx in the NWSA and the JM, respectively (Table 4.1). Dispersal data came mainly from radio-telemetry; additional information was available from cubs tagged at the den and later live-trapped or “captured” in a camera trap. Radio-marked lynx were relocated from the ground to a precision of 1 km^2 to 1 ha. We located dispersing lynx almost every day when they moved through new terrain, and at least every week once home ranges were established for more than one month. Each subadult was monitored until it occupied a definitive home range (see below), or was lost due to death or failure of the radio-collar. After independence subadult were considered “dispersers” when they had established a home range overlapping not more than 5% of their natal (= maternal) home range (based on 90% minimum convex polygon MCP) or were last located outside their natal area (Sweanor *et al*. 2000; Chapter 5). All other independent progeny – establishing home ranges with more than 5% overlap with their natal range – were considered philopatric. Dispersal started when a subadult made its first movement outside its natal home range without returning. Data were not available for all dispersing lynx for each of the questions, so sample sizes could differ for different analyses.

Table 4.1. Characteristics and fate of juvenile lynx followed in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). Type and order of information: den = individuals ear-tagged as kittens; rt = radio-telemetry; ct = camera-trap, cr = carcass retrieved. # days = number of days in maternal home range after separation. Fate: Alive = survived the whole year after separation from the mother; reproduced = strong evidence from genetic analyses or observations in the field that individual has reproduced; (reproduced) = lynx reached sexual maturity according to Kvam (1991) but there was no proof of reproduction.

Lynx	**Kitten of female**	**Date of first observation**	**Information**	**Date of last observation**	**Separation from mother**	**# days**	**Number of locations**	**Fate**
NWSA								
M18[1]	F37	22.01.97	rt, ct	16.05.99	06.03.97	77	94	Alive, (reproduced)
M20[1]	F30	25.03.97	rt, ct	02.12.98	25.03.97	-	15	Alive
M24[1]	F47	24.02.98	rt, ct	27.01.04	15.04.98	164	433	Alive, reproduced
M25	F33	28.06.97	den, rt	14.09.00	03.04.98	13	229	Alive, (reproduced)
M28	?	30.01.99	rt	12.02.99	?	-	9	Died, starvation
M29	F34	25.06.98	den, rt, ct	07.05.03	22.04.99	42	124	Alive, (reproduced)
M30[1]	?	05.03.99	rt	21.09.99	?	-	59	Died, disease
M31[1]	F52	08.12.98	ct, rt	10.08.00	26.04.99	64	210	Alive
M35	F35	31.10.98	ct, rt, ct	12.02.04	?	-	139	Alive, (reproduced)
F31[1]	F32	06.01.97	rt, ct	26.09.98	08.03.97	221	78	Alive, (reproduced)
F33[2]	?	14.01.97	rt	23.07.98	?	-	115	Alive, reproduced
F40	?	13.03.97	rt	20.03.98	?	-	42	Unknown
F42[2]	?	05.04.97	rt,ct	11.01.04	?	-	187	Alive, reproduced
F46[2]	?	15.11.97	rt	20.01.98	?	-	14	Died, car accident
F48	F38	05.07.97	den, rt	18.05.98	10.04.98	-	23	Unknown
F49	F34	23.06.97	den, rt	27.08.99	01.05.98	106	156	Alive, (reproduced)
F50	F37	13.03.98	rt	19.05.98	13.03.98	-	24	Unknown
F54[2]	?	14.08.99	rt	23.06.00	?	-	93	Alive, (reproduced)
F56	F32	08.02.00	rt	25.02.00	?	-	-	Unknown
F57[2]	?	08.05.00	rt	10.03.01	?	-	138	Alive
FB22	F34	25.06.98	den, ct, cr	18.10.01	?	-	-	Alive, (reproduced)
FB44	F34	11.12.01	ct	01.08.03	?	-	-	Alive, (reproduced)
JM								
M11	F21	19.06.93	den, rt, cr	08.02.02	?	-	337	Alive, reproduced
M13	F18	18.06.93	den, rt	27.06.95	?	-	45	Alive, (reproduced)
M14[1]	F21	31.12.95	rt	26.02.98	28.01.96	1	200	Alive, (reproduced)
M15	F18	23.06.95	den, rt	21.09.96	15.04.96	40	96	Died, illegal killing
M16	F11	08.03.90	rt	19.06.90	03.04.90	30	72	Died, disease
F12[1]	F11	20.04.88	rt	20.12.88	30.03.88	30	99	Died, illegal killing
F13	F11	23.03.89	rt	17.08.89	27.03.89	30	56	Died, disease
F17	F14	25.03.90	rt	23.05.90	10.04.90	12	23	Died, car accident
F19[1]	F18	04.03.91	rt	05.05.91	15.04.91	-	-	Unknown
F20	F11	16.03.91	rt	xx.11.95	24.03.91	65	393	Alive, reproduced
F22[1]	F18	04.03.92	rt	25.11.94	14.03.92	76	332	Alive, reproduced
F23[1]	F15	14.03.92	rt	15.02.95	12.04.92	-	423	Alive, reproduced
F25[1]	F30	20.12.95	rt	02.07.96	15.02.96	-	27	Unknown
F26	F18	23.06.95	den, rt, ct	08.01.03	15.04.96	-	354	Alive, reproduced
F27	F24	30.06.95	den, rt	27.04.96	10.04.96	-	6	Unknown
F28	F24	27.06.95	den, rt	04.03.96	?	-	-	Unknown
F36	F29	04.03.97	rt	24.06.98	26.03.97	14	152	Alive, (reproduced)

[1] exact birth date unknown and hence estimated as the mean birth date of all known births

[2] first observed as subadults after separation from mother

4.4.2. Dispersal and body condition

During each capture, lynx were weighed and different body measurements taken as for example the head-body length. Body condition was measured as the residual value obtained in a reduced major axis regression of log mass on log head-body length (Sokal & Rohlf 1995). Reduced major axis regression are recommended when both y and x variables are subject of errors. Regressions were fitted separately for males and females producing correlation indexes of 0.55 for females and 0.71 for males. Index of body condition was tested as a predictor of dispersal at a given age, dispersal distance, as well as dispersal duration. Only lynx weighing between 7 and 11 month old were considered in order to reduce possible effect due to age.

4.4.3. Temporal behaviour

If not exactly known, the date of separation, dispersal, death, or entry into a home range was calculated by the mid point between the closest known dates before and after the event. The time subadults separated from their mother was measured in days starting from the beginning of the year. The age at independence was calculated in months. The birth date, when not known, was estimated by using the mean birth date of all known litters in the JM (Breitenmoser-Würsten *et al*. subm.) and in the NWSA (Breitenmoser-Würsten *et al*. 2001). Three seasons characterized by different breeding and social events were considered. The first third of the year (January-April) mostly coincided with mating, pregnancy and separation of cubs from their mother, the second third (May-August) with births and lactation when females with cubs have a reduced mobility, and the last third (September-December) with the time when females with cubs use a larger part of their home ranges due to a higher mobility of their kittens (Fig. 4.2; Kaczensky 1991; Breitenmoser *et al*. 1993). The observed number of lynx dispersing during each season was compared with the expected number of dispersers according to the total radio-tracking days of lynx of dispersal-prone age gathered during each season. The age at start of dispersal as well as the duration of dispersal (time between start of dispersal and settlement), were also computed. The effects of area of origin (A), sex (S), condition (C), presence of a new progeny (P), and their second-order interactions on time of start at dispersal were analysed.

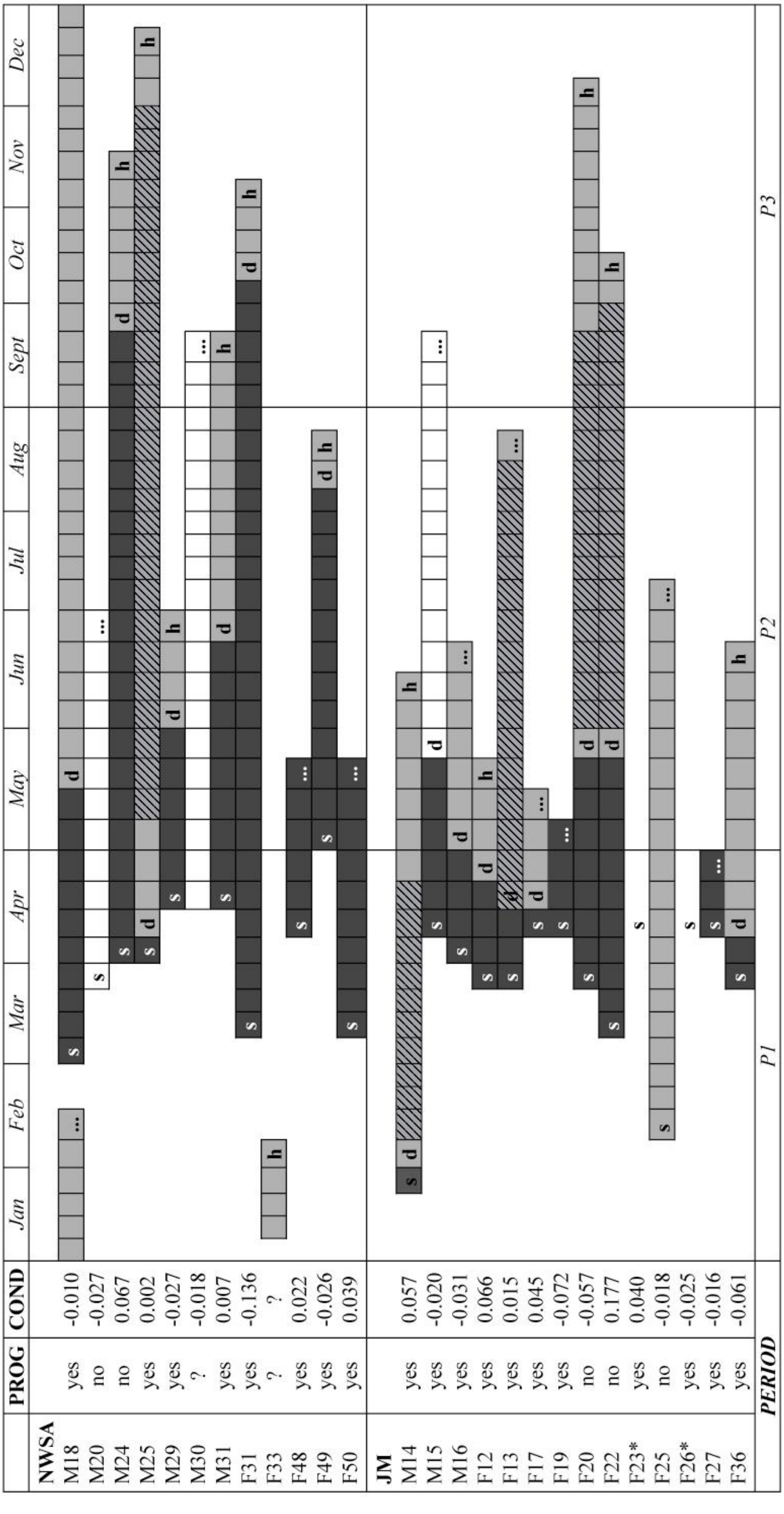

Figure 4.2. Temporal behaviour of subadult lynx that dispersed in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). M indicates males, F females, * individuals that remained philopatric. PROG = subadult's mother giving birth to a new litter, COND = body condition measured as the residual value obtained in a reduced major axis regression of log mass on log head-body length. s = separation from mother, d = subadults leave the maternal home range (HR) and disperse, h = establishment of a definitive home range, **…** = interruption of the radio collar, dark grey = time spent in the maternal HR, light grey = time spent dispersing, diagonally hatched = time spent in a transient home range (*THR*), white = status unknown (maternal HR unknown or survey period too short to know whether subadult established a transient or definitive HR). The year is divided into three periods (*P1*: mating, pregnancy and separation of cubs, *P2*: births and lactation and *P3*: females with cubs use a larger part of their ranges) according to breeding and social events.

4.4.4. Dispersal distances

Dispersal distance was defined as the distance from the arithmetic centre of a progeny's natal home range (natal centre) to the arithmetic centre of its independent home range (independent centre). When complete dispersal information was not available, dispersal distance was calculated based on one of the following combinations: natal centre to mortality site or last location; or capture site to independent centre, mortality site, or last location. Comparisons were made between: (i) all subadults including those that remained philopatric (recovery distance, according to Trewhella, Harris & MacAllister 1988), (ii) only individuals that dispersed (distance to the end of dispersal), and (iii) finally only those that completed dispersal (effective dispersal; see Chapter 5). We analysed the effects of area of origin (*A*), sex (*S*), body condition (*C*), and their second order interaction on dispersal distances (recovery distance, distance to the end of dispersal, and effective dispersal).

4.4.5. Transient home ranges (THR), definitive home ranges (DHR)

A temporary home range (*THR*) was retrospectively identified as the area an animal used after leaving its natal range but later abandoned (Beier 1995). The area a lynx used for ≥ 6 consecutive months without subsequent change in location was regarded as definitive home range (*DHR*). Home range sizes (*THR* and *DHR*) were computed by means of the 100% minimum convex polygon (*MCP*) method (Hayne 1949). The calculations were done in ArcView (ESRI 1996a, b, c) using the animal movement extension (Hooge & Eichenlaub 2000).

4.4.6. Diet

Lynx usually fed for several days on a kill, hiding during the day and returning to the carcass each evening. If a subadult lynx stayed for two consecutive days at the same spot, we located it precisely by homing in to a distance of 25-50 m the next night. The next day, this area was searched intensively, sometimes using a bloodhound in order to find a kill (see Jobin *et al.* 2000). The species of each kill was recorded. We compared the diet of the subadults in the

NWSA and the JM with the one of the resident lynx documented by A. Ryser (pers. comm.) and Jobin *et al*. (2000), respectively.

4.4.7. Statistical analysis

Linear regression was used to model effects on age at dispersal, recovery distances, dispersal distances, effective dispersal distances and duration of dispersal. The response variables were normalized as much as possible using the log transformation. Calculations were done in S-PLUS (MathSoft, Inc., Seattle, Washington, USA) using generalized linear models with the Gaussian family (GLM; McCullagh & Nelder 1983; see Nicholls 1989). Only biological meaningful models were built. The effects of area of origin (*A*), sex (*S*), condition (*C*), presence of a new progeny (*P*), and their interactions on age at dispersal were analysed as well as the effects of area of origin (*A*), sex (*S*), condition (*C*), and their interactions on dispersal distances. The best approximating model equation from the set was selected using a bias corrected Aikake's Information Criterion for fitted models (AIC_c)

$$AIC_c = n\log(RSS/n) + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where *RSS* is the residual sum of square, *n* the sample size, and *K* the number of parameters in the model including the intercept and the error (Burnham & Anderson 1998).

4.5. Results

4.5.1. Temporal behaviour

We studied the fate of 39 juvenile lynx in the NWSA and the JM (Table 4.1). For 24 animals (9 males and 15 females; Table 4.1, Fig. 4.2), which had been radio-tracked before and after becoming independent from their mothers, age at independence was comparable between the study areas. It ranged from 9.3–10.6 months (median = 10.0 months) in the NWSA (n = 10) and from 8.1–10.7 months (median = 10.1 months) in the JM (n = 14), respectively. Our sample size was small, but males appeared to become independent from their mothers at about the same age (NWSA: median = 10.3 months; JM: median = 10.0 months) as females

(NWSA: median = 10.0 months; JM: median = 10.2 months) in both areas. Independence started from the beginning of March to the beginning of May in the NWSA and from January to the beginning of April in the JM with a peak during April in both areas (Fig. 4.2). Subadult lynx did not separate earlier in the year from their mother in the JM than in the NWSA. The median was equal to 91 and 100 days since the beginning of the year for the JM and the NWSA, respectively. In the JM four out of seven radio-tracked adult females undertook excursions out of their home range just before the family break-up. This behaviour was only observed in one out of 10 females in the NWSA. In one case separation of lynx kittens from their mother occurred outside of the maternal home range (Molinari & Molinari-Jobin 2001). In two cases (F36 and M14) the mothers abandoned their kittens in the vicinity of a kill and in another case two subadult males (M25 and M29) left their mother when they made the first kill at their own. Anecdotic observations suggest that some young males actively left their mother, but in most cases, the mother seemed to have left the juveniles. Subadults usually stayed a few days close to the place where the separation occurred. Finally, they moved on. We have never observed females interacting aggressively with their kittens. Independency took place in the core area as well as in the periphery of the maternal home range. All subadults except one male (M14) spent some time in their maternal home range. Only three out of twenty-four were relocated together with their mother during this time.

The best approximating models explaining age at dispersal included the interaction of presence of a new progeny x area of origin, and the interaction of area of origin x sex, but neither area of origin nor progeny nor sex nor condition nor their interaction (Table 4.2). However, these results must be taken with care as there were only three females without progeny in our sample and the sex ratios were not similar between the study areas (Fig. 4.2). There was predominance of females in the JM and males in the NWSA. The factor “area of origin” was present in all models indicating its value as model predictor. Presence of progeny and gender may be relevant but a model including exclusively presence of progeny or gender showed less than < 0.001 confidence indicating that the effect of these variables was manifested only in conjunction with other factors.

After independence subadults in the NWSA stayed from 13 to 221 days (median = 77 days) in the maternal home range, in the JM from one to 76 days (median = 30 days). Lynx from the JM dispersed at younger ages (median = 10.9 months; range: 8.2–12.1 months) than those in the NWSA (median = 13.1 months; range: 10.4–16.6 months). In the JM, two females (F23 and F26) never left the maternal home range apart from an excursion in autumn. Both took over their mother's home range after those had died. One female (F25) in the JM, however, dispersed after her mother had been killed and left a vacant home range. In the NWSA all individuals of both sexes dispersed whereas in the JM a slightly greater proportion of males (5/5) than females (7/9) dispersed, but the difference was statistically not significant (two-tailed Fisher's exact test, p = 0.51).

Table 4.2. AIC_c-based comparison of linear regression models explaining variability in age at dispersal. Only the most parsimonious models classified in decreasing order of their Akaike weights are shown. *A*: area of origin; *S*: sex; *P*: presence of a new progeny; *C*: condition; *A:S, P:A* and *S:C*: interactions. AIC_c = bias corrected Akaike's Information Criterion for fitted models; $\Delta_i = (AIC_c)_i - (AIC_c)_{min}$; Akaike W_i = Akaike weights: R^2 *adj* = explained deviance.

Model	AIC_c	Δ_i	**Akaike** W_i	R^2 *adj*
P:A+A:S	-93.41	0	0.618	0.71
P+A:S	-91.33	2.07	0.219	0.67
A:S	-88.29	5.11	0.048	0.53
P+A+A:S	-86.97	6.44	0.025	0.64
P+S+A:S	-86.97	6.44	0.025	0.64
P:A	-86.81	6.60	0.023	0.49
C+A:S	-84.71	8.70	0.008	0.50
A+A:S	-84.66	8.75	0.008	0.50
A+S	-83.55	9.86	0.004	0.46
P+P:A	-83.17	10.24	0.004	0.45
A+P:A	-83.17	10.24	0.004	0.45
P+A	-82.99	10.42	0.003	0.44
A	-82.88	10.53	0.003	0.34
P+A+S:C	-81.91	11.50	0.002	0.50
P+S+A+S:A	-81.63	11.77	0.002	0.61
C+S+A:S	-80.34	13.07	< 0.001	0.46
C+A+A:S	-80.34	13.07	< 0.001	0.46
A+S+A:S	-80.30	13.11	< 0.001	0.46
C+A	-79.48	13.93	< 0.001	0.31

In the NWSA, subadults left the maternal home range between April to mid-October, in the JM between the end of January to the end of May with a peak in April and May (Fig. 4.2). Dispersal events were evenly distributed along the year, even after considering the seasonal differences in tracking days overall and in the NWSA, but not in the JM ($\chi^2 = 6.28$, df = 2, $p < 0.05$; Fig. 4.3). Subadults in the JM took more time to complete dispersal than their conspecifics in the NWSA (JM: n = 5, range: 20–190 days, median = 134 days; NWSA: n = 6, range: 1–251 days, median = 39 days), but the difference was statistically not significant.

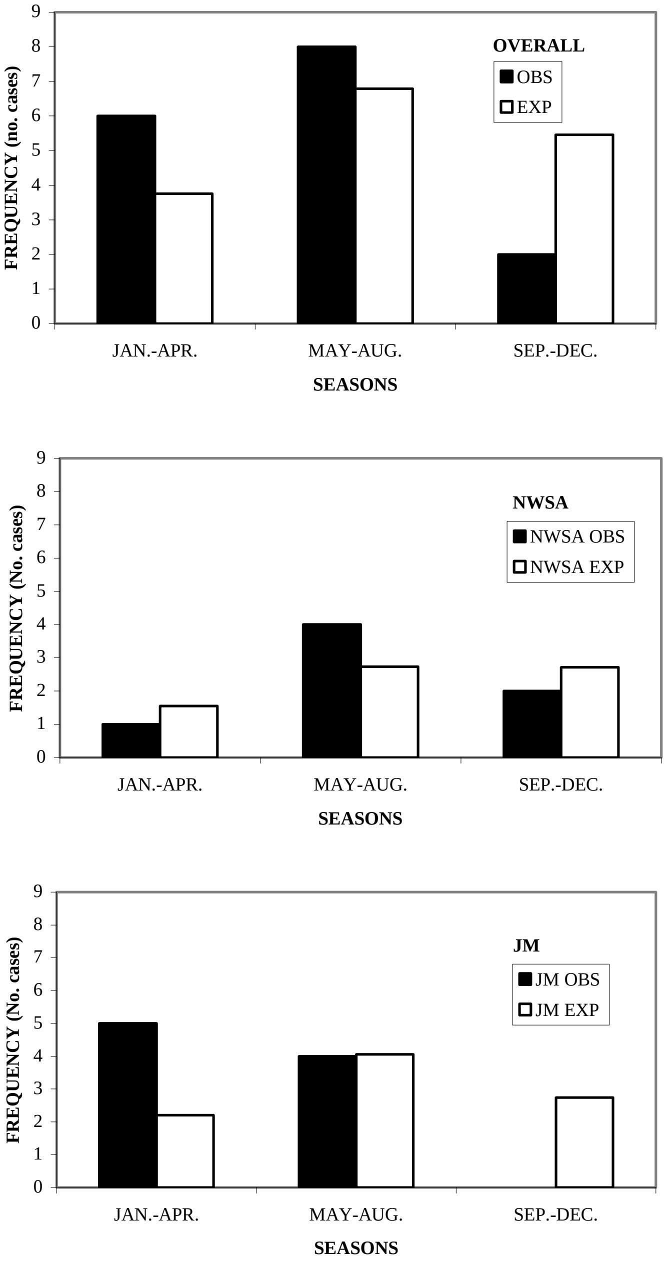

Figure 4.3. Seasonal pattern of observed (obs) and expected (exp) dispersal events, according to radio-tracking effort (proportion of radio-days during each season), in the overall sample (top), and in each area of origin (NWSA: middle graph; JM: bottom graph. The observed frequency significantly differs from the expected frequency for the dataset from the JM ($\chi^2 = 6.28$, df = 2, $p < 0.05$) but not for the remaining datasets (all $p > 0.1$).

4.5.2. Dispersal distances

Dispersal distances (recovery distance, distance to the end of dispersal, effective dispersal) were best explained by a model including only the interaction of area of origin x gender but neither area of origin nor gender nor condition nor their interaction (Table 4.3). However, caution is required as the sex ratios were not similar between the study areas. The factor area of origin was present in the first four most parsimonious models with the exception of the recovery distance indicating its value as model predictor. Gender may be relevant, but a model including exclusively gender showed less than < 0.02 confidence, with the exception of the recovery distance were it was equal to 0.11 (Table 4.3), indicating that the effect of this variable was manifested only in conjunction with other factors. Dispersing lynx from the JM were recovered farther (recovery distance: median = 29.5 km, n = 14) from their point of origin than those from the NWSA (median = 20.6 km, n = 13). Distances to the end of dispersal were also longer in the JM (median = 31.7 km, n = 12) than in the NWSA (median = 20.6, n = 13). Furthermore, lynx from the JM settled at farther distances (effective dispersal: median = 68.8, n = 7) than those from the NWSA (median = 21.4, n = 12).

Table 4.3. AIC_c-based comparison of linear regression models explaining variability in dispersal distances. Only the most parsimonious models classified in decreasing order of their Akaike weights are shown. *A*: area of origin; *S*: sex; *A*:*S*: interaction between area of origin and gender. AIC_c = bias corrected Akaike's Information Criterion for fitted models; $\Delta_i = (AIC_c)_i - (AIC_c)_{min}$; Akaike W_i = Akaike weights: R^2 *adj* = explained deviance.

Distance	**Models**	AIC_c	Δ_i	**Akaike** W_i	R^2 *adj*
Recovery distance	*A:S*	-45.84	0	0.49	0.076
	A	-44.44	1.40	0.25	0.027
	S	-43.06	2.78	0.12	-0.024
	S+A	-42.80	3.04	0.11	0.028
	S+A+A:S	-40.03	5.81	0.03	-0.004
Distance to the end of dispersal	*A:S*	-52.69	0	0.46	0.206
	A	-52.42	0.27	0.40	0.198
	S+A	-49.80	2.89	0.11	0.169
	S+A+A:S	-46.68	6.02	0.02	0.131
	S	-45.86	6.83	0.01	-0.043
Effective dispersal	*A:S*	-41.83	0	0.56	0.373
	A	-40.67	1.16	0.31	0.334
	S+A	-38.43	3.40	0.10	0.329
	S+A+A:S	-34.82	7.02	0.02	0.290
	S	-32.01	9.82	< 0.01	-0.051

4.5.3. Home range (*THR*, *DHR*)

NWSA – Most subadults established a definitive home range (*DHR*) directly after their dispersal (Table 4.4).

Table 4.4. Size (km^2, based on 100% minimum convex polygon) and duration of subadult home ranges in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). *THR* = transient home range, *DHR* = definitive home range, ? = unknown.

Lynx	Home range type	Size (km^2)	Number of locations	Days	Days/ Locations
NWSA					
M24	*DHR*	93	136	366	2.7
M25	*THR*	122	60	200	3.3
	DHR	149	71	360	5.0
M29	*DHR*	129	96	322	3.4
M31	*DHR*	150	118	327	2.8
F31	*DHR*	26	13	166	12.8
F33	*DHR*	69	53	364	6.9
F40	*DHR*	38	14	198	14.1
F42	*DHR*	57	41	364	8.9
F49	*DHR*	67	86	378	4.4
F54	*DHR*	55	86	315	3.7
F57	*DHR*	93	144	326	2.3
JM					
M14	*THR*	22	50	72	1.5
	DHR	133	76	185	2.4
M15	*?*	78	53	119	2.2
F12	*DHR*	223	80	216	2.7
F13	*THR*	120	33	114	3.5
F20	*THR*	230	56	109	1.9
	DHR	642	138	361	2.6
F22	*THR*	108	87	113	1.3
	DHR	109	76	363	4.8
F23	*DHR*	226	155	280	1.8
F26	*DHR*	68	192	365	1.9
F36	*DHR*	431	113	372	3.3

M25 was the only individual for which we were able to document a transient home range (*THR*). He established his 122 km^2 *THR* 15 km east of his natal range (Fig. 4.4). He then moved northwards and established a *DHR* of 149 km^2 in December, where he was illegally killed two years later. M24 made a circular dispersal and established a *DHR* of 93 km^2 just beside the one of his mother (Fig. 4.4). F31 settled down 22 km west from her natal range

(Fig. 4.4). Her radio-collar failed on 19th April 1998, one month before maturity. At this time she occupied a home range of 26 km^2 (Table 4.4). She was still present in this region on 26th September 1998 when she has been photographed by a camera-trap. F49 established a *DHR* of 67 km^2 just beside the one of her mother (Fig. 4.4). She made eight excursions out of her *DHR*. During her first rutting season she had a meeting with male M26 but she did not give birth in the coming year or lost the kittens very early. She died at the age of 26 months because of a bacterial infection (M. Janovsky, pers. comm.). All subadults established their *DHR* in the vicinity of home ranges of adult resident lynx of the same sex which were radio-tracked as well (e.g. M24, M25, F31, F49; Fig. 4.4) or in areas where signs of presence of conspecifics were reported within the same period (Breitenmoser-Würsten *et al*. 2001). None of the subadults established a *DHR* in an area without conspecifics.

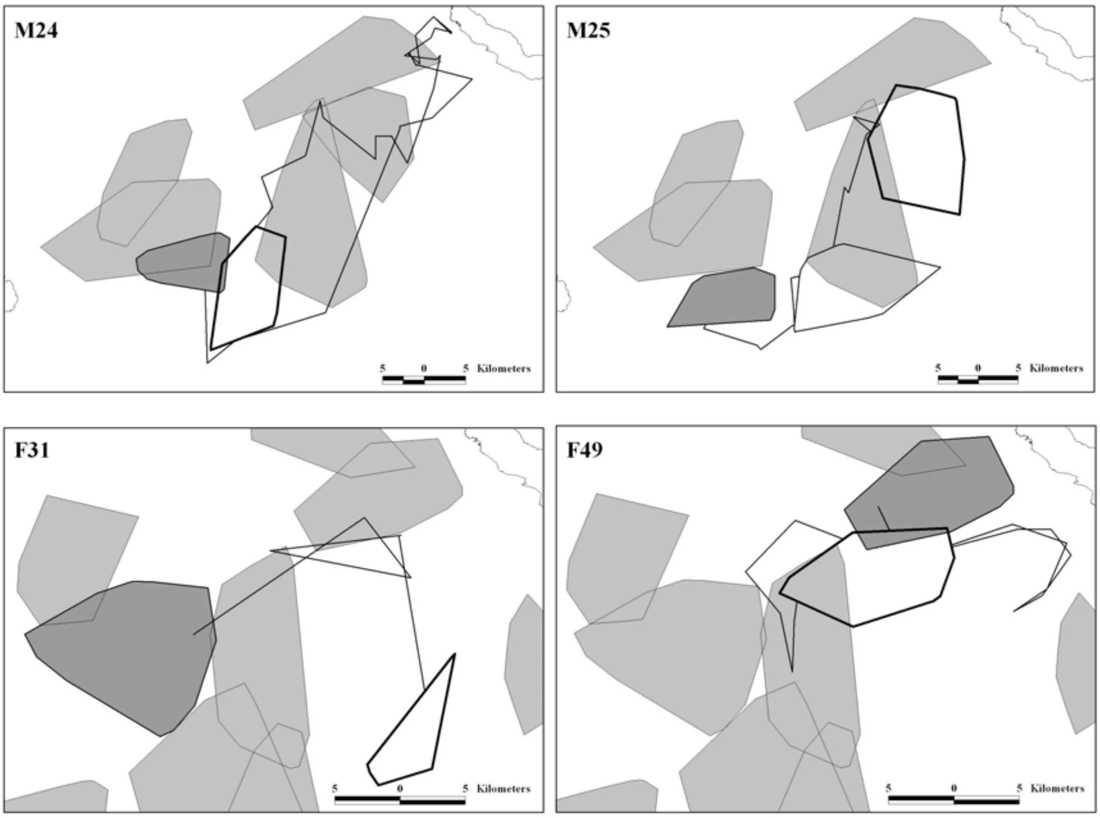

Figure 4.4. Dispersal trajectories and home range establishment of two males and two females from the north-western Swiss Alps (NWSA). Natal ranges are in solid gray. Thin and fat outlined polygons stand for transient home range (*THR*) and definitive home range (*DHR*), respectively. The black lines represent movement during dispersal. The home ranges of the residents of the same sex are shown in light gray.

JM – Subadult normally crossed the territories of resident lynx. Only one male (M16) from the six subadults that crossed known territories of resident lynx avoided the resident home ranges by following their borders (Fig. 4.5). He died after having spent 24 days in the Swiss Plateau. Three females (F13, F20 and F22) and one males (M14) established a *THR*. The orientation of the *THRs* was parallel to the mountain ridge. The area of the *THRs* ranged from 22 to 230 km^2 (Table 4.4). Subadults occupied their *THR* from 72 to 113 days. All females left their *THR* between mid-August and the end of September. F22 dispersed north-westwards and occupied a *THR* of 108 km^2 for 113 days until she moved southwards by the end of September and established a *DHR* of 109 km^2 (Fig. 4.5). M14 established a *THR* in mid-February just after he had stayed a week in private properties between a lake and the main road. The size of his *THR* was only 22 km^2. His daily movements were extremely short during this time (mean = 0.78 ± 0.67 km, n = 37) compared to those in the second home range (mean = 3.02 ± 3.34 km, n = 69). Sometimes he stayed more than a week at the same spot and we were not able to find any large kill such as roe deer or chamois, so that we were afraid he might not be well. He once fed on a roe deer killed by a resident female F29, obviously helping him to recover. He left the *THR* after 72 days by the end of April, and established a *DHR* of 133 km^2 in the northern part of the Swiss JM by mid-June. He stayed there for 185 days before returning into the range of F29 during the rutting season where we could located him together with her. He then moved back to his home range in the northern part of the JM but came to visit F29 again during the mating season one year later.

Six females (F12, F20, F22, F23, F26 and F36) established a *DHR*. Their areas ranged from 68 km^2 to 642 km^2 (Table 4.4). Two females (F23 and F26) took over their mothers’ home range after those had died. Both made an excursion outside of their home ranges in October. The maximum distance from the centroid of their home ranges was 34 km and 30 km, respectively. F23 dispersed south-westwards of her home range and turned back after 10 days. F26 and her mother with two new kittens occupied the same home range during ten months. The overlap of their core area (Kernel 50%) was about 48%. The adult female spent more time on the northern slope of her range than in the previous year. Her daughter on the other hand spent most of her time on the southern slope of her mother’s range. F26 finally left the maternal home range in autumn and dispersed northwards. She made a kill in the home range of the neighbouring resident female F21. Two days later we located F21 instead of F26 at the kill site. The kill was almost completely eaten. F26 was relocated 7 km north of the kill site, still in the home range of F21. She had probably been chased away by the resident female F21. She came back to her maternal home range after 13 days. During February the next winter, her mother in turn left her home range together with her kittens for an area towards France where she had never been located before. The separation from her kittens probably occurred in France (Molinari & Molinari-Jobin 2001). At the beginning of April she came back alone to her previous range. One week later she had been located in the same square kilometre as her daughter F26. She died three weeks later because of a bacterial infection at the border of her home range when she was 14 years old. All subadults (e.g. M14, F22, F26; Fig. 4.5) established their *DHR* in the vicinity of home ranges of adult resident lynx of the same sex followed by means of radio-telemetry during the same time or in respectively close to areas where signs of presence of conspecifics have been reported within the same period (Vandel 2001; Capt subm.).

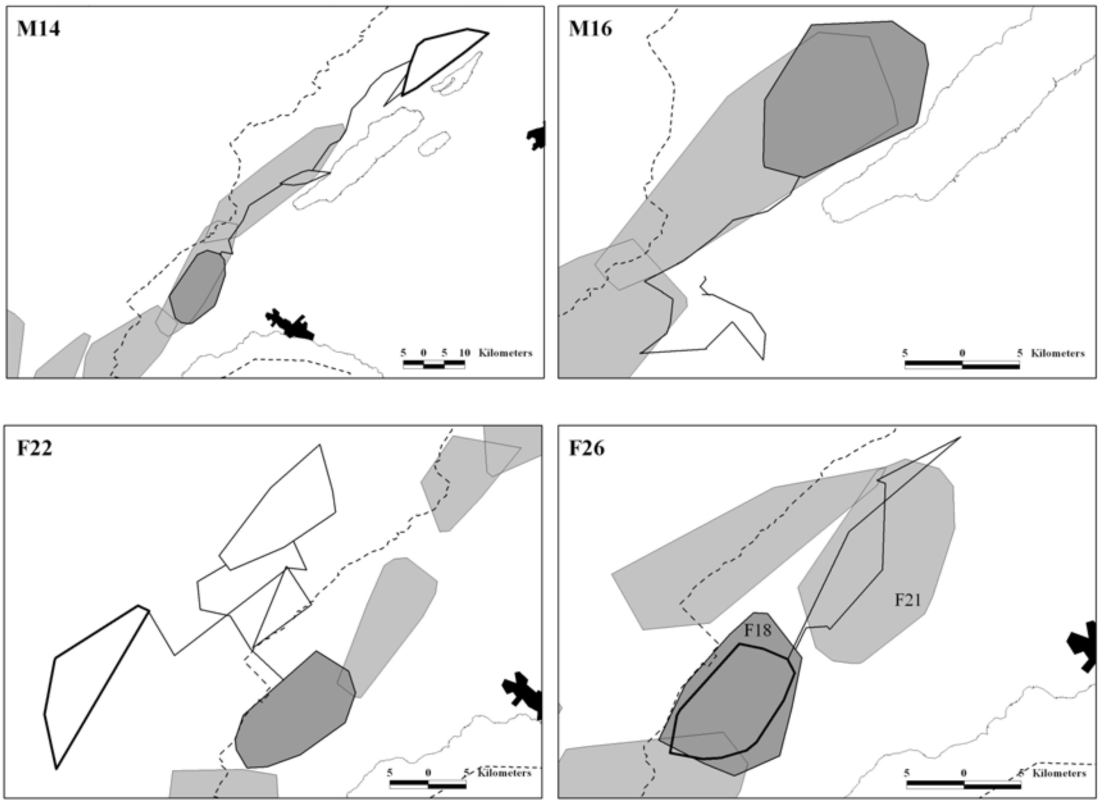

Figure 4.5. Dispersal trajectories and home range establishment of two males and two females from the Jura Mountains (JM). Natal ranges are in solid gray. Thin and fat outlined polygons stand for transient home range (*THR*) and definitive home range (*DHR*), respectively. The black lines represent movement during dispersal. The home ranges of the residents of the same sex are shown in light gray.

4.5.4. Diet

Data on the diet (Table 4.5) have been divided into three categories according to the prey size: roe deer, chamois, and the remaining smaller preys such as foxes (*Vulpes vulpes*), hares (*Lepus europaeus, Lepus timidus),* and marmots *(Marmota marmota),* which have been pooled into one category. Roe deer is the most common prey of all lynx age classes in the NWSA and the JM. Alternative preys to roe deer are either larger (chamois) or smaller prey. In the JM, subadult lynx take less larger (G = 18.9, df = 1, $p < 0.001$), but more smaller prey than resident (G = 4.7, df = 1, $p < 0.05$). In the NWSA subadults killed also significantly more smaller prey (G = 3.9, df = 1, $p < 0.05$), and tended to take less larger prey than residents (G = 3.1, df = 1, $0.05< p < 0.01$). In the JM, the first adult chamois was killed by a female at the end of the first year of independence, whereas in the Alps three individuals (M25, F59 and M29) killed a chamois just after separation from their mother. Prominent haematomas on the throat of the ungulates killed by subadults suggest that they are not as efficient hunters at the beginning of their first year of independence as residents.

Table 4.5. Number of kills of 14 and 10 subadult lynx found from January 1997 to May 2001 and from April 1988 to February 1998 in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM), respectively. Data on the diet of adult lynx in the NWSA came from A. Ryser (pers. comm.) and in the JM from Jobin et al. (2000). In brackets the percentage of prey items.

	NWSA		**JM**	
Prey species	Subadult	Adult	Subadult	Adult
Wild prey[1]				
Roe deer *Capreolus capreolus*	**30** (51.7)	**80** (51.6)	**54** (79.4)	**374** (68.8)
Red fox *Vulpes vulpes*	**8** (13.8)	**6** (3.9)	**10** (14.7)	**27** (5.0)
Chamois *Rupicapra rupicapra*	**12** (20.7)	**52** (33.5)	**2** (2.9)	**131** (24.1)
Brown hare *Lepus europaeus*	**4** (6.9)	**2** (1.3)	**2** (2.9)	**11** (2.0)
Mountain hare *Lepus timidus*	**2** (3.4)	**9** (5.8)	-	-
Marmot *Marmota marmota*	**2** (3.4)	**6** (3.9)	**0** (0.0)	**1** (0.2)
Total	**58** (100.0)	**155** (100.0)	**68** (100.0)	**544** (100.0)

[1] in bold prey species occurring in both study areas

4.6. Discussion

Most behavioural studies on dissolution of lynx litters come from observations in captivity (e.g. Jonsson 1984; Sokolov, Naidenko & Serbenyuk 1994; Naidenko 2001), there are only a few anecdotal observations from the wild (e.g. Molinari & Molinari-Jobin 2001). Even in our study where direct observations were rare and the results principally relied on radio-telemetry data, different aspects of the spatio-temporal behaviour suggest that disintegration of litters in free-ranging lynx is not caused by female parent aggression as pointed out by Stroganov (1962) and later by Jonsson (1984): (i) aggressive interactions between female parents and juvenile lynx were never observed in the wild (Schmidt 1998; Molinari & Molinari-Jobin 2001; this study), it is unlikely that they have been missed as aggressive encounters between adults of the same sex have been reported (Wölfl & Wölfl 1996; Sunde *et al*. 2000; A. Burri pers. comm.), (ii) separation occurred at the periphery as well as in the core area of the maternal home range, (iii) all subadults except one stayed a few weeks in the maternal home range and even close to the spot of separation before they started dispersal, and none was chased away by its mother during this time, and (iv) a few subadults were occasionally during one day relocated with their mother after separation. A few anecdotal observations suggest that contacts are getting looser close to the separation time. Females sometimes make parallel kills to ensure constant access to food for their kittens (Molinari & Molinari-Jobin 2001). While the female is already at the new kill, the kittens are still feeding at the old one, spending more time away from their mother. Family break-up may be initiated by the female abandoning the kittens at a kill. On some occasions, subadults separated from their mother when they made their first own kill as shown by two juvenile males (M29 and M25) in the NWSA. The cause in either separation case may be the shortage of food in the sense that females may not be able to kill enough prey to feed their almost adult offspring, and not because resources are limited. The start of the mating season in February-March may also induce the process, as most family break-ups occurred in March and April (Schmidt 1998; Sunde *et al*. 2000; this study). The majority of the literature on juvenile dispersal suggests that resource and/or reproductive competition occur between adults and juveniles, thus juvenile dispersal being forced by resident adults of the same sex. However, Wolff (1993) pointed out that only 4 out of 49 mammal studies have documented that juvenile dispersal results from parental aggression. The dispersal of a female even in the absence of her mother and our observations on family breakdowns corroborate these findings. In cougars (*Puma* *concolor*) Beier (1995) did not observe aggression of females towards her kittens either: the mother often left her kittens from 0–3 km at the edge of her home range while she moved to the opposite edge of her home range. Anecdotic observations of interactions between non-related territorial adults and subadults at a kill site during dispersal suggest that residents do not show aggressive behaviour towards subadults of the opposite sex but towards individuals of the same sex.

In both areas, subadults stayed a few months in the maternal home range after separation. Making their first hunting experiences in a familiar environment is certainly an advantage as prey-catching techniques may be expected to take time to acquire. Interactions with their mother is also reduced at this time, as most females give birth to a new litter on June and therefore only use a reduced part of their home range until September (Kaczensky 1991). Such an initial phase of independence was also observed in a former study in the Alps (Haller & Breitenmoser 1986) but not in the autochthonous population in Bialowieza, Poland, where all subadults left the maternal home range just after separation (Schmidt 1998). During the peak of the lynx density in the NWSA, subadults stayed longer in the maternal home range and dispersal onsets were distributed over a longer time period than in the JM (Fig. 4.2). In the Iberian lynx (*Lynx pardinus*), seasonality was more marked in the area where lynx and rabbit densities were low (Ferreras *et al*. 2004). In contrary to the Iberian lynx, intraspecific competition for resource seems not to be the ultimate cause of dispersal in Eurasian lynx. Delayed dispersal at high density is an important factor in the evolution of cooperative breeding in birds and mammals (Brown 1987), but it has also been reported from non-social species (see Lambin *et al*. 2001). Among carnivores it has been observed in black bear (*Ursus americanus*; Lindzey & Meslow 1977a, 1977b) and in Canada lynx (*Lynx canadensis*) where yearlings of both sexes still remained in the mother’s home ranges one year after the hare peak (Breitenmoser, Slough & Breitenmoser-Würsten 1993). If a resident is forced to share its once exclusive home range with conspecifics as a consequence of increased density, it may be more advantageous to share it with its own offspring.

Subadults’ diet in both study sites consisted of smaller prey (e.g. foxes, hares) and less large prey (e.g. chamois) than residents. It is difficult to conclude whether this is a consequence of differences in food preferences or in hunting skills as these results were based on radio-telemetry and not on direct observations of subadults hunting attempts. In Poland, Okarma *et al*. (1997) reported that the brown hare was a buffer prey in subadult lynx, probably crucial for their survival during the first year of independence. In cheetah (*Acinonyx jubatus*), prey of older females tended to be larger than those of adolescents, and younger females chased after inappropriate prey (e.g. dangerous prey such as adult zebra) or very small prey (mainly birds) more often than adults (Caro 1994). Female cheetahs became increasingly successful at catching hares and neonate gazelles as they matured. Such an improvement of the hunting skills has also been reported for leopards (*Panthera pardus*; Bailey 1993), lions (*Panthera leo*; Schaller 1972), and bobcats (*Lynx rufus*; Bailey 1972).

The duration of dispersal was short, with a median of 39 in the NWSA and 134 days in the JM, suggesting that subadults in both areas were quickly integrated into the population. Both sexes established a *THR* in the JM, whereas only one male established a *THR* in the NWSA. In puma, only males established a *THR*, while females were more quickly integrated in the resident population (Beier 1995). Such a difference was not seen in the JM, and is consistent with the previous findings that in lynx both sexes actually disperse. In the JM, most individuals left their *THR* from mid August to the end of September coinciding with the time resident females with kittens start to occupy a larger part of their home range (Kaczensky 1991). The small *THR* of one male (M14) was probably the result of restricted movement abilities after a vehicle collision. This has also been reported in male puma (Beier 1995). All subadults established their *DHR* in the vicinity of known adult lynx home ranges or close to areas with known lynx occurrences. Individuals in solitary territorial species define their home range borders in relation to the spatial distribution of conspecifics. This propensity combined with a low ability of subadults to cross unfamiliar land and barriers (Chapter 5) hamper the expansion of lynx populations. Lynx is a conservative disperser when compared to wolf and bear. The males of the later are able to move long distances even through unoccupied suitable habitat searching for females.

Dispersal distances in the NWSA were shorter than those reported from other studies on Eurasian lynx (Schmidt 1998; Sunde *et al*. 2000; J. Linnell pers. comm.) as well as from other solitary felids of related size such as Canada lynx (Poole 1997) and bobcat (Knick & Bailey 1986; Knick 1990). In the NWSA, dispersal distances were close to those reported by Ferreras *et al*. (2004) in a critically endangered Iberian lynx population in the Coto del Rey area of the Doñana National Park. Differences in dispersal distances between the NWSA and the JM are probably related to the size and arrangement of suitable habitat in each area as well as linear barriers (e.g. fenced highways). Severe habitat restrictions (suitable habitat as well as linear barriers) led to circular dispersal in males in the NWSA (Chapter 5). A similar dispersal pattern has also been reported in two endangered cats: the Florida panther (*Puma concolor coryi*; Maehr, Land & Roof 1991; Maehr *et al*. 2002) and the Iberian lynx (Ferreras *et al*. 2004). However, intrinsic demographic differences and the prospect that dispersal rates and distances may be negatively correlated with density (Chapter 5) may also be relevant. Furthermore we do not know how dispersal would look like in areas continuously occupied by lynx. There is virtually no data on dispersal from a situation comparable to the Alps. The sparse information available is either from the central European lowland (Schmidt 1998) or from Norway with its very low lynx density (Sunde *et al*. 2000; J. Linnell pers. comm.). At the present stage of knowledge, we cannot assess the respective importance of population status (e.g. abundance and distribution), habitat distribution and fragmentation, and landscape features (topography) for shaping the dispersal of lynx. There are however good reasons to suppose that dispersal in the Alps may look different once the entire range is settled by lynx.

Dispersal in solitary felids is usually biased towards males with most of the females remaining philopatric, and dispersal distances are generally larger for males than for females (Logan, Irwin & Skinner 1986; Anderson, Bowden & Kattner 1992; Lindzey *et al*. 1992; Ross & Jalkotzy 1992; Smith 1993; Beier 1995; Sweanor *et al*. 2000; Maehr *et al*. 2002). In Poland, dispersal distances in Eurasian lynx ranged from 5 to 129 km (Schmidt 1998). The maximum distance was reached by a male. Although sample size was limited, it appeared that males dispersed for long distances, whereas females remained philopatric. In our study, there was no significant sex bias in the proportion of individuals that dispersed although only females took over the maternal home range. Furthermore gender by itself did not affect the recovery distance, the distance of settlement from the natal home range (effective dispersal) nor the distance travelled until dispersal ended (distance to the end of dispersal). This pattern has also been observed in the Iberian lynx (Ferreras *et al*. 2004). It has been hypothesized that sex-biased dispersal is linked to the mating system (Greenwood 1980). Polygyny, the predominant mating system among mammals, favours the evolution of male biased dispersal because of intrasexual competition among males for mates (Dobson 1982; Greenwood 1980). In contrary to the Iberian lynx (Ferreras *et al*. 2004), the mating system of the Eurasian lynx in the NWSA did not tend to monogamy in spite of the saturation of breeding territories. Male bias in dispersal may be less pronounced in Eurasian lynx compared to other felids, and therefore our sample size too small to detect sex specific differences. The small residual deviance explained by the models indicates that other factors not included in the models may be relevant. Extrinsic factors, such as habitat fragmentation (Chapters 5 and 8), the size of settled areas, and poaching may shape the dispersal distances in lynx. Furthermore, their constraints may vary between males and females (e.g. only males moved through unfamiliar habitat and turned back at the highways in the NWSA) making it difficult to reveal any sex-specific differences in dispersal distances.

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Chapter 5. Importance of dispersal for the expansion of an Eurasian lynx (*Lynx lynx*) population in a fragmented landscape

5.1. Abstract

Dispersal allows a species to recolonize former habitats after severe range depression. However, the significance of dispersal for the spread of a population is less obvious in felids. There is little evidence for the general belief that subadult felids would conquer new areas, although this is a crucial assumption in re-introduction or recovery projects. Eurasian lynx were reintroduced into the Swiss Alps and have subsequently spread over the north-western part of the Alpine arc, but the expansion halted in the mid-1980s, although suitable habitat was still available. We postulated that high lynx density would lead to an expansion of the population. Five predictions were tested with dispersal data from the north-western Swiss Alps (NWSA) where from about 1995 a strong increase in lynx abundance took place, and from the Jura Mountains (JM), an area with low to average lynx density. Dispersal characteristics were collected for 22 and 17 lynx most were radio-tagged, in the NWSA and JM respectively. Dispersal rate and distances for subadults that completed dispersal were lower in the NWSA than in the JM. In the NWSA, subadults showed a low ability to cross major barriers like highways, which led to circular dispersal in the case of two males. The general hypothesis that high population density will foster the expansion of the population was not confirmed. This has consequences for the re-introduction and recovery of (solitary) carnivores in a fragmented landscape. To establish one strong source population in one place might not be an optimal strategy. Rather, population nuclei should be founded in several neighboring patches. Exchange between established neighboring subpopulations (e.g. to maintain genetic diversity) will later on take place, as resident adult lynx show a higher propensity to cross barriers than subadults.

5.2. Introduction

Dispersal, the movement of subadult animals from their natal range to the place where they will breed, is an important mechanism in the process of colonization of new areas. In territorial species, individuals compete for local resources, and dispersers need to get access to unexploited resources. In a saturated population, those are to be found at the edge or outside the colonized area. Hence, dispersal leads to dispersion (see general comments in Stenseth & Lidicker 1992). Dispersal allows a species also to recolonize former habitats after a severe population and range depression. This is presently observed in large carnivores in Europe and North America. Brown bears (*Ursus arctos*), nearly extinct in the early 20th century, have recolonized important parts of Scandinavia (Swenson *et al*. 1995). The range outside the core areas was occupied by young bears, predominantly by males of 2-4 years, the age of most active dispersal (Swenson, Sandegren & Söderberg 1998). Wolves (*Canis lupus*) reappeared in the Swiss Alps, where the species had been eradicated in the 19th century (Breitenmoser 1998). The Alps have been recolonized from the Italian Apennine population, mainly by subadult males (Crettenand & Weber 2000). The recolonization of lost areas by wolves dispersing from their natal ranges was also observed in Minnesota (male-biased; Mech 1987), and in the central Rocky Mountains (both sexes; Boyd & Pletscher 1999).

The significance of dispersal for the spread of a population is less obvious in cats. Long-range dispersal has been described in Eurasian lynx (*Lynx lynx*; J. Linnell, pers. comm.), in Canada lynx (*Lynx canadensis*; review in Mowat, Poole & O'Donoghue 2000), and in puma (*Puma concolor*; Sweanor, Logan & Hornocker 2000), but these were animals dispersing between or within extant populations. There is little evidence for the general belief that dispersing subadult cats would conquer new lands, although this is a crucial assumption e.g. in re-introduction or recovery projects.

Eurasian lynx were reintroduced into the Swiss Alps and have subsequently spread over the north-western part of the Alpine arc (Breitenmoser, Breitenmoser-Würsten & Capt 1998), but the expansion slowed down in the mid-1980s, although areas with suitable habitat were still available, and from some regions already colonized, little or no evidence for lynx presence was available in the 1990s (Molinari-Jobin *et al*. 2001). After about 1995, monitoring data signaled an increase in lynx abundance in the north-western Swiss Alps (NWSA), finally resulting in a controversy with hunters who claimed that lynx was reducing the roe deer and the chamois populations (Breitenmoser *et al*. 1999; Breitenmoser-Würsten *et al*. 2001). After an increasing number of lynx attacks on livestock (Angst, Olsson & Breitenmoser 2000), the wildlife management authorities of the canton of Fribourg asked the Swiss Agency for Environment, Forest and Landscape (SAEFL, the federal office in charge) for permission to remove problem lynx. Such permission was however not given at that time, as it was the aim of the policy of the SAEFL to have lynx spread throughout suitable habitats in the Alps, and there was a general belief that the "population pressure" in the NWSA would further the expansion of the populations. Instead, the SAEFL funded a research project to understand the dynamics of the ongoing process. In 1997, we started to capture and radio-tag lynx in the NWSA. One target group consisted of juvenile lynx just before separation from their mothers, in order to observe them during dispersal.

The assumption that population pressure would result in an expansion of the occupied area (Hell 1961) implies two hypotheses: 1. the lynx population expands through dispersal (of subadult lynx), and 2. dispersal is density dependent, so both the rate and the mean distance of dispersal are higher in a situation of high lynx abundance. To assess dispersal in the NWSA, we compared it with data from an earlier, similar study in the Jura Mountains (Zimmermann 1998) with low to average lynx density (Breitenmoser-Würsten *et al.* subm.) and tested the following predictions: 1. All subadult lynx in the NWSA will disperse due to local resource depletion. 2. Most subadults will leave the saturated compartment of the NWSA and settle in neighboring areas. 3. Mean dispersal distances will be longer than in a low-density situation. 4. A larger proportion of dispersers from the NWSA will move through unfavorable habitat and cross barriers. 5. As a consequence, we expected that the standard monitoring system for lynx in Switzerland (Capt, Breitenmoser & Breitenmoser-Würsten 1998) would reveal an increase of lynx presence in the geographic compartments adjacent to the NWSA after a time lag of some years.

5.3. Study areas

5.3.1. North-western Swiss Alps

The Alpine landscape is fragmented both by high altitude ridges above the timberline and valleys with dense human settlements and main traffic arteries. Our study was conducted in the north-western Swiss Alps (NWSA), a 2,800 km^2 patch more or less isolated from the rest of the Alps (Fig. 5.1).

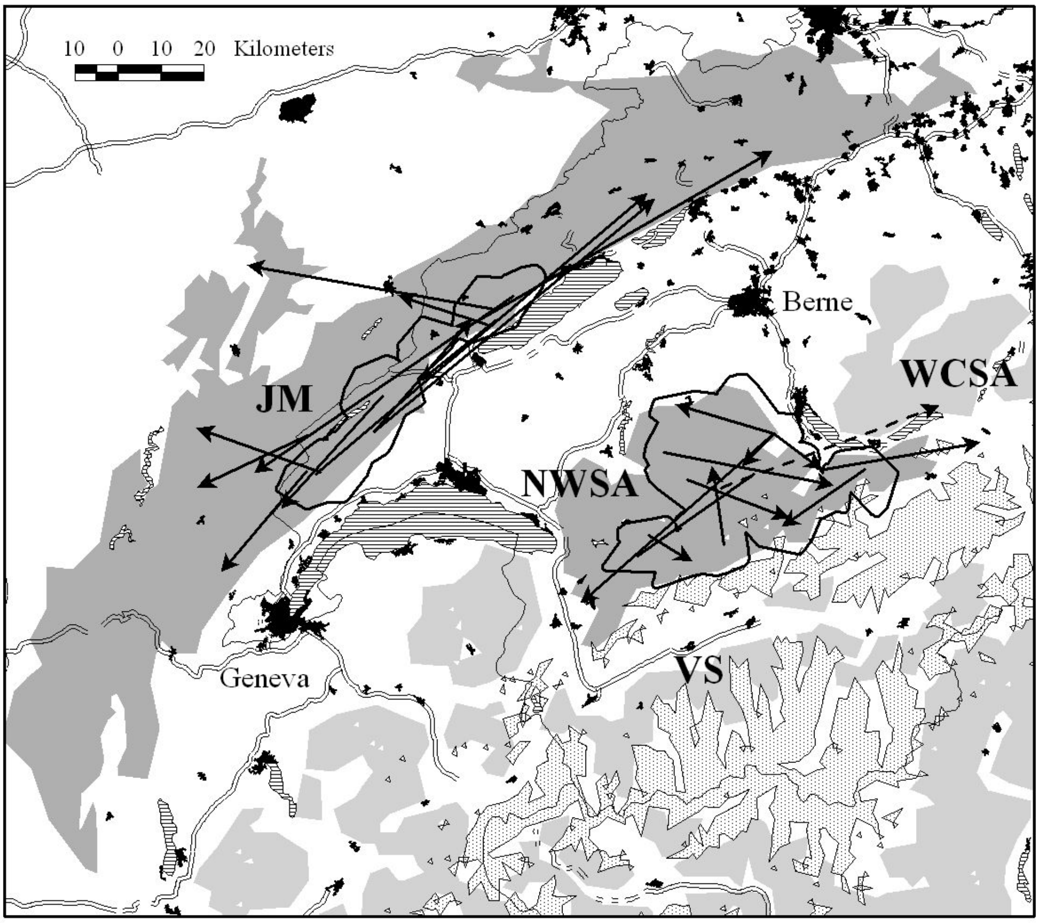

Figure 5.1. Suitable habitat patches in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM) are highlighted in dark; the adjoining patches Valais (VS) and western central Swiss Alps (WCSA) in light gray. Thick lines in compartment NWSA and JM show the main study areas of the *Swiss Lynx Project* (*SLP*), where the subadults were caught. Arrows indicate dispersal directions, distances and endpoints for 14 lynx from compartment NWSA and 12 from compartment JM. Movements are shown as straight lines from a lynx's natal home range center or its capture site to its independent home range center, mortality site, or last location. All subadults settled down in their natal habitat patch (NWSA or JM), except one male that left the NWSA for a new area (dashed line). Dotted = Elevation >2,400 m; horizontally hatched = lakes; double lines = highways; thin lines = international boundaries; black spots = major agglomerations.

It is limited in the north-east by the valley of the Aare river with the lakes of Brienz and Thun, in the north-west by the Swiss Plateau, in the west by the Rhone valley with the Lake of Geneva, and in the south by the Bernese Alps rising to 4,000 m. The valley bottoms have been deforested and are densely populated. The human population reaches a density of 140/km^2 in most parts of the study area and people living in the lowlands use the Alps intensively for recreation (skiing, hiking). Forests cover 30% of the study area but are highly fragmented. They extend along steep slopes up to the timberline at 1,800-2,200 m. Lower ridges and gentle slopes were deforested early on and provide summer pastures for cattle and sheep. From late spring to autumn, domestic sheep graze unguarded on remote mountain meadows. Lynx's main prey in the study area are roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) (Breitenmoser & Haller 1987). On rare occasions lynx prey upon sheep. In 1999, the year with the highest loss, 157 sheep were killed that is 0.4% of the 39,000 sheep aestivated in the study area (Angst *et al*. 2000). The overall lynx density in the north-western Swiss Alps, based on the distribution of radio-collared animals and information about additional, untagged individuals from photo-trapping, was estimated at 1.4–1.5 resident lynx/100 km^2 (Breitenmoser-Würsten *et al*. 2001; Molinari-Jobin *et al*. 2001). Adjacent lynx areas to the NWSA are the compartments Valais (VS) in to the south and western central Swiss Alps (WCSA) in the east (Fig. 5.1).

5.3.2. Jura Mountains

The study was performed from 1988 to 1999. The Jura Mountains (JM) are a secondary limestone mountain chain forming the north-western border of Switzerland with France (Fig. 5.1). They are less fragmented than the Alps, forming basically a block of contiguous suitable habitat of 6,670 km^2 (Chapter 7). The altitude ranges from about 500 m to 1,718 m (Crêt de la Neige). Deciduous forests along slopes and coniferous forests on the ridges cover 53% of the study area. Agricultural areas are typically pastures. The human population is more clustered than in the Alps and reaches a density of 120/km^2 in most parts of the JM. People living on the Swiss Plateau use the highlands intensively for recreation. As in the Swiss Alps, roe deer and chamois are the main prey of lynx (Jobin, Molinari & Breitenmoser 2000; Molinari-Jobin *et al*. 2002). The overall lynx density in the main study area remained fairly constant over the whole study period (Breitenmoser-Würsten *et al*. subm.) and was estimated at 0.7–0.8 resident/100 km^2 (Breitenmoser *et al*. 1993a, Molinari-Jobin *et al*. 2002, Breitenmoser-Würsten *et al*. subm.).

5.4. Material and method

5.4.1. Field Study

Dispersal characteristics (Table 5.1) were obtained for 22 and 17 lynx in the NWSA and the JM, respectively. Dispersal data came mainly from radio-telemetry; additional information was available from cubs tagged at the den and later live-trapped or “captured” in a camera trap. Details of capture, handling, and radio-telemetry can be found in Jobin *et al*. (2000) and Breitenmoser-Würsten *et al*. (subm.). Radio-marked lynx were relocated from the ground to a precision of 1 km^2 to 1 ha. We located dispersing lynx almost every day when they moved through new terrain, and at least every week once home ranges were established for more than one month. Subadults after independence were considered “dispersers” when they established a home range that overlapped not more than 5% of their natal (= maternal) home range (based on 90% minimum convex polygon MCP) or were last located outside their natal area (Sweanor *et al*. 2000). Percent overlap of total ranges and home ranges between animals A and B was calculated as

$$\sqrt{overlapAB / rangeA * overlapAB / rangeB}$$

All other independent progeny – establishing home ranges with more than 5% overlap with their natal range – were considered philopatric (Ph in Table 5.2). Dispersal began when a subadult made its first move outside its natal home range without returning.

Dispersers were classified in two categories: (1) dispersers (Di in Table 5.2) = individuals that most likely completed their natal dispersal and exhibited six months of site fidelity suggestive of home range (HR) establishment and/or reached sexual maturity, and (2) failed dispersers (fD in Table 5.2) = dispersers that exhibited less than six months site fidelity and/or died before they established a HR. Lynx reach sexual maturity at the age of 2.7 years for males and 1.75 years for females. Although, some males and almost 50% of the females reached sexual maturity one year earlier in a study by Kvam (1991), we never observed early maturity in the field. A limit of six months for site fidelity was chosen because all dispersers with the exception of one male, which stayed for 200 days, left their transient home range after 72 to 114 days (median = 113 days, N = 5; Chapter 4). The main study area in each region was defined as the area formed by the 1 km buffered 100% MCP of all adult resident females from which juveniles were caught and observed during dispersal.

Table 5.1. Characteristics and fate of juvenile lynx followed in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). Type and order of information: den = individuals ear-tagged as kitten; rt = radio-telemetry; ct = camera-trap, cr = carcase retrieved. Alive = survived the full year after separation of the mother. Reproduced = strong evidence from genetic analyses or observations in the field that individuals have reproduced, (reproduced) = lynx reached sexual maturity according to Kvam (1991) but their was no proof for reproduction.

Lynx	**Kitten of female**	**Date of first observation**	**Information**	**Date of last observation**	**Fate**
NWSA					
M18	F37	22.01.97	rt, ct	16.05.99	Alive, (reproduced)
M20	F30	25.03.97	rt, ct	02.12.98	Alive
M24	F47	24.02.98	rt, ct	27.01.04	Alive, reproduced
M25	F33	28.06.97	den, rt	14.09.00	Alive, (reproduced)
M28	?	30.01.99	rt	12.02.99	Died, starvation
M29	F34	25.06.98	den, rt, ct	07.05.03	Alive, (reproduced)
M30	?	05.03.99	rt	21.09.99	Died, disease
M31	F52	08.12.98	ct, rt	10.08.00	Alive
M35	F35	31.10.98	ct, rt, ct	12.02.04	Alive, (reproduced)
F31	F32	06.01.97	rt, ct	26.09.98	Alive, (reproduced)
F33*	?	14.01.97	rt	23.07.98	Alive, reproduced
F40	?	13.03.97	rt	20.03.98	Unknown
F42*	?	05.04.97	rt,ct	11.01.04	Alive, reproduced
F46*	?	15.11.97	rt	20.01.98	Died, car accident
F48	F38	05.07.97	den, rt	18.05.98	Unknown
F49	F34	23.06.97	den, rt	27.08.99	Alive, (reproduced)
F50	F37	13.03.98	rt	19.05.98	Unknown
F54*	?	14.08.99	rt	23.06.00	Alive, (reproduced)
F56	F32	08.02.00	rt	25.02.00	Unknown
F57*	?	08.05.00	rt	10.03.01	Alive
FB22	F34	25.06.98	den, ct, cr	18.10.01	Alive, (reproduced)
FB44	F34	11.12.01	ct	01.08.03	Alive, (reproduced)
JM					
M11	F21	19.06.93	den, rt, cr	08.02.02	Alive, reproduced
M13	F18	18.06.93	den, rt	27.06.95	Alive, (reproduced)
M14	F21	31.12.95	rt	26.02.98	Alive, (reproduced)
M15	F18	23.06.95	den, rt	21.09.96	Died, illegal killing
M16	F11	08.03.90	rt	19.06.90	Died, disease
F12	F11	20.04.88	rt	20.12.88	Died, illegal killing
F13	F11	23.03.89	rt	17.08.89	Died, disease
F17	F14	25.03.90	rt	23.05.90	Died, car accident
F19	F18	04.03.91	rt	05.05.91	Unknown
F20	F11	16.03.91	rt	xx.11.95	Alive, reproduced
F22	F18	04.03.92	rt	25.11.94	Alive, reproduced
F23	F15	14.03.92	rt	15.02.95	Alive, reproduced
F25	F30	20.12.95	rt	02.07.96	Unknown
F26	F18	23.06.95	den, rt, ct	08.01.03	Alive, reproduced
F27	F24	30.06.95	den, rt	27.04.96	Unknown
F28	F24	27.06.95	den, rt	04.03.96	Unknown
F36	F29	04.03.97	rt	24.06.98	Alive, (reproduced)

*first observed as subadults after separation from mother

Table 5.2. Dispersal distances (*CD*: centroid distance; *TD*: total distance; *MD*: maximum distance; MPD_1, MPD_2: maximum possible distances according to two habitat models; see Method for details) for 13 subadult lynx in the north-western Swiss Alps (NWSA) and 14 in the Jura Mountains (JM). *DT* = dispersal type: Ph = remained philopatric, Di = individuals that most likely completed their dispersal (six months of site fidelity suggestive of home range (HR) establishment and/or surveyed until sexual maturity), fD = failed dispersal (exhibited less than six months site fidelity and/or died before established a HR). ♀HR and ♂HR diameter = *CD* expressed in number of mean circular resident female and male home range diameter, respectively. Percentage of overlap with maternal home range (90%MCP). + = overlap, but maternal HR not exactly known.

Lynx	***DT***	**Centroid distance**			***TD*** **(km)**	***MD*** **(km)**	MPD_1 **(km)**	MPD_2 **(km)**	**Overlap (%)**
		CD **(km)**	**Number ♀HR diameter**	**Number ♂HR diameter**					
NWSA									
M18	Di	50.7	5.0	3.5	-	-	50	50	0
M20	Di	15.2	1.5	1.0	-	-	53	53	0
M24	Di	4.5	0.4	0.3	157	43.2	68	68	0.8
M25	Di	33.1	3.3	2.3	36	28.8	73	73	0
M29	Di	56.0	5.6	3.8	81	68.2	65	65	0
M30	fD	5.1	0.5	0.3	62	17.2	65	4	+
M31	Di	36.7	3.6	2.5	164	51.2	63	63	0
M35	Di	20.1	2.0	1.4	-	-	76	-	0
F31	Di	22.1	2.2	1.5	55	22.0	58	58	0
F40	Di	33.3	3.3	2.3	69	35.9	68	25	0
F49	Di	7.4	0.7	0.5	2	17.4	65	65	0
FB22	Di	10.7	1.1	0.7	-	-	65	-	0
FB44	Di	20.6	2.0	1.4	-	-	65	-	0
median		*20.6*	*2.0*	*1.4*	*65.5*	*32.4*	*65*	*60.5*	
JM									
M11	Di	31.4	2.1	1.6	-	-	156	-	0
M13	Di	97.3	6.6	5.1	-	-	173	-	0
M14	Di	81.1	5.5	4.3	86	75.7	156	156	0
M15	fD	27.0	1.8	1.4	14	21.0	175	104	0
M16	fD	19.1	1.3	1.0	52	28.0	157	157	0
F12	Di	80.7	5.5	4.2	70	68.9	150	128	0
F13	fD	18.4	1.3	1.0	19	18.4	155	155	0
F17	fD	31.9	2.2	1.7	68	51.0	151	127	0
F20	Di	54.9	3.7	2.9	99	45.7	159	159	0
F22	Di	27.6	1.9	1.4	72	35.5	172	105	0
F23	Ph	11.0	0.7	0.6	51	34.0	143	143	12.2
F25	fD	24.9	1.7	1.3	91	46.8	170	112	0
F26	Ph	2.1	0.1	0.1	52	30.0	176	176	47.2
F36	Di	68.8	4.7	3.6	110	53.3	164	164	0
median		*29.5*	*2.0*	*1.5*	*69*	*40.6*	*158*	*149*	

5.4.2. Data analysis

The dispersal direction is defined as the vector from the centre of the natal home range (arithmetic centre) to the centre of the dispersal home range. Directional data from dispersers were transformed to unimodal data and subjected to Rayleigh's test (Zar 1984) to examine whether dispersal directions were distributed uniformly or not. Centroid distance (*CD*) was the distance from the arithmetic centre of a progeny's natal home range (natal centre) to the arithmetic centre of its independent home range (independent centre). When complete dispersal information was not available, dispersal distances and direction were calculated based on one of the following combinations: natal centre to mortality site or last location, or capture site to independent centre, mortality site, or last location. The dispersal distance was also expressed relatively as the number of sex-specific home ranges crossed during dispersal movements. The size of male and female home ranges, respectively, was calculated as the diameter (*d*) of a circle with an area equal to the average home range size (*HR*) for adult male and female lynx in the study areas (NWSA: Breitenmoser-Würsten *et al*. 2001; JM: Breitenmoser-Würsten *et al*. subm.):

$$d = 2\sqrt{HR/\pi}$$

The total distance (*TD*) was the sum of distances between consecutive locations (only one fix per day considered) of the subadults during their dispersal. The measures were taken from the point the subadult left the maternal home range to the point when entering its subsequent home range. When subadults established more than one home range, the total-distances between the ranges were summed. The maximum distance (*MD*) was the largest distance a dispersing lynx was ever located from the centroid of its mother's home range. We compared the *MD* with two maximum possible distances (MPD_1) and (MPD_2), calculated as the distance from the centroid of the natal range to the farthest edge of good lynx habitat that could be accessed within the same compartment (MPD_1) and to the most distant good lynx habitat edge in the initial dispersal direction chosen by the respective subadult (MPD_2). The areas of good lynx habitat were derived from lynx habitat models developed for the Alps (Chapter 8) and the Jura Mountains (Chapter 7). We used Mann-Whitney U-test (Zar 1984) to compare dispersal distances between sexes and study areas, and Wilcoxon paired-sample test (Zar 1984) to compare the $MPD_{1,2}$ with the *MD*. Comparisons were made between: (i) all subadults (dispersal of Ph, fD and Di in Table 5.2), (ii) only individuals that dispersed (fD, Di in Table 5.2) and (iii) finally only those that completed dispersal (Di in Table 5.2). *CD* dispersal distance of Ph, Fd and Di is equivalent to the recovery distance according to Trewhella, Harris & McAllister (1988) whereas *CD* dispersal distance of Di is equivalent to the effective dispersal distance.

To assess the effect of increased lynx abundance in and dispersal form the NWSA on lynx presence in neighboring compartments, we used information from a standardised monitoring. Monitoring of lynx in Switzerland is based on four data sets (see Capt *et al*. 1998, for details): (1) records of lynx killed or found dead or young orphaned lynx discovered, (2) records of livestock killed by lynx, (3) records of wild prey remains, tracks, scats, sightings, and vocalizations, and (4) periodic qualitative inquiries among game wardens. All monitoring data were calibrated according to the criteria defined for the pan-Alpine monitoring (Molinari-Jobin *et al*. 2001), which defines three levels of reliability: Quality 1 (Q1): “hard facts”, such as dead or captured lynx or photographs; Quality 2 (Q2): confirmed records such as cases of depredation, wild prey remains, tracks and scats assessed by trained staff; Quality 3 (Q3): all unconfirmed or unverifiable reports, including direct observations. We considered only confirmed data (Q1 and Q2) to compare lynx presence and population trends in neighboring areas, but excluded depredation reports, as livestock is not consistently available in all areas.

5.5. Results

Only two females out of 14 subadults in the JM and one male out of 13 subadults in the NWSA (F23, F36 and M30; Table 5.2) remained philopatric. The latter died after a short circular dispersal (Fig. 5.2). Seven out of 9 subadults from the JM that completed dispersal left the main study area whereas 3 out of 12 did so in the NWSA. None of the subadults left the compartment of the JM whereas one (M18) left the compartment of the NWSA.

Dispersal directions of individuals that either failed or completed dispersal (fD, Di; Table 5.2) were randomly distributed over the cardinal points in the NWSA, but not in the JM (Rayleigh test; NWSA: $Z=2.1$, $N=12$, $p>0.1$; JM: $Z=5.5$, $N=12$, $0.002<p<0.005$; Fig. 5.1). The main dispersal direction in the JM was south-west and north-east oriented. This corresponds approximately to the orientation of the predominant ridgelines of this mountain range (Fig. 5.1).

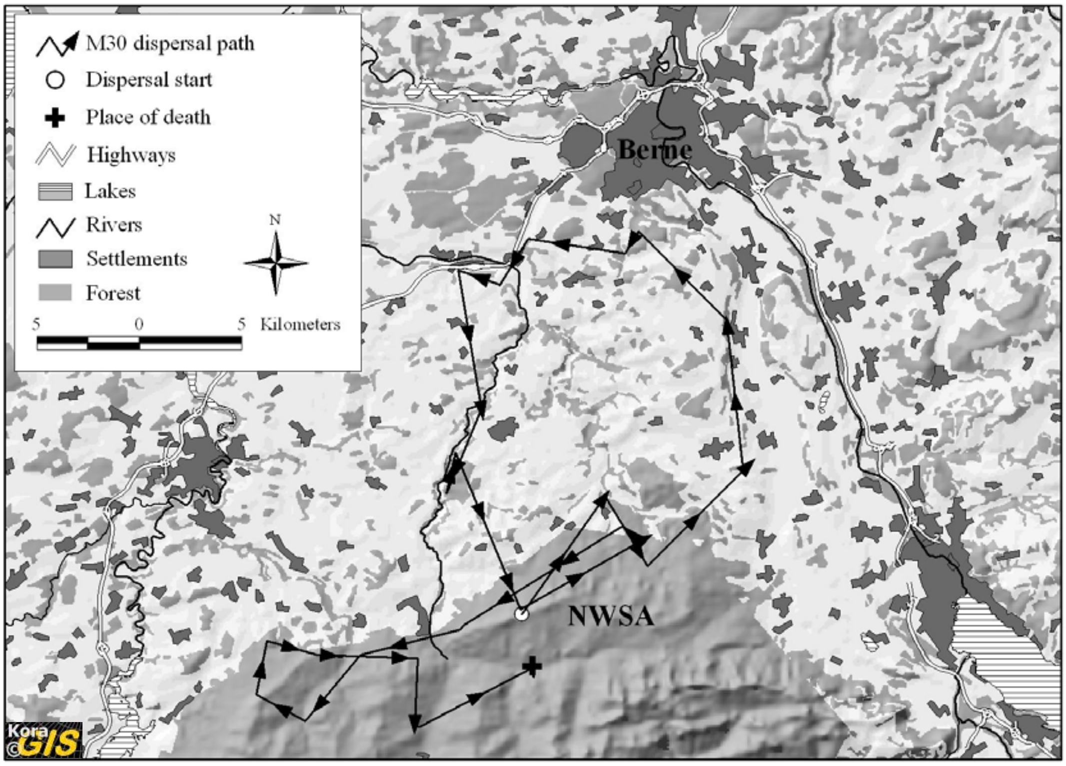

Figure 5.2. Dispersal path of M30 who traversed part of the Swiss Plateau an area with limited forest cover. He moved northward until he reached the surroundings of Berne where he turned west. He followed the highway for over 4.5 km and returned to the north-western Swiss Alps (NWSA) along a river-bed. M30 used mainly small ribbons of forests when moving. The ultimate trajectory of M30's movements was circular.

Males did nowhere disperse further than females (Mann-Whitney U test, $p>0.05$). Both sexes have therefore been pooled for further analyses. The centroid distances (*CD*) ranged from 4.5 to 56 km in the NWSA (median=20.6 km, N=13) and from 2.1 to 97.3 km (median=29.5, N=14) in the JM when all individuals were considered (Table 5.2). Subadult lynx that completed and/or had a fatal dispersal dispersed further in the JM than in the NWSA: *CD* was higher in the JM than in the NWSA when either both fatal (fD) and completed dispersal (Di) or when only completed dispersal (Di) was considered (Mann-Whitney U test, Table 5.3), but did not differ when all (Ph, fD, Di) individuals were included in the analyses.

Recovery distance (*CD*, Ph, fD and Di) in the NWSA was 2.0 (range=0.4–5.6) times the mean circular resident female's home range diameter and 1.4 (range=0.3–3.8) times the mean circular male's home range diameter. In the JM, it was 2.0 (range=0.1–6.6) and 1.5 (range=0.1–5.1) times the respective means. Effective dispersal distance (*CD*, Di) was 2.1 (range=0.4–5.6) times the mean resident female's home range diameter and 1.5 (range=0.3–3.8) times male's home range diameter in the NWSA. In the JM it was 4.7 (range=0.1–6.6) and 3.6 (range=0.1–5.1) times the respective means.

The total distances (*TD*) ranged from 2 to 164 km (NWSA: median=65.5 km, N=8), and from 14 to 110 km (JM: median=69 km, N=12), whereas the maximum distances (*MD*) ranged from 17.2 to 68.2 km (NWSA: median=32.4 km, N=8), and from 21 to 75.7 km (JM: median=40.6 km, N=12) in the NWSA and the JM, respectively. Dispersal potential did not differ between the JM and the NWSA: *TD* and *MD* were not significantly different between the two areas (Mann-Whitney U test, Table 5.3) whichever dispersal category was considered.

Table 5.3. Comparison between the dispersal distances in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). Median with sample size in bracket. NS = non significant. All = recovery distance, all individuals were considered including those that completed dispersal (Di, effective dispersal), had a fatal dispersal (fD) or remained philopatric (Ph).

	Centroid Distance (km)			***Total Distance*** (km)			***Maximum Distance*** (km)		
	NWSA	**JM**	**P**	**NWSA**	**JM**	**P**	**NWSA**	**JM**	**P**
Ph+fD+Di	20.6 (13)	29.5 (14)	NS	65.5 (8)	69 (12)	NS	32.4 (8)	40.6 (12)	NS
fD+Di	20.6 (13)	31.7 (12)	P=0.05	65.5 (8)	71 (10)	NS	32.4 (8)	46.3 (10)	NS
Di	21.4 (12)	68.8 (7)	P<0.01	68.5 (7)	86 (5)	NS	35.9 (7)	53.3 (5)	NS

In the NWSA, *CD* was smaller than *MD*, indicating a circular dispersal, when all individuals and individuals that exhibited fatal or completed dispersal (fD, Di, Table 5.2) were compared (Wilcoxon paired-sample test, Table 5.4), but did not differ for individuals that completed dispersal (Di, Table 5.2). There was no significant difference between *CD* and *MD* in the JM. In both areas, the maximum distance (*MD*) was smaller than the maximum possible distance 1 (MPD_1) whichever dispersal category was considered (Wilcoxon paired-sample test, Table 4). *MD* was significantly smaller than the maximum possible distance 2 (MPD_2) for all comparisons in the JM (Wilcoxon paired-sample test, Table 5.4) but did not differ in the NWSA, indicating that in the NWSA most of the subadults reached the edge of suitable habitat during their dispersal. The MPD_1 and MPD_2 were significantly higher in the JM than in the NWSA (Mann-Whitney U test, $p<0.05$), which means that the suitable habitat patch in the JM is larger than that in the NWSA.

Table 5.4. Comparison between the centroid distance (*CD*) and the maximum distance (*MD*) and between the maximum distance (MD) and the maximum possible distances (*MPD1* and *MPD2*) in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). Sample size in bracket. NS = non significant. All = recovery distance, all individuals were considered including those that completed dispersal (Di, effective dispersal), had a fatal dispersal (fD) or remained philopatric (Ph).

	CD/MD		***MD/MPD1***		***MD/MPD2***	
	NWSA	**JM**	**NWSA**	**JM**	**NWSA**	**JM**
Ph+fD+Di	P<0.05 (8)	NS (12)	P<0.05 (8)	P=0.005 (12)	NS (8)	P<0.005 (12)
fD+Di	P<0.05 (8)	NS (10)	P<0.05 (8)	P<0.01 (10)	NS (8)	P<0.01 (10)
Di	NS (7)	NS (5)	P<0.05 (7)	P<0.05 (5)	NS (7)	P<0.05 (5)

In the NWSA, four out of nine subadults – all males (M18, M24, M29 and M30) – went beyond the edge of good lynx habitat while dispersing. Only M18 however was successful and reached the neighboring compartment WCSA (Fig. 5.1). The three other males (M24, M29 and M30) returned to the NWSA after having spent a few days in the vicinity of a highway. Two of them (M24 and M30) turned back to the place where they initially started their dispersal. M24 dispersed northwards and was located close to a fenced highway 43 km from his natal range. He spent a week in the vicinity of the highway in a military training area. He was once located 50 m away from a bridge over the highway without lighting, but he did not attempt to cross it. Finally, he returned to the vicinity of his maternal home range. M29 tried to cross the valley of the Rhone river but stopped at the highway and turned back to the NWSA. M30 made an excursion to the Swiss Plateau and was located in the surroundings of Berne (Fig 5.2). He moved in an area lying 8 km west of Berne and stayed a week in the vicinity of a highway and railway. He returned to the NWSA moving along a river-bed before he died from cat-mange (Ryser-Degiorgis *et al*. 2002). During his dispersal, he crossed a minimum distance of 650 m in arable lands. On their dispersal, subadult lynx were mostly traveling through areas occupied by adult resident conspecifics. Only one male (M16) of 11 subadults in the JM avoided the resident home ranges by following their borders and leaving the good lynx habitat. He spent 24 days on the Swiss Plateau and died of *Pneumonia* (Breitenmoser *et al*. 1993a).

Quality 1 and Quality 2 monitoring data showed a significant increase of lynx abundance in the NWSA from the middle to the end of the 1990s followed by a decrease (Fig. 5.3b, Molinari-Jobin *et al.* 2001; Zimmermann *et al.* 2003). No significant increase of lynx abundance could however be observed in the neighboring compartments VS and WCSA, even after a time lag of some years following the peak in the NWSA (Fig. 5.3a, c).

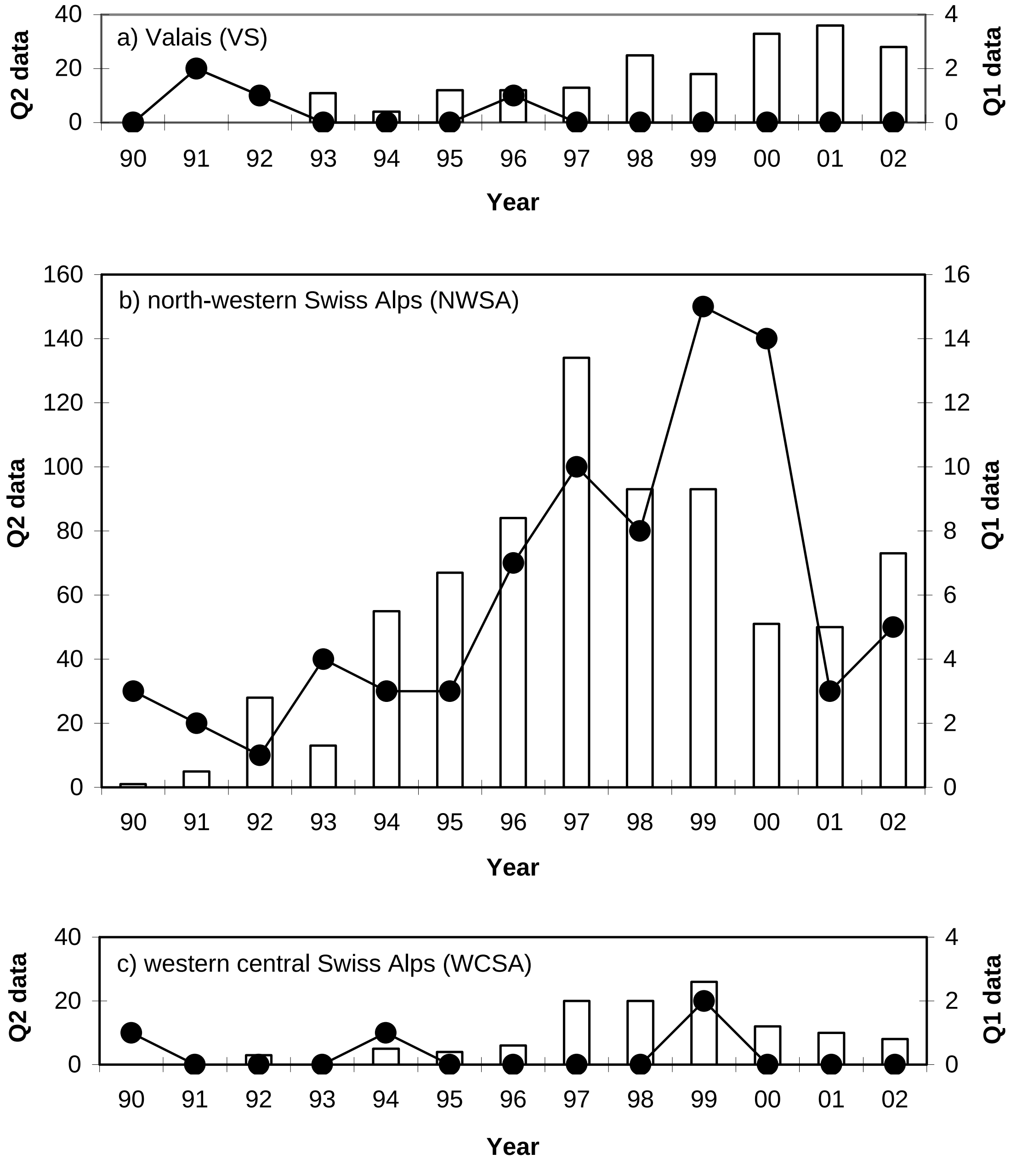

Figure 5.3. Evolution of two data sets from 1990-02 in a) the Valais, b) the north-western Alps and c) the western central Swiss Alps. Reports of lynx killed or found dead, or young orphaned lynx caught and put into captivity (Quality 1, continuous line), records of wild prey remains, tracks, scats, sightings, and vocalisation confirmed by trained people (Quality 2, columns).

5.6. Discussion

5.6.1. Hypotheses and predictions

Prediction 1, stating that all subadults in the NWSA will disperse due to local resource depletion, was not supported, as a high proportion of subadults also dispersed in the JM, an area with a lower lynx density and relative high prey density during the study period (Molinari-Jobin, Molinari & Breitenmoser subm.). Prediction 2, asserting that most subadults will leave the compartment of the NWSA, was also rejected as only one individuals out of 12 that completed dispersal, indeed left its natal compartment. The number of individuals leaving the main study area in the NWSA was even smaller than in the JM. Prediction 3, stating that the dispersal distance in the NWSA will be larger than in a low-density situation, was rejected, as centroid dispersal distances (*CD*) did not differ between the JM and the NWSA when all individuals were considered (Ph, fD, Di, Table 5.2). *CDs* in the NWSA were significantly smaller than in the JM when only individuals that most likely completed dispersal were considered (Di, Table 5.2). Prediction 4 – a larger proportion of dispersers in the NWSA will move through unfavorable habitat and cross barriers – was partly confirmed. A larger proportion of individuals in the NWSA, all males, moved through unfavorable habitat, but all stopped at fenced highways and turned back to the NWSA. Two of them settled down in or in the vicinity of their maternal home range. Finally, the prediction that dispersal would lead to an increase of lynx presence in the geographic compartments adjacent to the NWSA (Prediction 5) was so far not confirmed.

5.6.2. Why did our hypotheses and predictions not turn out to be right?

Subadults from the NWSA and the JM seem to have the same dispersal potential, as there was no significant difference between the total distance (*TD*) and the maximum distance (*MD*) between the two areas. Subadult lynx have a low capability to move through unfavorable habitat and to cross barriers such as highways as shown by our results. Observations from adult radio-tagged lynx, which sometimes roam far outside their home ranges, demonstrated however that lynx in principle easily cross such obstacles. The reduced ability of the subadult led to circular dispersal in the case of two males in the NWSA. Severe habitat restriction led to male philopatry in Florida, where male cougars (*Puma concolor coryi*) returned to the vicinity of their natal areas after frustrated dispersal attempts (Maehr 1997; Maehr *et al*. 2002). A similar process has also been described for the Iberian lynx (*Lynx pardinus*; Ferreras *et al*. 2004). Habitat quality and barriers not only shaped dispersal distances but also directions. In the NWSA, dispersal directions were oriented randomly in space, but not in the JM. The ridges of the JM run south-west to north-east and the predominant orientation of mountain appeared to shape the movements of dispersing subadult lynx. The compartment of the NWSA is in contrast less elongated and there are no parallel ridgelines (compared to the JM) inducing lynx dispersal in a particular direction (Fig. 5.1). The lack of south-east dispersal in the JM may indicate hesitance to leave the continuous forest and travel over open agricultural areas. Similar behavior has been reported in American black bears from western Virginia which used the predominant ridgelines of the Appalachian Mountains as corridors (Lee & Vaughan 2003), and in red fox (*Vulpes vulpes*) in North Dakota where dispersal directions were altered by a 4-lane interstate highway (Allen & Sargeant 1993).

The most important outcome from our study however was that we failed to detect any density-dependent aspects in lynx dispersal and hence cannot confirm the general hypothesis that high population density – “population pressure” – will foster the expansion of the population. High lynx abundance can locally depress the numbers of roe deer und chamois, lead to an increase of depredation on livestock, and ultimately diminish the acceptance of lynx by local people (Breitenmoser 1998; Breitenmoser & Breitenmoser-Würsten 2001). There was little evidence of illegal killing in the NWSA until 1999. In 2000, however, at least eight individuals were known to have been illegally killed (Breitenmoser-Würsten *et al*. 2001). In addition, four animals were removed as stock raiders from 1997 to 2001, and six lynx were taken from the NWSA in 2001 for a translocation program into the eastern Swiss Alps (Molinari-Jobin *et al*. 2001) leading to a considerable reduction of the population pressure (Fig. 5.3).

In principle, there is good evidence from most groups of organisms considered that dispersal (emigration) rate increases with increasing competition for limited resources (examples in Lambin *et al*. 2001). On the other hand, dispersal rates have also been reported to be negatively density dependent, so that a smaller fraction of individuals disperses at higher densities (Wolff 1997; Lambin, Aars & Piertney 2001). Furthermore, those that disperse may be expected to move relatively short distances (McCarty 1997). This pattern has been reported for different mammal species, for example red foxes (Trewhella *et al*. 1988), roe deer (Linnell, Aanes & Anderson 1995, Wahlström & Liberg 1995), Townsend's voles (*Microtus townsendii*; Lambin 1994), and Canada lynx (*Lynx canadensis*) (after the hare crash both female and male yearlings were tolerated in the parental home ranges; Breitenmoser, Slough & Breitenmoser-Würsten 1993b), and seems also to be true for the Eurasian lynx. The few data sets available (Schmidt *et al.* 1997; Sunde *et al.* 2000; Table 5.5) indicate that median recovery distance may be negatively correlated with lynx density. With the exception of the hunted Norwegian population, lynx dispersed roughly 1.5 male or 2.0 female home range diameters when recovery distances were considered. If dispersal is negatively correlated with density, the longest dispersal distances should be observed in areas where the lynx density is low and the home ranges large. Anecdotal observations of a low-density population (large home ranges: 709 km^2 for males and 407 km^2 for females; Linnell *et al.*, 2001) in the Sarek national park in Sweden were consistent with this hypothesis: a high number of individuals moved long distances e.g. more than 100 km (J. Linnell pers. comm.), and the record animal, a male, was shot 10 months later in Norway 450 km from its natal range.

Table 5.5. Data on dispersal distances of Eurasian lynx across Europe. Data are sorted according to the density (low to high). Given are: mean resident male and female home range diameters (HR ø) and population densities (number of resident lynx/100 km^2); recovery distances and effective dispersal distances expressed in kilometres and in median number of mean circular resident female (♀HR) and male home range (♂HR) diameters. Sample size are given in brackets.

Location	Mean HR ø (km)		Density	Recovery distance Median (km)		Recovery distance Median # of HR ø crossed		Effective dispersal Median (km)		Effective dispersal Median # of HR ø crossed	
	♂	♀				♂HR	♀HR			♂HR	♀HR
Norway[a]	48.4	26.2	0.3*	40.6	(6)	0.8	1.6	41.2	(5)	0.9	1.6
Jura Mountains[b]	19.1	14.7	0.8	29.5	(14)	1.5	2.0	68.8	(7)	3.6	4.7
Poland[c]	16.9	13.0	-	25.0	(6)	1.5	1.9	50.5	(4)	3.0	3.9
Alps[d]	14.6	10.1	1.5	20.6	(13)	1.4	2.0	21.4	(12)	1.5	2.1

[a]Sunde *et al.* 2000, [b]Breitenmoser-Würsten *et al.* 2004, [c]Schmidt *et al.* 1997,[d]Breitenmoser-Würsten *et al.* 2001
*hunted population

5.6.3. Conservation and management implications

Despite a high population density during the radio-telemetry study we did not observe an expansion of the population in the NWSA. Contrary to wolf and bears, which can disperse over long distances through unsettled areas, subadult lynx are conservative dispersers from their life history and land tenure system and therefore maintain close contact to conspecifics due to their territoriality (Chapter 4). Their low ability to cross major barriers like fenced highways hampers the natural colonization of unsettled areas in a fragmented landscape such as the Alps. The spread of the population may still happen in the long-term, but for practical reasons (prey depression, conflicts with local people), high population density is not to be maintained over a long period. During the last peak to date in the NWSA, not only hunters and sheep-breeders, but also the authorities of the respective cantons demanded that the lynx population in this area be reduced (Breitenmoser 1998; Breitenmoser & Breitenmoser-Würsten 2001; Jobin-Molinari *et al*. 2001).

The natural spread could be favored through corridors (“green bridges”) but parameters needed for effective corridor use by lynx have still to be determined. Riparian vegetation may serve as natural corridors as shown by the dispersal path of M30 (Fig. 5.3). In mountain populations, connectivity may be enhanced if corridors are established in the direction of predominant ridgelines or other landscape level features (e.g. forests, riparian vegetation) which may aid or direct dispersing lynx.

Our findings may have consequences for the design of re-introductions of (solitary) carnivores (overview in Breitenmoser *et al*. 2001) or recovery programs in fragmented landscape. To create a strong source population in one place might not be the best strategy. Rather, population nuclei should be founded in several neighboring patches through re-introductions or artificial transfer of individuals to neighboring compartments. To compensate for the lack of expansion of the Swiss populations, six lynx from the NWSA and three from the JM were translocated to the eastern part of Switzerland during the winters 2000/01 and 2002/03. This allowed reduction of locally high abundance in the NWSA and accelerating the desired spread of the species. Almost paradoxically, we cannot ever exclude the possibility that the intervention in the NWSA and the resulting disturbance of the population will now lead to an increased dispersal rate, as discussed by Macdonald & Johnson (2001) and Woodroffe (2001). Exchange between established neighboring populations will certainly take place later on, as resident adult lynx, especially males, show a higher propensity to cross barriers than subadults, particularly during the mating season. One male from the NWSA crossed a fenced high-speed road at least four times (P. Molinari, pers. comm.) and once a fenced highway (A. Ryser, pers. comm.) using an underpass. This will be sufficient to grant genetic exchange between established sub-populations; since as little as one breeding migrant per generation can render the population effectively panmictic (Lande & Barrowclough 1987).

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Chapter 6. Present status and distribution of the lynx in the Swiss Alps

6.1. Abstract

To evaluate the population trend of lynx in the Swiss Alps, we analysed the spatial and numerical development of signs of presence found from 1995 to 1999 and compared them with previous years. Three sources of information on the presence of lynx are available: (1) reports of lynx killed or found dead; (2) records of livestock killed by lynx; (3) records of wild prey remains, tracks, scats, sightings, and vocalisations. We distinguished three levels of reliability: Quality 1 represent the hard facts, e.g. all reports of lynx killed or found dead, photographs of lynx as well as young orphaned lynx caught in the wild and taken into captivity. Quality 2 include all records of livestock killed, wild prey remains, tracks and scats reported by people who have attended special courses, e.g. mainly game wardens. Quality 3 are all wild prey remains and tracks reported by the general public as well as all sightings, scats and vocalisations, e.g. signs that cannot be verified. More than 1,600 signs of presence were recorded in the Swiss Alps in this 5-year-period. A high number of quality 1 and 2 records showed that (1) the lynx population in the north-western Swiss Alps increased from 1994 to 1999, that (2) there is a moderate presence of the species in the central and south-western parts and (3) none or hardly any lynx are found in the eastern Alps of Switzerland. Based on a radio-telemetry study and the number of quality 2 data, we were able to estimate the number of lynx in the Swiss Alps at 70 individuals. To counterpart the uneven distribution of lynx in Switzerland, lynx are being translocated from the north-western Alps to the eastern Swiss Alps, as the expansion of the Swiss lynx population is crucial for the conservation of the lynx in the whole Alps.

6.2. Introduction

Lynx were re-introduced in the Swiss Alps from 1971-1980 (Breitenmoser; Breitenmoser-Würsten & Capt 1998). After a swift expansion over part of the potential range in the first decade, Breitenmoser and coauthors (1998) reported a stagnation of the lynx population in the Swiss Alps from 1985-1994, although there was still suitable habitat in the east and in the south. The reason for this is unclear, but most likely, it was due to the natural and artificial barriers that hindered individual lynx dispersal, and, maybe more importantly, illegal killings destroyed the population pressure needed for an expansion. Nevertheless, the population in the Swiss Alps was judged to be one of the most vital of all lynx occurrences in the Alps.

Since about 1993/94, a second increase of the lynx population in the north-western Swiss Alps has been observed, leading again to another controversy about the return of the lynx. Not only hunters and sheep-breeders, but also the authorities of the respective cantons have demanded that the lynx population in this area be reduced. To respond to this situation, a research project was started in the north-western Swiss Alps. From 1997 to 1999, 40 individual lynx were radio-collared. This allowed us to directly estimate the number of lynx in the north-western Swiss Alps.

To evaluate the population trend of lynx in the Swiss Alps in the late 1990s, we first analysed the development in the number of signs of presence found from 1995 to 1999 and compared them with previous years. Secondly we analysed the spatial trend of the population and estimated the number of lynx in the Swiss Alps.

6.3. Methods

From 1992 onwards, the network of game wardens in Switzerland was used to survey the development of lynx in Switzerland. Annual questionnaires have been sent out to all game wardens in order to obtain a systematic monitoring (Capt, Breitenmoser & Breitenmoser-Würsten 1998). To instruct game wardens how to recognise signs of presence of lynx, special courses were organised and instructive material was produced (e.g. Molinari *et al.* 2000). Three sources of information on the presence of lynx are available: (1) reports of lynx killed or found dead or young orphaned lynx caught and put into captivity; (2) records of livestock killed by lynx; and (3) records of wild prey remains, tracks, scats, sightings, and vocalisations. The best evidence of lynx presence is a lynx found dead or a lynx captured. The reliability of all other records varies greatly. We distinguished three levels of reliability according to the possibility to verify an observation: Quality 1 (Q1) represent the hard facts, e.g. all reports of lynx killed, found dead or captured, photographs of lynx as well as young orphaned lynx caught in the wild and put into captivity. Quality 2 (Q2) represent all records of livestock killed, wild prey remains, tracks and scats confirmed by people who attended special courses, e.g. mainly game wardens. As all game wardens were instructed how to recognise lynx signs of presence, these records are mostly an objective proof of lynx presence, though both errors and even deception may occur. Quality 3 (Q3) represent all wild prey remains and tracks reported by the general public as well as all sightings, scats and vocalisations, e.g. mainly signs that cannot be verified. When studying distribution, isolated data of Q3 are of reduced significance. However, their repeated occurrence in the same areas may attract attention to the possible presence of the species.

Subsequently, Switzerland was divided into 9 geographical compartments according to habitat connectivity and administration units (Fig. 6.1). To estimate the potential lynx habitat within each compartment, we used squares with the probability of ≥ 0.5 of a previously modelled suitability map (Breitenmoser *et al*. 1999) computed with Biomapper 1.0 (Hirzel, Hausser & Perrin 1999).

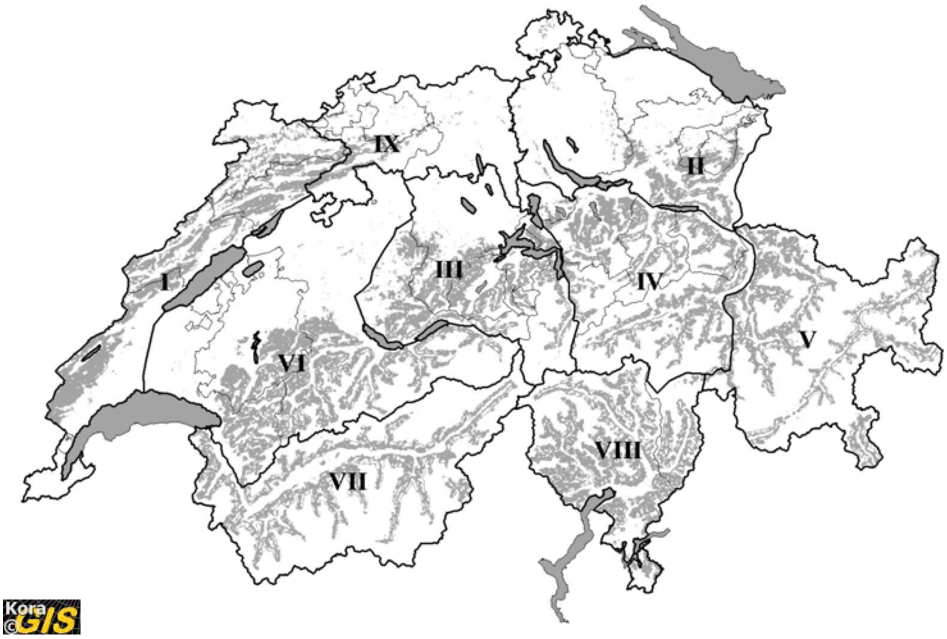

Figure 6.1. Potential lynx habitat (grey) and division of Switzerland into 9 management compartments (black outlines).

We applied our knowledge of the land tenure system of resident lynx (Breitenmoser *et al*. 1993; Breitenmoser-Würsten *et al*. 2001) to estimate the number of lynx in each compartment. All estimations of the population size have been made under the assumption that the number of lynx in each compartment is proportional to the number of cells ≥ 0.5 within it. Lynx numbers in the north-western Alps were estimated by means of radio-telemetry and confirmed presence of unmarked lynx (Fig. 6.2; Breitenmoser-Würsten *et al*. 2001). We then compared the number of Q2 data reported from this compartment with known lynx density and number of lynx present and extrapolated to all other compartments where only the number of Q2 data reported was available. Thus, we used Q2 data recorded as an index of lynx abundance and the findings from the radio-tracking to calibrate the data.

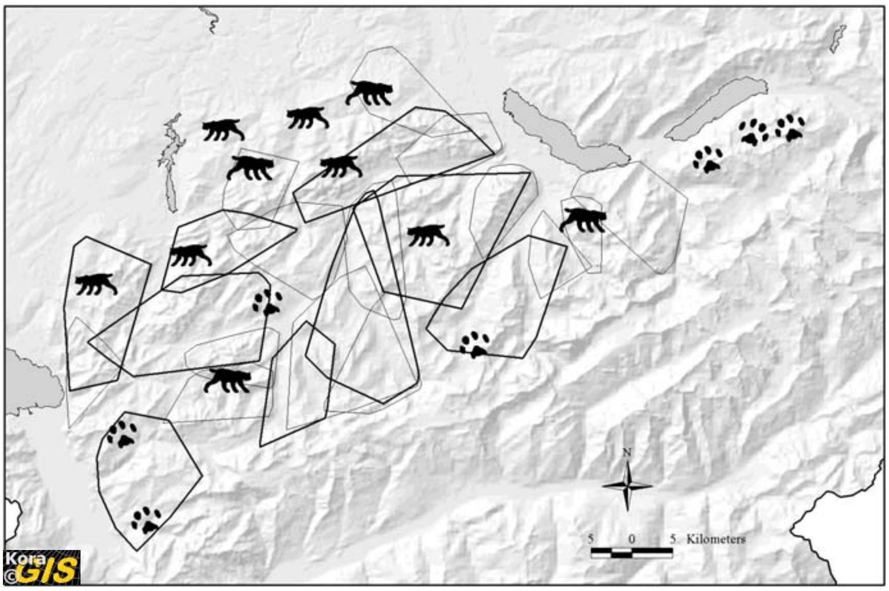

Figure 6.2. Home ranges (100% convex polygons) of radio-tagged male (thick line) and female (thin line) lynx and confirmed presence (lynx symbol) of untagged lynx in the north-western Swiss Alps (compartment VI). Suspected presence of lynx is shown with the lynx print symbol. Symbols facing right stand for male lynx, symbols facing left for female lynx.

6.4. Legal situation

Switzerland has signed and enforced both the Washington convention (CITES, in 1975) and the Bern Convention (in 1982), which require the conservation of lynx population. Lynx are protected year-round by the *Federal Law on the Hunting and Protection of Free Living Mammals and Birds* (JSG). The according ordinance to this law defines that all domestic animals killed by lynx are reimbursed by the federal and the cantonal governments. Cantonal game wardens are in charge of the evaluation of every attack on livestock reported. Permits to remove lynx who attack livestock may be issued by the Swiss Agency for Environment, Forest and Landscape (SAEFL) in order to stop attacks in high damage areas. From 1995 to 1999, three lynx have been shot for this reason. The Swiss hunting ordinance obliges the SAEFL to establish a management plan for the lynx. The *Swiss Lynx Concept* was implemented in August 2000 and defines the general conservation and management goals, the co-operation between the SAEFL and the cantons, and criteria for interventions.

6.5. Results

From 1995 to 1999, more than 1600 signs of presence were recorded in the Swiss Alps. More Q1 data were reported than in any previous 5-year-period. The number of lynx found dead (including the illegally killed individuals) more than doubled compared to the previous five years (Table 6.1), indicating the possibility of an increased population trend.

Table 6.1. Number of lynx found dead and livestock killed for different periods. Data from 1971 to 1994 derived from Breitenmoser et al. (1998).

Period	Number of lynx found dead	Number of livestock killed
1971-79	7	9
1980-84	11	171
1985-89	9	303
1990-94	16	162
1995-99	41	519
Total	84	1,164

Most lynx mortalities occurred in the region of the north-western Swiss Alps (Fig. 6.3a). Only one dead lynx was reported from the canton of Valais and one north of the Aare river. Both mortalities occurred close to the compartment VI. Besides, one orphaned lynx was caught north of the Aare river and put into captivity. The number of lynx found dead peaked in 1999 (Table 6.2). Even though three times more hard facts were reported for the 1995-99 period than for 1990-94, the polygon drawn around the signs of lynx presence of Q1 decreased from 7,590 km^2 to 3,800 km^2.

Quality 2 data were most often reported, representing 68% of all records. Almost half of these records were cases of livestock depredation, mainly sheep (Table 6.2). This is obviously the most complete category because livestock killed by lynx are reimbursed, and thus announced. The number of wild prey remains reported increased considerably, doubling from 1995 to 1999 (Table 6.2). The number of lynx tracks reported however peaked in 1997. The distribution of the Q2 data indicates an expansion of the lynx population into the northern part of the canton Ticino, compared to the previous 5-year-period (Breitenmoser *et al*. 1998). Furthermore, even though isolated, one confirmed track was recorded from the eastern part of the canton of St. Gallen (Fig. 6.3b). The polygon drawn around the signs of lynx presence of Q2 increased from 10,500 km^2 in 1990-94 to 16,400 km^2 in 1995-99. Even though the number of records of Q2 tripled from 315 in 1990-94 to 1115 in 1995-99, the area of lynx distribution increased only by 50%.

In areas where lynx presence was regularly confirmed, the effort to report Q3 data decreased considerably. That’s why tracks and wild prey remains reported by people other than game wardens were only small in number (Table 6.2). Most of the Q3 data were sightings. When considering also Q3 data in the distributional analyses (Fig. 6.3c), lynx appear to have immigrated to the Swiss Plateau south of the Lake of Neuchâtel in the past 5 years where they did not occur before. This new appearance still has to be confirmed with Q1 or Q2 data.

Table 6.2. Number of records collected per year. Data from radio-tracking was not considered in this analysis.

Quality 1	**1995**	**1996**	**1997**	**1998**	**1999**	**Total**
lynx found dead	3	8	8	7	15	41
capture			2	2	2	6
photo				2		2
Total	3	8	10	11	17	49
Quality 2						
livestock killed	52	72	104	104	187	519
wild prey remains	65	76	96	88	104	429
tracks	17	24	70	31	25	167
Total	134	172	270	223	316	1,115
Quality 3						
wild prey remains	0	1	1	13	3	18
tracks	0	4	3	9	6	22
sightings	31	61	142	70	113	417
vocalisations	0	3	7	1	1	12
Total	31	69	153	93	123	469

To obtain a rough estimation of the number of lynx living in the Swiss Alps, we extrapolated the very detailed knowledge from the north-western Swiss Alps (compartment VI) to the whole of the Swiss Alps by comparing the potential habitat and the Q2 data available. The estimation of the size of the potential lynx habitat per compartment is shown in Table 6.3.

Table 6.3. Estimated and potential number of lynx in the Swiss Alps. The compartments of the Jura Mountains (Nr. I & IX) were not considered in this analysis.

Nr. of compartment	**Potential habitat (km^2)**	**Quality 1**	**Quality 2**	**Quality 3**	**Estimated nr of lynx**	**Potential nr of lynx**
II	510	0	1	4	0	18-19
III	1,057	3	98	38	6	37-40
IV	1,294	0	14	7	1	46-49
V	1,207	0	0	0	0	43-46
VI	1,552	45	909	346	55-59	55-59
VII	1,213	1	89	71	5-6	43-46
VIII	1,336	0	4	3	0	47-51
Total	8,169	49	1,115	469	67-72	289-310

We estimated the number of self-provisioning lynx, e.g. adults and subadults (kittens < 1 year old are excluded), in compartment VI to be 55 – 59 individuals. In the same compartment, 909 Q2 data were recorded. Therefore we calculated one self-provisioning lynx per 16 Q2-data gathered. In the adjoining compartments III and VII, where 98 and 89 Q2 data were recorded, we estimated the lynx number to be 6 and 5-6 individuals, respectively (Table 6.3). According to our model, the lynx population in the Swiss Alps was estimated at roughly 70 individuals, even though the potential habitat could host about 300 self-provisioning lynx.

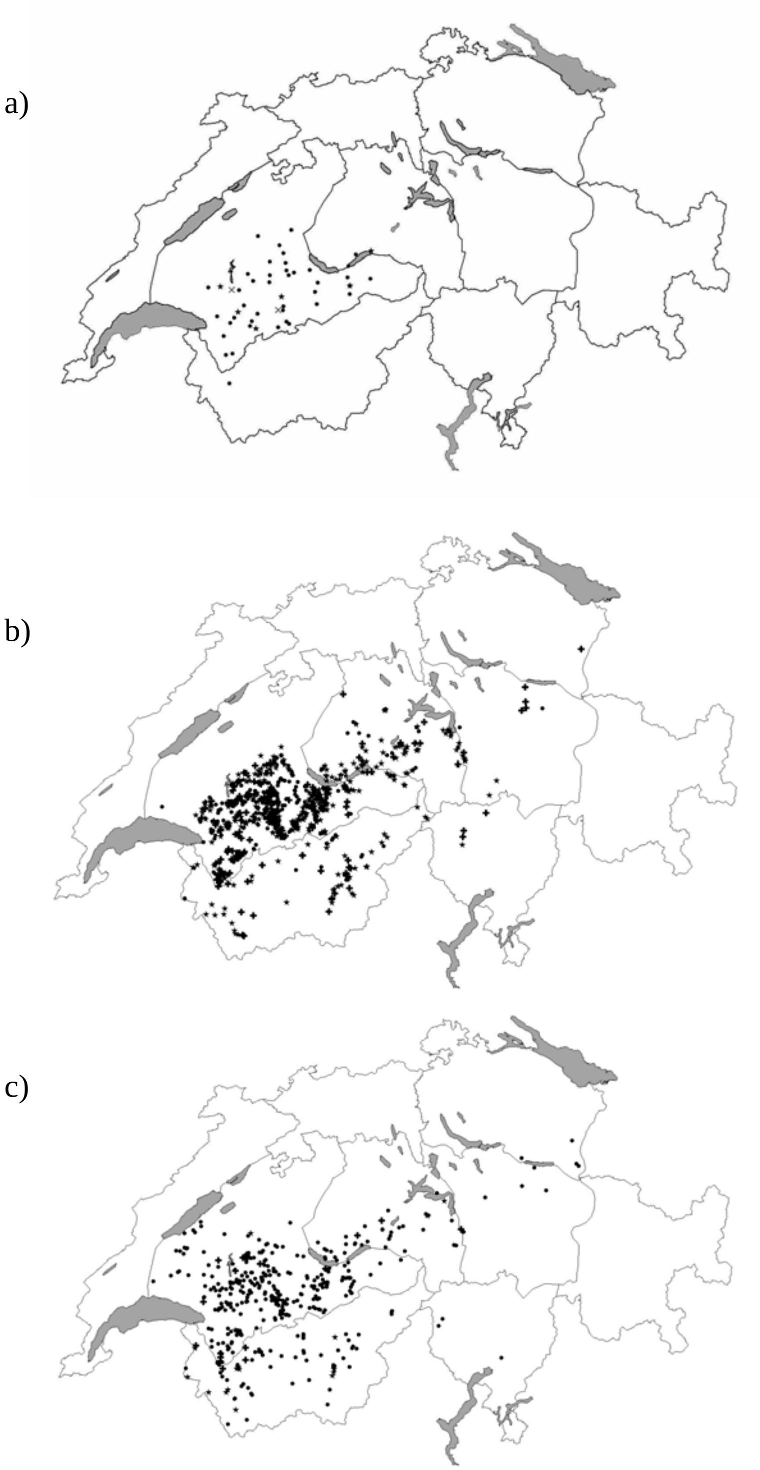

Figure 6.3. Distribution of the lynx in the Swiss Alps for the five-year period 1995-99. (a) Quality 1 data: dead lynx found (dots), photos (crosses) and captures (stars). (b) Quality 2 data: killed livestock (dots), wild prey remains (stars) and tracks (crosses). (c) Quality 3 data: wild prey remains (stars), tracks (crosses), sightings (dots) and vocalisations (squares).

6.6. Discussion

The monitoring system established in 1992 showed its effectiveness already in 1994, when an increase in the north-western Swiss Alps was detected, due to an increase in the number of signs of presence reported by game wardens (Breitenmoser *et al*. 1998). Since hard fact data were not available in all areas of lynx occurrence, the Q2 records became extremely important for the assessment of the lynx distribution. A network of trained people that cover the whole area is a prerequisite to ensure the reliability of the observations reported. Kills and tracks may then be verified by the game wardens. This “professional” approach is important because the number of data reported by the general public can vary, e.g. the fluctuations in the number of observations may also reflect changes in public awareness. The Austrian experience has shown that intensified publicity can immediately produce more records (Huber & Kaczensky 1998) without there being more lynx present.

The trends of Q1 and Q2 records showed that (1) the lynx population in the north-western Swiss Alps increased from 1994 to 1999, that (2) there is a moderate presence of the species in the central and south-western parts and (3) none or hardly any lynx are found in the eastern Alps of Switzerland. The Q2 data recorded from the northern part of the canton Ticino, may indicate a southward expansion of the Swiss population. New lynx occurrences in the Ossola and Aosta valley in Italy confirm this trend (Molinari *et al*. 2001). However, single lynx who left the closed population can roam for many years through a not really settled compartment. Such individuals can produce signs of presence at low density and over a huge area, as they search for conspecifics.

The mortality in the north-western Alps was very high. Besides, the losses given in Table 6.1 are minimum estimates. Undoubtedly, the number of unknown cases of lynx illegally killed is quite large. For example, only four out of nine radio-tagged lynx that were killed would have been found if untagged. We assume illegal killing to be the most important single cause of mortality. Some hunters and sheep breeders still consider lynx as a pest and openly state that they would shoot any lynx given the opportunity.

The high increase in the number of signs of presence of Q1 and Q2 data from 1995-99 compared to the previous pentad was translated only into a marginal increase in the area colonised by lynx. Observations to the east of the river Reuss still remained scattered and well separated by wide areas without any record. The analysis of the distribution and number of lynx signs of presence indicate that lynx seem to be “trapped” in the geographical area of the north-western Swiss Alps (compartment VI). This hypothesis was confirmed by the reports of lynx reproduction (Fig. 6.4) and by the telemetry study that revealed that the lynx density in this area was much higher than in previous years. But still, only 2 out of 40 radio-tagged lynx left the compartment VI (Chapter 5).

We distinguished four different categories of lynx status in the Swiss Alps (Fig. 6.5): in compartment VI, we observed a population at high density that may have acted as a source population. Lynx in compartments III and VII were found to be in a population low (sink). We attribute the few Q2 records from compartments IV and VIII to single individuals only, whereas in compartments II and V no lynx occurred.

We estimated the number of lynx in the Swiss Alps to be 70 individuals assuming that lynx numbers in the compartment VI (Fig. 6.2) were estimated correctly and the number of Q2 data reported in the same area was representative for all other compartments as well. Our method for the estimation of the lynx number is very much depending on the quality of the monitoring data. For future validation of the index it is desirable to compare our results with other areas where monitoring programs include radio-tracking and a “verification network”.

Breitenmoser *et al*. (1998) estimated the lynx number in the Swiss Alps at 50 individuals in the years from 1990-94 compared to our recent estimate of 70 individuals.

Figure 6.4. Comparison between the distribution of known lynx mortality (Quality 1, dots) and records of reproduction (Quality 3, triangles).

This increase is only caused by higher lynx abundance in the compartment VI, whereas the lynx numbers in the compartment III and VII decreased. Despite a locally high lynx density in the north-western Alps, the estimated lynx numbers are far from the potential capacity. To counteract the uneven distribution of lynx in Switzerland, 3 male and 3 female lynx were translocated from compartment VI to compartment II in spring 2001 (Fig. 6.5). We believe that the expansion of the Swiss lynx population is crucial for the conservation of the lynx in the whole Alps.

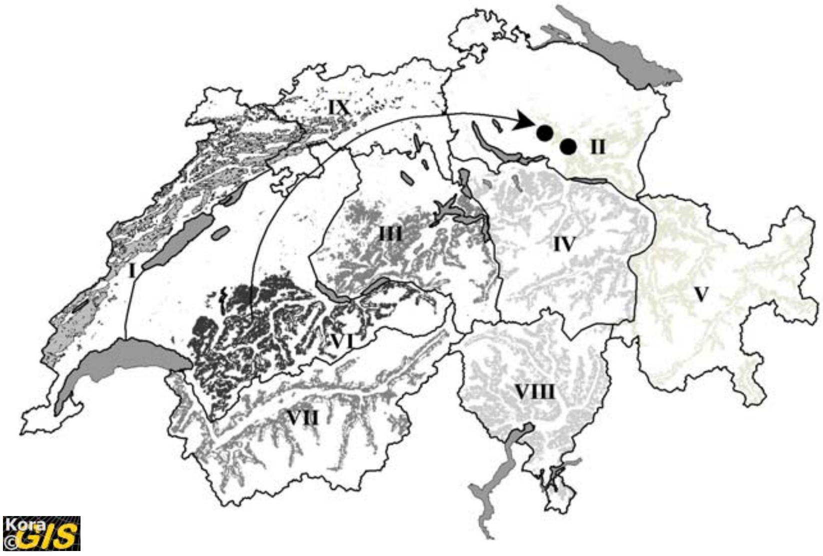

Figure 6.5. Distinction of compartments with different levels of lynx abundance: source population (compartment VI), sink population (compartments III and VII), single individuals without the typical social organisation (compartments IV and VIII), and compartments with no lynx (compartments II and V). The status of the lynx in the Swiss Jura Mountains is unknown (compartments I and IX). The dots mark the release sites 2001. See text for further details.

6.7. References

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Chapter 7. Potential distribution and population size of the Eurasian lynx (*Lynx lynx*) in the Jura Mountains and possible corridors to adjacent ranges

7.1. Abstract

To estimate the potential population size of the lynx in the Jura Mountains and to assess possible corridors between this population and adjacent areas (Vosges Mountains, Black Forest and Alps), we adapted a previously developed Geographic Information system (GIS) probability model for lynx distribution and extrapolated it over the entire mountain range. The model was based on knowledge of the habitat use and land tenure system of resident animals from the central part of the Jura Mountains, where lynx were followed by means of radio-telemetry. Corridors were computed in the GIS using a friction grid and a cost distance function. The friction value attributed to each land use variable was assessed from our observations of lynx dispersal. Our model predicts a breeding population in the Jura Mountains ranging from 74–101 individuals and from 51–79 individuals when continuous habitat patches < 50 km^2 are disregarded. The Jura Mountains population lies in the range of a viable population if only demographic aspects are taken into account, but is far too small from a genetic prospect. The genetic viability would be granted if the Jura lynx were part of a larger meta-population. Potential corridors exist from the Jura Mountains to the Vosges Mountains, the Black Forest and the Chartreuse (French Alps). Observations in the Chartreuse indicate that lynx may have immigrated from the Jura Mountains, but there is no evidence for the use of northern corridors, as the population has not yet completely settled this area. As an alternative to spontaneous migration, artificial transfer of lynx between the adjacent sub-population should be considered in the long term. We conclude that the monitoring of the population size, its spatial expansion, and the genetic surveillance in the Jura Mountains must be continued, as the status of the population is still critical. Only a good surveillance would allow initiating conservation measures in time if necessary.

7.2. Introduction

Eurasian lynx (*Lynx lynx*) were re-introduced to the Swiss Alps and the Swiss Jura Mountains in the 1970s (Breitenmoser, Breitenmoser-Würsten & Capt 1998). Although the Swiss re-introductions were considered rare examples of successful translocations of large predators (Yalden 1993), these still small populations cannot yet be considered viable. The expansion is very slow; the population in the Jura Mountains has – after almost thirty years – not yet occupied the entire mountain range (Capt, subm.). The reasons for the lack of vitality are not known; they may include ecological, anthropogenic, and intrinsic (genetic) factors. For the conservation of a large carnivore species in a limited living space – the Jura Mountains extend over some 14,000 km^2 (Breitenmoser *et al*. subm.) – it is however important to know the potential size of the whole population and the possible connections to neighbouring populations.

We recalibrated a previously developed Geographic Information System (GIS) probability model for lynx distribution (Zimmermann & Breitenmoser 2002) based on habitat information and radio-telemetry data from the Swiss Jura Mountains and extrapolated it over the entire Jura Mountains in order (i) to estimate the population size, based on knowledge of the land tenure system of resident lynx (Breitenmoser *et al*. 1993; Breitenmoser-Würsten *et al*. subm.), and (ii) to assess the possible corridors between the Jura Mountains and adjacent "lynx areas" (Vosges Mountains, Black Forest and Alps).

7.3. Material and methods

7.3.1. Study area

The study was performed in the Jura Mountains, a secondary limestone mountain chain forming the northwestern border of Switzerland with France (Fig. 7.1). The altitude varies from 372 m (Lake of Geneva) to 1,718 m (Crêt de la Neige). Mixed forests along slopes and coniferous forests on the ridges cover 53% of the highlands. Cultivated areas are typically pastures (for a more detailed description see Breitenmoser *et al*. subm.). Roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) are the main prey of lynx in the Jura Mountains (Jobin, Molinari & Breitenmoser 2000, Molinari-Jobin *et al*. 2002). The main area of sheep breeding is situated in France, along the south-western foothills of the mountain chain, at elevations from 400–700 m. Most lynx attacks on livestock occur in this area (Stahl et al. 2001). In Switzerland, only the Clos du Doubs in the canton of Jura was affected by attacks (Angst, Olsson & Breitenmoser 2000).

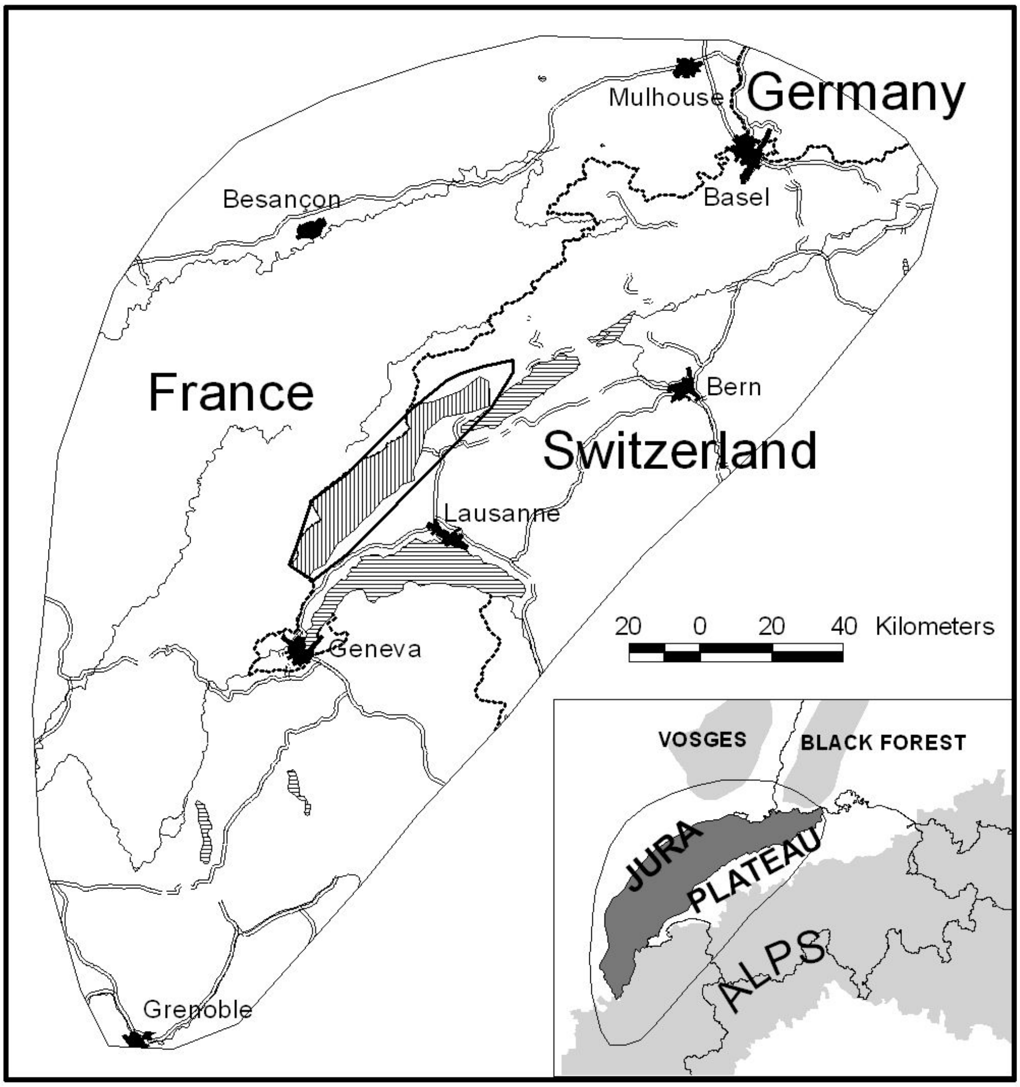

Figure 7.1. Reference areas in the Jura Mountains. The polygon in the large map shows the intensive study area of the *Swiss Lynx Project* (*SLP*) in the Swiss part of the Jura Mountains, where the radio fixes for the calibration of the model were gained. Vertically hatched is the area used for the calibration of the lynx density. To avoid an arbitrary limitation of the potential population, the total area for the model (outer polygon in the large map) exceeded the Jura Mountains (dark area in the small map) according to the definition in Breitenmoser *et al*. subm.. Horizontally hatched = lakes, simple lines = rivers, double lines = highways, broken lines = international boundaries, black patches = major agglomerations.

7.3.2. Data sets

We used a total of 6,282 radio fixes accurate to the ha and the km^2, respectively, from eleven resident lynx followed from 1988–1998 to generate and/or validate the model. The response variable was the presence/absence of lynx in each 1x1-km cell. Lynx was considered to be present in each cell containing one or more telemetry fix. A data set of highly reliable monitoring records (Capt subm.), independent from the radio telemetry data, and presence data from two subadult female lynx (F_{NADA}, F_{WINA}; *Swiss Lynx Project,* unpublished data) dispersing to France, were subsequently used to evaluate the model. The 13 environmental predictors (Table 7.1) came from the CORINE land use data (European Topic Center on Land Cover, Environment Satellite Data Center, Kiruna, Sweden) and the GTOPO30 database (U. S. Geological Survey's EROS Data center in Sioux Falls, South Dakota). The CORINE and the GTOPO30 database had an accuracy of 250x250-m and approximately 1x1-km (grid spacing 30-arc seconds), respectively.

Table 7.1. The thirteen predictors used in the logistic regression analysis. Sources: CORINE LAND COVER database (ETC/LC 1997; resolution 250 x 250 m) and GTOPO30 (EROS Data Center 1993; resolution 1 x 1 km).

Predictor	Unity	Sources
1. Urban fabric	frequency	CORINE
2. Industrial	frequency	CORINE
3. Artificial areas	frequency	CORINE
4. Arable land	frequency	CORINE
5. Permanent crops	frequency	CORINE
6. Pastures	frequency	CORINE
7. Forests	frequency	CORINE
8. Shrub	frequency	CORINE
9. Open space	frequency	CORINE
10. Wetlands	frequency	CORINE
11. Water	frequency	CORINE
12. Elevation	meter	GTOPO30
13. Slope	degree	GTOPO30

Both were in digital form and ready to be analysed by the GIS ArcView (Esri 1996a,b,c). All data were geo-referenced on a Lambert Equal-Area Azimuthal (central meridian: 14.37 degree; reference latitude 49.82 degree). From the 250x250-m information and the 1x1-km, we computed for each km^2 raster cell (1) the proportion of the different land use predictors; and (2) the mean value in the case of the quantitative predictors: elevation, declivity (predictors 1–13; Table 7.1).

7.3.3. Methods

We adapted an earlier probability model for lynx distribution in the Swiss Jura Mountains (Zimmermann & Breitenmoser 2002) to the new environmental data and extrapolated it over the entire Jura Mountains. The Generalized Linear Models (GLM) were calibrated in the S-Plus software (Mathsoft Inc.) by using a binomial distribution and a stepwise variable selection procedure. Because of the high sensitivity of the stepwise process – which eliminates a part of the input predictors to retain only the most relevant – to the input order of the predictors, we tested several sequences and retained the model explaining the highest proportion of variance.

7.3.4. Potential distribution and population size

The potential distribution area of lynx was estimated for each threshold value ranging from 0–1. In the first step, we considered every raster of the grid. Consecutive areas <50 km^2 were disregarded in the second step. We used two different approaches to set the cut-off value. In each round, we estimated an optimistic and a pessimistic cut-off value. In the first approach, we set the threshold so that the maximum proportion of correctly classified cases was reached (P_{opt}) to estimate the optimistic cut-off value (Schröder & Richter 2000). To estimate the pessimistic cut-off value, we set the threshold cut-off value in a way that false presence predictions and false absence predictions had the same probability to occur (P_{fair}). In a second approach (here called the “ratio method”), we plotted the ratio:

$$\frac{\text{area of lynx distribution predicted by the model}}{\text{area used by resident lynx within the main study area}}$$

in relation to the threshold to estimate the pessimistic cut-off value ($Thres_{pess}$). We set the $Thres_{pess}$ value so that the ratio was equal to 100%. A ratio of 100% means that the potential lynx distribution area (= number of occupied cells) predicted by the model is equal to the number of cells effectively occupied by lynx in the main study area. It would not make sense to go beyond this value. We used data from two subadult females (F_{NADA}, F_{WINA}) dispersing to France to estimate the optimistic cut of value ($Thres_{opt}$). This value was fixed in a way that the percentage of cells visited by these two females was the same as the percentage of presence cells within the study area when the threshold value is set to $Thres_{pess}$.

We used our knowledge of the land tenure system of resident lynx (Breitenmoser *et al.* 1993; Breitenmoser-Würsten *et al*. subm.) to estimate the size of the lynx population in the Jura Mountains. The lynx is a solitary, territorial species, and subadult lynx have to leave the parental home range at the age of about 10 months. Molinari-Jobin *et al.* (2002) estimated a number of 7 individuals (4 females, 2 males, 1 subadult) in a study area of 710 km^2 (Fig. 7.1). All estimations of the population size have been done under the assumption that the number of lynx is proportional to the amount of good habitat, and that the prey base is not a limiting factor for the lynx in this mountain range (Molinari-Jobin, Molinari & Breitenmoser subm.).

7.3.5. Corridors

The land use and land cover type at any given location influences the relative ease or difficulty of a species to move through the matrix. Using the CORINE data set, we specified the relative resistance to movement for each land use category according to our observations of dispersing lynx pers. obs.. The higher the value, the higher the resistance to movements. Lynx used principally vegetation cover when roaming through the landscape and moved never more than 400–500 m away from the closest vegetation cover. Several observations showed that lynx swam across rivers of 30 m (P. Molinari, pers. comm.) and still waters of up to 200 m (J.-M. Vandel, pers. comm.). In the study area in the Jura Mountains, radio-tagged animals used to cross (fenced) highways. We cannot expect that dispersing lynx find the optimal connection between two patches as indicated by the cost-path analyses. However, the cost-path analysis delivers a relative measure for comparing the connectivity between different patches (see Ferreras 2001). We set arbitrarily a value of 1,000 points (= high resistance) to settlements, industrial, mining, and artificial non-agricultural vegetated areas, lakes, glaciers and perpetual snow; 120 to highways and large rivers; 40 to medium rivers and main roads; 30 to arable land and heterogeneous agricultural areas; 10 to permanent crops, pastures, and inland wetlands; 1 to forests and shrubs. We then calculated the distance based on matrix quality using the cost-distance extension in the GIS ArcView (see Chapter 1), where the patches resulting from the distribution model with the threshold fixed at 0.35 (P_{opt}) considering only uninterrupted areas ≥ 50 km^2 are the source patches for the cost-distance function to assess the possible corridors between the Jura Mountains and the adjacent areas of the Vosges Mountains, the Black Forest and the Alps. The corridors were then evaluated by comparing them with the characteristics (length, barriers and costs) of known passages used by radio-collard lynx when roaming outside their prime habitat.

7.4. Results

7.4.1. Distribution model

Four out of 13 predictors were selected in our final model. They were: forest (18.8% of the deviance explained), elevation (11%), slope (7.6%) and shrubs (2.7%). GLM models are readily implemented in a GIS by building a single formula for the linear predictor *LP*:

$$LP = -4.5391 + (0.0152 \times shrub) + (0.0016 \times altitude) + (0.1337 \times declivity) + (0.0472 \times forest)$$

where each coefficient is multiplied with its related predictor variable (e.g. *shrub*) (Guisan, Weiss & Weiss 1999). The results of the calculations are obtained to the scale of the linear predictor so that the inverse logistic transformation

$$p(y) = \exp(LP)/(1 + \exp(LP))$$

is then necessary to obtain the probability values $p(y)$ between 0 and 1 at every raster of the grid. The proportion of deviance significantly explained ($adj\text{–}D^2$) in the model was 0.4, corresponding to a medium fit of the model. We used the Receiver Operating Characteristic (ROC; Fielding 2002), a threshold-independent measure of accuracy, to evaluate our models. The area under the ROC function (AUC) at calibration and evaluation was 0.81 and 0.78, respectively. The percentage of Swiss monitoring data correctly classified in relation to the threshold fitted exactly the curve of the percentage of presence cells within the main study area, but the classification of the presence cells of the two subadult females were less accurate (Fig. 7.2). For the threshold fixed at 0.5 (Fig. 7.2), 82.4% of the cells from the monitoring data and 81.2% of those from the telemetry data inside the study area, but only 68.6% of the cells from the lynx in the French Jura Mountains were correctly classified. When we used point data instead of presence cells in the validation process, the results increased to 89% for the telemetry data from the study area, and to 72.5 % for those from the French part, but did not change for the monitoring data (81.3%).

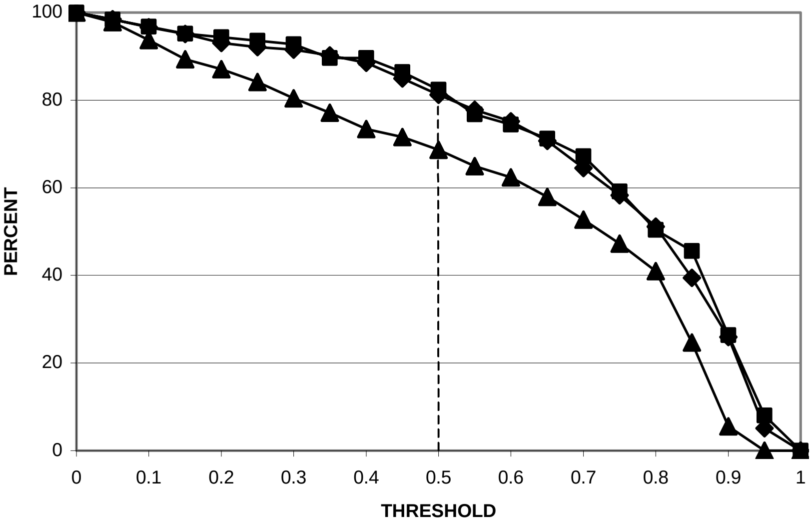

Figure 7.2. Percentage of correctly classified cells in relation to the threshold. The two upper curves show presence cells in the main study area (◆) and monitoring data from the Swiss Jura Mountains (■). The (▲) shows presence data from two subadult females (F_{NADA}, F_{WINA}) that dispersed towards France.

7.4.2. Potential distribution and population size

Figure 7.3 shows the pattern of the curve of the potential lynx distribution area from a threshold of 0 (the total area considered is good lynx habitat) to a threshold of 1 (no part is good lynx habitat). In the optimistic approach (P_{opt}; maximum proportion of correctly classified cases), the threshold was 0.35 and 0.54 in the pessimistic approach (P_{fair}; same probability for false presence and false absence predictions; Fig. 7.4). 89.6% (monitoring data Swiss Jura), 90.2% (telemetry data study area), and 77.1% (dispersing females) of presence cells were correctly classified with the threshold of 0.35. These figures – with the exception of monitoring locations, which remain almost stable at 88.7% – increase to 94.4% (radio fixes study area) and 78.9% (dispersing females), when point data instead of presence cells were used. The cut-off values obtained with the second (the "ratio") method were very similar: 0.33 for the optimistic, and 0.54 for the pessimistic threshold. This indicates that the estimation is robust.

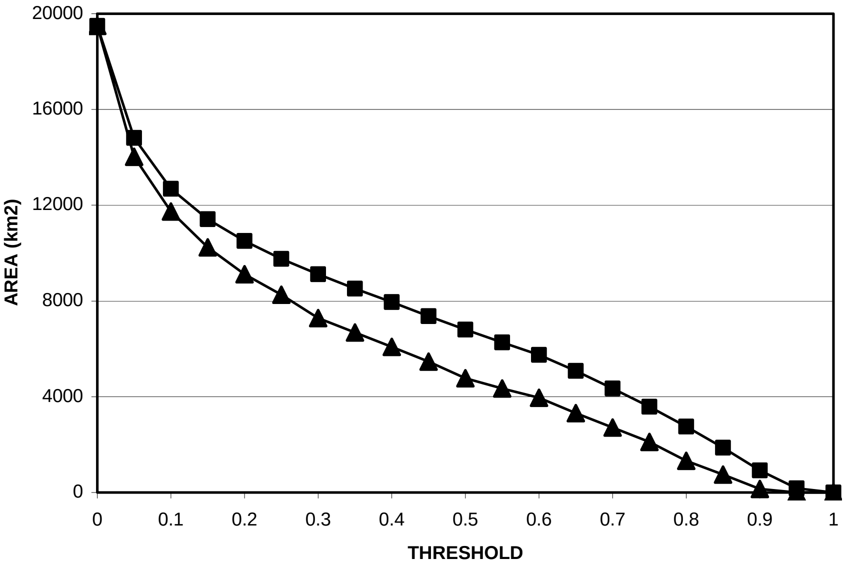

Figure 7.3. Potential lynx distribution area in relation to the threshold value. In the upper curve, every cell was considered, whereas in the lower curve, only consecutive areas ≥ 50 km^2 were considered.

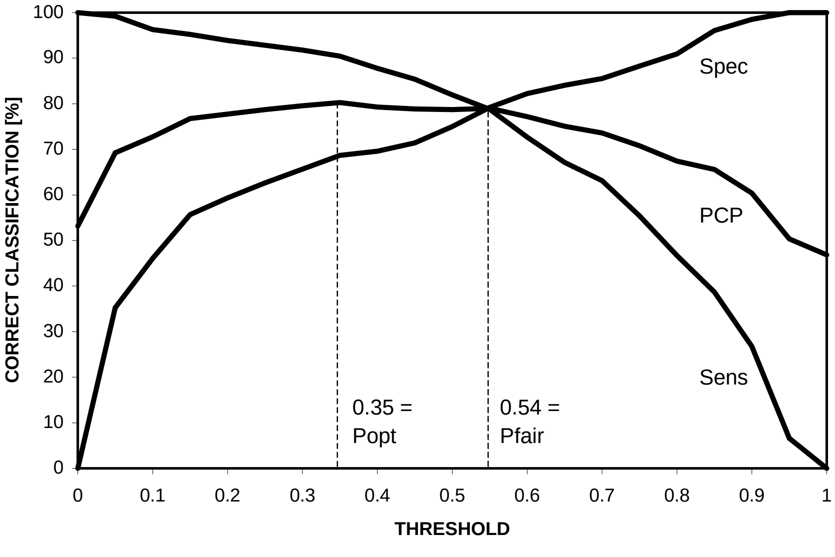

Figure 7.4. Estimation of the cut-off values based on P_{opt} (0.35) and P_{fair} (0.54). Percentage of correct prognoses (PCP) of the total model, sensitivity (Sens) and specificity (Spec) classification in relation to the threshold.

The threshold values of 0.35 and 0.54 (Fig. 7.4) corresponded to an area of good lynx habitat of 8,437 km^2 and 6,342 km^2, respectively. When considering only continuous areas ≥50 km^2 (thus eliminating small and isolated patches of good habitat), the area of good habitat was reduced to 6,670 km^2 and 4,406 km^2, respectively (Fig. 7.5). From data of radio-tracked lynx in the study area (Breitenmoser *et al*. 1993; Breitenmoser-Würsten *et al*. subm.), we estimated a density of 1.19 resident lynx/100 km^2 good lynx habitat. As all resident lynx potentially reproduce, we estimated for the whole Jura Mountains a breeding population of 74–101 resident animals taking into account all suitable habitat. This number decreased to 51−79, when we considered only continuous areas ≥ 50 km^2.

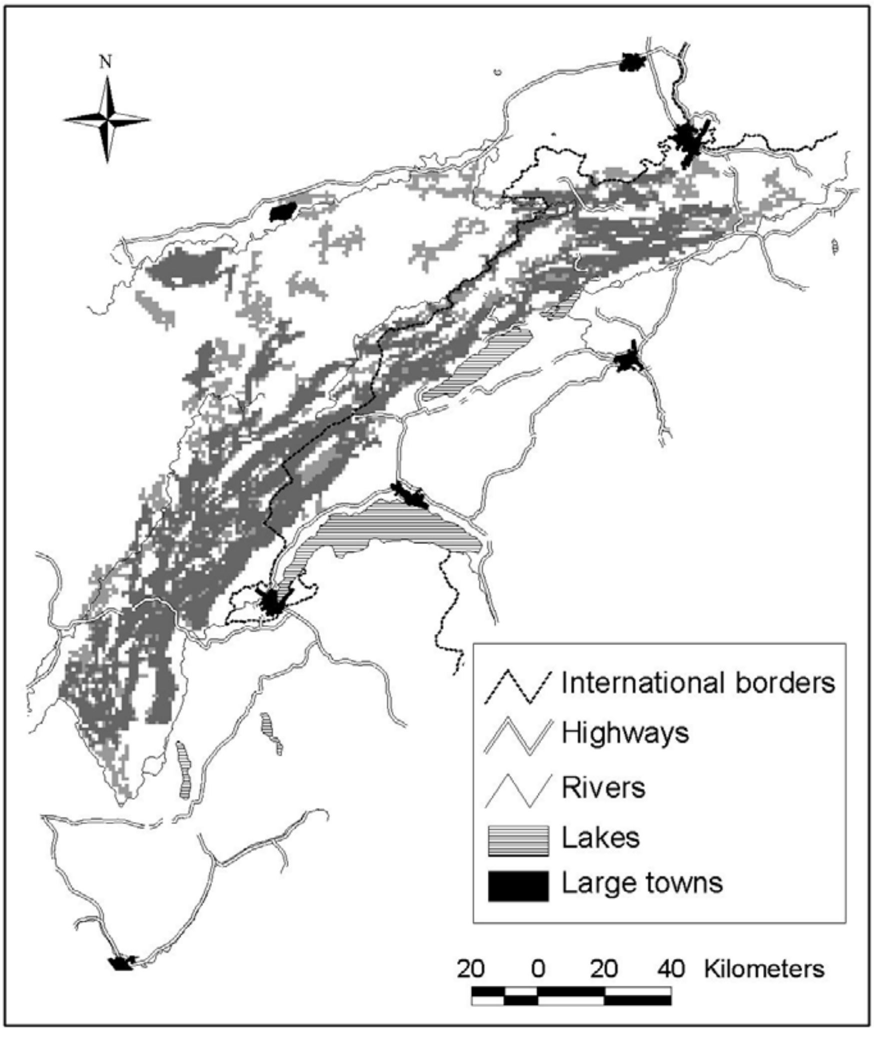

Figure 7.5. Optimistic and pessimistic estimation of good lynx habitat in the Jura Mountains considering all continuous areas ≥50 km^2. Dark grey: pessimistic estimation (P_{fair} threshold 0.54), light plus dark grey: optimistic estimation (P_{opt} threshold 0.35).

7.4.3. Corridors

Three neighbouring mountain ranges, the Alps, the Vosges Mountain and the Black Forest, are real or potential living space for the lynx next to the Jura population. The Vosges Mountains and the French Alps have a permanent lynx occurrence (Stahl & Vandel 2002), whereas in the Black Forest, occasional observations of lynx of unknown origin were reported (T. Kaphegyi, pers. comm.). Four possible corridors (A, B, C, D; Fig. 7.6 and Table 7.2) connect the Jura Mountains to the adjacent ranges.

Corridor A connects the Jura Mountains with the Vosges Mountains. This 23.9 km long corridor passes a highway, a minor river and two main roads. Corridor B is 23 km long and connects the Jura Mountains to the Black Forest. The barriers here are the river Rhine, three main roads and the proximity to human settlements (Table 7.2, Fig. 7.6). The Jura Mountains are separated from the French Alps by a 7.3 km long corridor passing by the Rhone River and a main road, no insurmountable dispersal barriers to lynx (Corridor D, Fig. 7.6, Table 7.2). Two other connections exist between the Jura Mountains and the French Alps (Corridors C1-C2 and C1-C3, Fig. 7.6, Table 7.2). Corridor C1 connects the Jura Mountains to the Salève, a 5 km^2 wooded mount south of Geneva (Fig. 7.6, Table 7.2).

Table 7.2. Characteristics of the corridors from the Jura Mts to the Black Forest, the French Alps and the Vosges Mountains. No = number of detail map in Fig. 7.6. Costs are a relative value describing the resistance of a corridor to lynx movement.

No	Connection	Length (km)	Costs	Costs/ km	Major Barriers
A	Jura/Vosges	23.9	372	15.6	One highway
B	Jura/Black Forest	23.0	341	14.8	One major river (Rhine), passes close to human settlements
C1	Jura/Salève	27.3	437	16.0	One major river (Rhone), highway
C2	Salève/Alps	7.8	234	30.0	One highway, passes close to human settlements
C3	Salève/Alps	10.0	397	39.7	One highway, passes close to human settlements
D	Jura/Alps	7.3	194	26.6	One major river (Rhone)
E	Alps$_{\text{Chartreuse}}$/Alps	6.5	286	44.0	One highway, passes close to human settlements
F	Alps$_{\text{Chartreuse}}$/Alps	4.5	279	62.0	One highway, 500 m in arable land

This corridor is about 27.3 km long and crosses two major barriers, the Rhone River and a highway. The Salève, on the other hand, is connected to the French Alps through two corridors (C2 and C3, Fig. 7.6, Table 7.2).

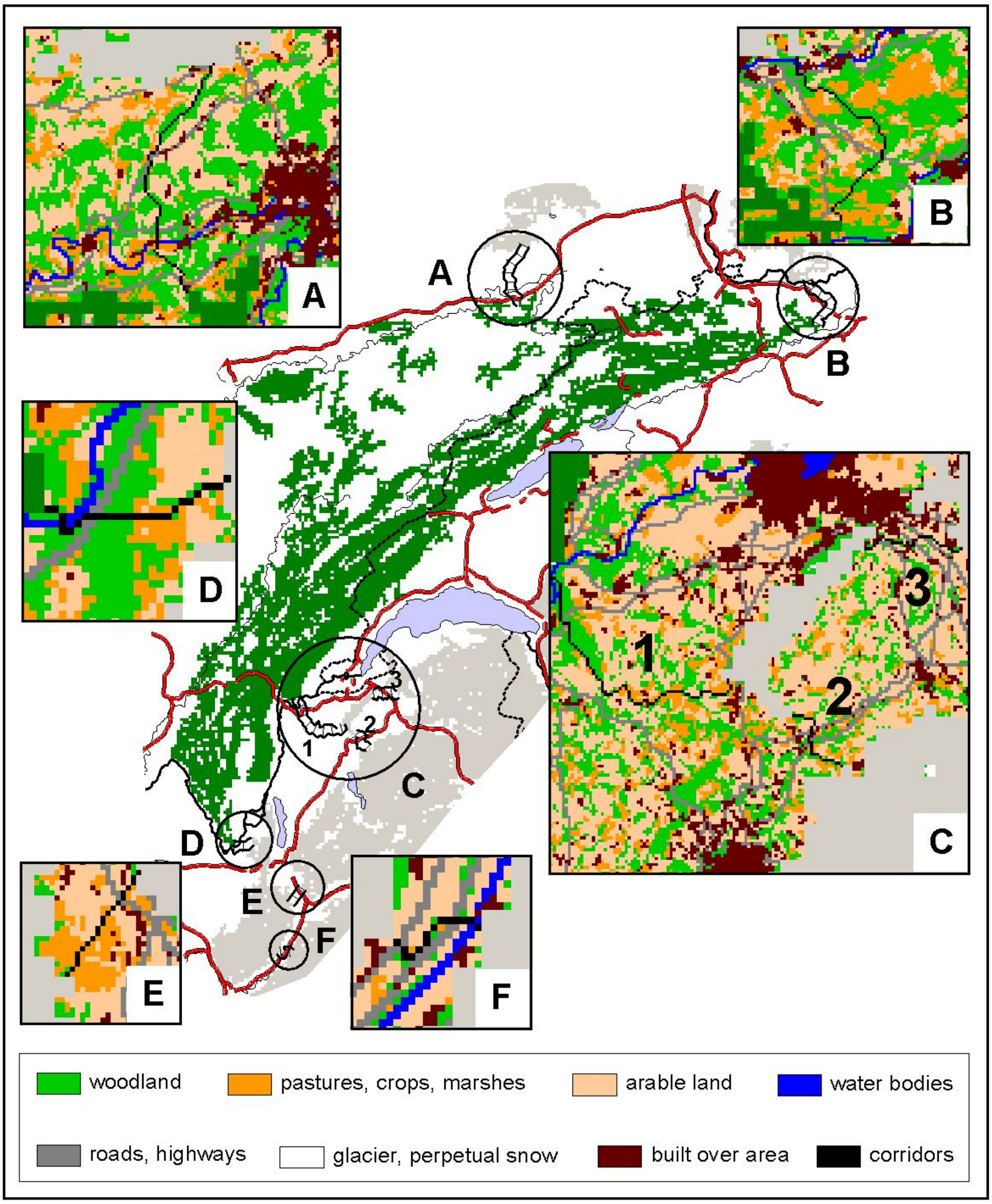

Figure 7.6. Potential corridors between the Jura Mountains and the adjoining areas Vosges Mountains (A), Black Forest (B) and French Alps (C-F). Continuous areas ≥50 km^2 with habitat probability greater than 0.35 are shown in dark green for the Jura Mountains and light grey for the adjacent areas (1x1-km grid). The 250x250-m grid in the small maps shows the environmental variable categories used for the computation of the friction grid and the resulting potential corridors.

A highway and the proximity to human settlements impede both corridors. Corridors E and F connect the Alps and the Chartreuse, a 688 km^2 mountain more or less isolated from the rest of the French Alps (Fig. 7.6, Table 7.2). These corridors are the shortest, with 6.5 km and 4.5 km, respectively. On the other hand, they have the highest cost per km with an average cost of 43/km and 62/km, respectively. Only 60% of corridor A and 40% of corridor F are within the forest and shrub category, whereas all other corridors (A-D) are above 77%.

To assess the relevance of the values computed for the corridors (which were, at this stage of the research, mainly based on assumptions), we analysed the dispersal costs of four male lynx moving through unfavourable habitat using the same resistance values. Three individuals were followed in the Alps, one in the Jura Mountains. One dispersing young male, who spent most of its time in suboptimal habitat, moved a minimum distance of 3 km across arable land and turned back at a highway in the open plain. He had travelled 20.9 km outside the prime habitat (less than 20% of the corridor was within the forest and shrub category) with a total cost of 1163 (55.6/km), but did not survive (Zimmermann & Breitenmoser 2002). The other three were successful – that is surviving – dispersers, using corridors of 18.8 km length (total costs 264; average cost 14/km), 60.6 (828; 13.7/km), and 2.2 (294; 133.6/km), respectively. They travelled distances of up to 600 m through arable land. The percentage of the corridor within the forest and shrub category ranged from 40% to 75.9%. One lynx crossed a medium river as large as 30 m. On the other hand, highways were important barriers to dispersal. Three out of 4 dispersing lynx did not cross highways and turned back after they spent a few days in their vicinity (Breitenmoser-Würsten *et al*. 2001). One adult male, however, crossed four times the valley of the Aare, which is 1 km wide and comprises a railway, a medium river and a fenced highway in an open habitat. These anecdotal observations demonstrate that the capacity to cross barriers may differ considerably between individuals. The passages actually used by dispersing lynx were within the range of the costs of the corridors A to E (Table 7.2, 7.3; Fig. 7.6) or even more expensive.

7.5. Discussion

7.5.1. Distribution model

The distribution of large carnivores depends *a priori* on habitat and prey availability, and is limited through anthropogenic pressure. Data on number and distribution of prey are presently not available in an accurate and comparable form for the Jura Mountains (Breitenmoser *et al.* subm.) to be incorporated in a GIS analysis. However, as ungulate distribution is habitat dependent by itself, we argue that the presence/absence data of lynx reflects also prey availability. It must also be stressed that ungulate abundance was not a limiting factor during our study time (Jobin *et al.* 2000; Stahl *et al.* 2001; Molinari-Jobin *et al.* 2002, Molinari-Jobin *et al.* subm.). In our model, we assume that disturbances are reflected by variables describing land use (e.g. urban fabric, industrial, artificial areas in Table 7.1).

Top predators are generally not very sensitive to a particular habitat structure, vegetation or ecosystem type (Mladenoff *et al.* 1995). But among the European large carnivores, lynx is certainly the one with the most specific demands regarding habitat and prey (Breitenmoser 1997). On the other hand, lynx are able to adapt to semi-natural landscape and their permanent disturbances (Breitenmoser-Würsten *et al.* 2001). Radio-tagged lynx stayed close to human settlements or main roads if they were able to find secure day resting places. In a habitat evaluation for all Switzerland (Chapter 3), distance to road was found to be a poor predictor for lynx habitat quality. Lynx do not care about human presence (e.g. recreational areas, hunting, logging) as we concluded from many anecdotic observations. Radio-tagged lynx were often located in a military exercise site when shooting was going on. A female with her two kittens once had a day resting place in brushwood in the middle of a golf course where she had killed a roe deer. It was not uncommon to locate lynx close to loggers, next to a mountain restaurant, ski lifts or recreational areas. The lynx seemed to be aware of the human activities, whereas people very rarely noted the presence of the elusive cat.

The AUC at calibration and evaluation indicates a good discrimination of our model. Presence cells as point location from monitoring data from the Swiss Jura Mountains (Capt subm.) are comparably well classified as the presence cells in the study area, from where data have been used to calibrate and validate the model (Fig. 7.3). Habitat models are sensitive regarding the origin of observations used to calibrate the model (Guisan & Zimmermann

2000). Our prediction should be good, as the model has been calibrated in one part of the Jura Mountains (polygon in Fig. 7.1) and extrapolated over the rest of the mountain range, which, however, have the same habitat characteristics as the reference area.

7.5.2. Present distribution and viability of the population

Our model predicts that the breeding population in the Jura Mountains ranges from 74–101 individuals and from 51–79 individuals when continuous areas <50 km^2 are disregarded. The maximum number of 101 individuals computed in the first approach is certainly too optimistic, as numerous small and isolated patches which are not suitable for permanent lynx home-ranges were included. The density estimation computed for our model (1.19 resident lynx/km^2 for good lynx habitat) was slightly higher than the average densities given by Breitenmoser-Würsten *et al.* subm.: 0.7–0.8 ind/km^2, or 1.0–1.1 ind/100 km^2 for good habitat only. The minimum value of 51 individuals, on the other hand, seems to be too restrictive. Vandel 2001 reports for the western Jura Mountains not only lynx observation in the “pessimistic range” (dark grey area in Fig. 7.5), but also in the “optimistic” areas (light grey area in Fig. 7.5). The most plausible number may indeed lie between the lower value of the first and the higher value of the second estimation, hence 74–79 individuals. The resident lynx form the reproducing population. In addition to the breeding animals, there will be a number of subadult lynx on dispersal. For the Jura Mountains, this shadow population was estimated to be about 6–35% of the resident population, depending on the status of the population (Breitenmoser-Würsten *et al.* subm.). Will such a population be viable?

As pointed out by Thomas (1990) there is no single “magic” population size that guarantees the persistence of an animal population. No empirical data are available on Minimum Viable Population (MVP) size of carnivores (Ballou 1998). Models estimated the minimum number for viable populations – from a demographic point of view – to be at least 50–100 individuals (Seidensticker 1986; Schaffer 1978), and up to 1,000 individuals when genetic, environmental variations and natural catastrophes are taken into account (Thomas 1990). Our results show that the Jura population lies in the “demographic” viability range. In one empiric example, Saether *et al.* (1998) estimated the minimum viable size for the brown bear in Scandinavia to be even lower.

However, the potential Jura population is far from the size of a long-term secure population considering genetic aspects and catastrophic events. We do not know how relevant such considerations are in the real world, yet, the reintroduced lynx population in the Jura Mountains has indeed a genetic load to bear. The number of founder individuals was low (Capt subm.), and preliminary genetic analysis (Breitenmoser-Würsten *et al*. 2001) revealed that the population underwent a genetic drift and has a reduced genetic variability compared to the Slovakian source population. The genetic viability would be granted if the Jura population were a part of a larger meta-population, allowing the exchange of individuals between neighbouring sub-populations. Such a network of populations is not unrealistic, as our analyses of corridors demonstrated. At present, we cannot assess the functionality of these corridors, as most of the bridgeheads on either side are not really colonised. According to Vandel (2001) and Capt (subm.), we estimate that 92% of the potential distribution area in the Jura Mountains is actually occupied by lynx. The existing gaps are in the north of the range. Lynx have been reintroduced in the Vosges Mountains (Stahl & Vandel 2002). According to Stahl & Vandel (2002), the southern edge of the population in the Vosges Mountains is more than 100 km distant from the Jura Mountains, but the authors mention observations in the wooded hills of the *Haute Saône* between the two mountain ranges. Lynx have been observed in the Black Forest, it is, however, unlikely that they originated from the Jura Mountains (T. Kaphegyi, pers. comm.). The corridor most likely used by lynx so far is the one between the Jura Mountains and the Chartreuse (D in Fig. 7.6). Stahl & Vandel (2001) assume that lynx signs found in the Chartreuse actually came from immigrating lynx from the Jura Mountains. The Chartreuse occurrence, however, has so far been isolated from the Alpine lynx population.

As an alternative to the spontaneous migration of lynx between the adjacent sub-populations, we may have to consider an artificial transfer of individuals. Such measures should be considered at least during the recovery phase of the lynx population over a large area, as it is now done in the Alps, where lynx are being translocated to the eastern Swiss Alps (Molinari-Jobin *et al*. 2001). If once the neighbouring areas of the Alps, the Jura and the Vosges Mountains, and the Black Forest (the single sub-populations) are occupied, the likeliness that individuals will disperse through the existing corridors and hence guarantee the genetic exchange will increase considerably.

7.5.3. Conclusions

Our habitat and distribution model – together with MVP and meta-population considerations – can help to develop concepts for the conservation and the management of the lynx population in the Jura Mountains and adjacent ranges. In practice, the results of our model suggest that the monitoring of the size and the spatial expansion as well as a genetic surveillance of the population should be continued, as the population is (still) in a critical status. It furthermore suggests that the migration between adjacent sub-populations is important for the long-term stability of the population(s), and that suitable corridors indeed exist. In turn, the recovery of the lynx in this part of Western Europe offers the chance to assess the practical use of certain theoretical models. As a subsequent step we could combine the GIS model (habitat and land tenure system of the lynx) with population viability considerations into a meta-population model, and hence bring such theoretical approaches closer to the real world.

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Chapter 8. Potential Distribution, Fragmentation and Population Size of the Eurasian Lynx (*Lynx lynx*) in the Alps

8.1. Abstract

Forest cover throughout the Alps has considerably increased since the eradication of the lynx in the early 20th century. But the mountain range is more fragmented than ever; high altitude ridges above the timberline and valleys with human settlements and traffic lines hinder the movements of forest living species. Re-introductions programmes in the 1970s resulted in two still relatively small and isolated populations of lynx in the Swiss Alps and in the Dinaric Mountains. For the long-term conservation of the species in the Alps, spatial expansion and fusion of the population is crucial. We evaluated the habitat suitability and connectivity for the lynx in the Alps by means of GIS-based models using radio-telemetry data from the Swiss Alps and the Jura Mountains, in order to reveal (1) the suitable habitat patches (sub-populations), (2) the potential size of the sub-populations, and (3) connections between sub-populations. Ecological Niche Factor Analysis (ENFA) was used to predict the potential distribution of lynx in the Alps. The first factor, called marginality, accounted for 29% of the total specialization and showed that lynx preferred forest, shrubs and herbaceous vegetation, but avoided areas of heterogeneous agriculture. The second, the third and the fourth factor accounted for more specialization, mostly regarding distance to towns, heterogeneous agriculture, forest and open space frequencies. The cut-off value of the habitat suitability map was fixed so that 80% of the "presence cells" were included. The resulting map was smoothened and overlaid with the barrier map in order to identify sub-units. The resulting model divided the Alps in 37 suitable habitat patches ranging from 50 into 18,711 km^2, when all patches smaller than 50 km^2 were ignored. The total area of suitable habitat in the Alps is about 93,600 km^2. Using the range of densities found in field studies in Switzerland, we estimate that the Alps could host a population of 961 to 1,827 resident lynx. Connectivity was calculated in the GIS using a friction grid and a cost-distance-function. The results of the cost-distance analysis revealed that all patches were within the reach of dispersing lynx, as the connection costs were in the range of dispersal cost of radio-tagged subadult lynx moving through unfavourable habitat. But experience suggests that only few dispersers will cross unsuitable areas and barriers such as highways. This low migration rate may be enough to grant genetic exchange between established sub-populations, but seems too low to allow the spontaneous foundation of a new

population in an un-settled areas. As an alternative to natural dispersal, artificial transfer of individuals across the barriers should be considered.

8.2. Introduction

Human development and other alteration of natural environment tend to fragment habitats and animal populations, and to restrict movements of terrestrial animals. Fragmentation results from direct destruction of important habitat and/or linear infrastructure development such as roads, railways, and trails, which often prevent the movement of terrestrial animals and reduce habitat connectivity. These changes can be gradual or abrupt, natural or anthropogenic. Roads lead to increased human access to wildlife habitat which can disturb animals (e.g. Cederna & Lovari 1985; Lamerenx *et al*. 1992; Andersen, Linnell & Langvatn 1996; Mace *et al*. 1996; Primm 1996; Linnell *et al*. 2000), forcing them to invest energy to avoid people. More specifically in large carnivores, roads can have a major effect on mortality directly by vehicle collision, and indirectly by illegal killing as well as reduced prey availability due to greater access for hunters and poachers (e.g. Mattson *et al*. 1987; Mech *et al*. 1988; Noss *et al*. 1996). As habitat is reduced, either directly or indirectly, wildlife populations become smaller in size and more isolated. This increases the risk of local extinction (Shaffer 1987). Mammalian carnivores are thought to be particularly vulnerable to local extinction in fragmented environment because they have large spatial requirements, exist at low abundance and suffer from direct persecution (Noss *et al*. 1996; Woodroffe & Ginsberg 1998). Crooks (2002) showed that carnivore species differed regarding their sensitivity to habitat fragmentation. Large-bodied specialized carnivores (e.g. puma or bobcat) were more sensitive than small-sized generalists (e.g. domestic cats, grey fox, and opossum). The later even profited from habitat alteration.

The extinction risks may be reduced by rescue effects due to dispersal between local populations (Hanski, Moilanen & Gyllenberg 1996). This process depends on (i) the number of dispersers available in the population, (ii) the distance between the source and the target population, and (iii) the permeability of the habitat matrix to movements by the species under consideration (Fahrig & Merriam 1994; Wiens 1997). The distance between source and target population increases with habitat destruction, whereas matrix permeability is altered through modification in the land use and construction of linear barriers. Globally, large and medium sized carnivores have experienced severe range depression in the past and occur in very small populations if they were not completely exterminated (e.g. Breitenmoser 1998; Gittleman & Gomper 2001). The management policy (Linnell, Swenson & Anderson 2001) as well as habitat quality (Breitenmoser 1998) have improved considerably in many regions in Europe and North America, and large carnivores are about to recolonize their former ranges naturally, or artificially through re-introductions (Boitani & Cuicci 1993; Swenson *et al*. 1995; Adamic 1996; Breitenmoser 1998; Bader 2000). In such cases the recolonization process of former habitat is even more shaped by habitat fragmentation, as only few source populations are left or a small number of individuals were released. Therefore, good knowledge on the spatial distribution, size and connectivity of suitable habitat patches is required when planning re-introduction or recovery programs as the choice of the release sites may strongly influence the recolonization dynamics of a fragmented landscape. Such knowledge should allow developing conservation strategies to maximize the success of the population restoration. Lynx have been re-introduced in different parts of the Alps in the 1970s (reviewed in Breitenmoser *et al*. 2001) and currently occur in two small populations in the Swiss Alps and Dinaric Mountains. A recent analysis of the status and distribution of the Alpine lynx populations has revealed that (1) the lynx population in the north-western Swiss Alps increased while the Slovenian population was at best stable, and (2) that there was hardly any spatial expansion of the Slovenian and Swiss populations (Molinari-Jobin *et al*. 2003). The expansion and the merging of the two populations was recognized an important prerequisite for the long-term survival of the lynx in the Alps. The Alps, though wild ungulate populations and forest cover within all massifs have recovered since the eradication of the species in the early 20th century (Breitenmoser 1998), are more fragmented than ever. Ancient natural barriers (e.g. high altitude ridges, lakes) and recent artificial barriers (e.g. valleys with extended human settlements and traffic lines) hinder the further spread of terrestrial animals. Besides, lynx does not tend to very intensive dispersal (Chapters 4 and 5). An important step towards the convergence of the two existing Alpine populations is the assessment of biological, ecological and geographic possibilities and constraints.

To formulate recommendations for the unification of the western and eastern lynx population in the Alps we evaluate the habitat suitability and connectivity of the Alps. The objectives are (1) to identify the suitable habitat patches (sub-populations), (2) to estimate the potential size of the sub-populations, and (3) to assess the connections between sub-populations. This should provide insights into the potential recolonization of the Alps by the lynx and allow to identify areas for further re-introductions to support the recolonization. A Geographic Information System (GIS) model represents a cost-effective way of maximizing the information on which to base conservation strategies and actions. We present a model map to predict the possible spread of the lynx populations. The aim of this habitat suitability model is to plot possible corridors interconnecting the existing populations in order to identify future focal areas for conservation and management actions.

8.3. Material and methods

The Ecological Niche Factor Analysis (ENFA, Hirzel *et al*. 2002, see Chapter 1 for details) uses presence data only. This approach is recommended when absence data are not available (most data banks, radio-telemetry), unreliable (most cryptic and rare species) or meaningless (invaders) (Hirzel, Helfer & Metral 2001b). The ENFA computes a habitat suitability model by comparing the environmental niche of the species to the environmental characteristics of the entire study area. The analyses have been performed with *Biomapper 2.1* (Hirzel, Hausser & Perrin 2002).

8.3.1. Data sets

The whole Alps were chosen as reference area, and modelled as a raster map based on Lambert Equal-Area Azimuthal projection (central meridian: 9 degree; reference latitude 48 degree), comprising 321,060 squares of 1 kilometre.

The land use data came from GEOSTAT for Switzerland (Swiss Federal Statistical Office) and from CORINE for the remaining areas (European Topic Centre on Land Cover, Environment Satellite Data Center, Kiruna, Sweden), which classify the land use types on a 100x100-m and a 250x250-m grid, respectively.

A fundamental difference between the investigation methodologies of the two classification systems (GEOSTAT, CORINE) lies in the delineation of land use and land cover types. While the Swiss Land Use Statistics identifies land use utilization at each sample point, CORINE Land Cover divides the surface area into more or less homogenous units of 25ha or lager which are then assigned the corresponding type of land cover. The different methods of delineation result in differences in the nomenclature and thereby make it difficult, if not impossible, to translate the Swiss Land Use Statistics into corresponding classes of Level 3

(44 land cover classes) of the CORINE Land Cover (Klaus & Finger 1998). For this reason, it was preferred to relate the base categories of the Swiss Land Use Statistics with Level 2 (15 land cover classes) of CORINE Land Cover. Whichever procedure is used during generalization of point or grid data, it is inevitable that the area statistic will change. Generalized data are secondary data which means that the percentage of each individual usage is no longer accurate in the results. Therefore we used the CLCBN85B 100x100-m grid CORINE base data set for Switzerland (GEOSTAT base data set, Swiss Federal Statistical Office) to compute the surface area statistics of the different land use categories for Switzerland. We pooled the 15 categories into 10 variables (Table 8.1) according to similarities between categories and our knowledge of lynx biology.

Table 8.1. Land-use categories used in the analyses. The fourteen land-use categories of the CORINE database have been combined in ten categories according to similarities between categories and our knowledge of lynx biology.

CORINE land-use categories compiled for the analyses	14 original land-use categories of the CORINE
Town	Urban fabric Industrial Mine Artificial non-agricultural vegetated areas
Arable land	Arable land
Permanent crops	Permanent crops
Pastures	Pastures
Heterogeneous agricultural areas	Heterogeneous agricultural areas
Forests	Forests
Shrubs	Shrubs and/or herbaceous vegetation
Open spaces	Open spaces with little or no vegetation
Inland wetland	Inland wetland
Water	Coastal wetlands Inland waters

Only vector information of forest cover was available for Liechtenstein. This vector file has been converted in a 250x250-m grid.

Elevation came from the MONA elevation model, a 250x250-m grid (GEOSYS, Geographic Information for the Rural Environment).

Vector files on roads, human settlements and rivers came from the Vector 200 database for Switzerland (Swiss Federal Topographic Office) and from the Bartholomew's 1:1,000,000 European database for the remaining areas. All databases were in digital form and ready to be used in the GIS ArcView (ESRI 1996a,b,c) and IDRISI 2.0 (Eastman 1997).

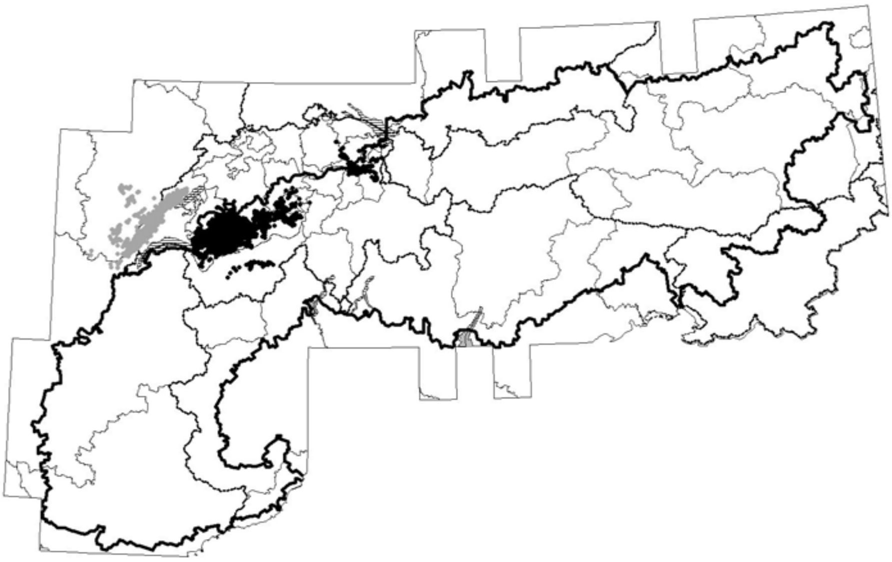
From the 100x100-m and the 250x250-m information, we computed a summary statistics to each square-kilometre cell: (1) the frequency in the case of the different land use predictors and roads; and (2) the mean value in the case of distance to large and medium town (eco-geographical variables 1-7 in Table 8.2). The environmental predictors have been normalized using the Box-Cox transformation (Box & Cox 1964) prior to the analyses. Frequencies of water, inland wetland, arable land, permanent crops, and towns were not continuous enough and have therefore been removed from the analyses.

Table 8.2. Source of the seven predictors used in the ENFA analysis. Land use: CORINE (European Topic Center on Land Cover, Environment Satellite Data Center, Kiruna, Sweden) or CLCBN85B for Switzerland, Swiss Federal Statistical Office (SFSO GEOSTAT). CORINE data have an accuracy of 250x250-m and CLCBN85B of 100x100-m. Vector files on roads, railways and settlements came from the Bartholomew's 1:1,000,000 European database and vector 200 1:200,000 Federal Office of Topography for Switzerland.

Variable category	Predictor	Sources
Biological	1. Forest [frequency]	CORINE/ CLCBN85B
	2. Shrub and/or herbaceous vegetation [frequency]	CORINE/ CLCBN85B
	3. Open spaces [frequency]	CORINE/ CLCBN85B
	4. Pastures [frequency]	CORINE/ CLCBN85B
Anthropogenic	5. Roads [frequency]	Bartholomew's/Vector 200
	6. Distance to large and medium town [mean]	Bartholomew's/Vector 200
	7. Heterogeneous agricultural areas [frequency]	CORINE/ CLCBN85B

The only radio-telemetry data available in the Alps are from Switzerland. However, due to the high heterogeneity of the Alps, presence data obtained by radio-telemetry both from the

Alps (Haller & Breitenmoser 1986; Breitenmoser & Haller 1987; Haller 1992; Breitenmoser-Würsten *et al.* 2001; Ryser *et al*. 2004; KORA unpublished data) and the Jura Mountains (Breitenmoser *et al*. 1993; Stahl *et al*. 2001a; Stahl *et al*. 2001b; Stahl *et al*. 2002; Breitenmoser-Würsten *et al*. subm.) were included in our model (Fig. 8.1). Thus we combined data sets from areas with high and low forest cover (Jura Mountains *versus* Swiss Alps). A total of 13,380 radio fixes accurate at least to the square kilometre of 75 resident lynx followed from 1983 to 2002 and 1,611 kill site locations were used to generate and/or to validate the models. The response variable is the presence of lynx in each kilometre square. Lynx was considered to be present in each square containing one or more telemetry fix/kill site.



Delimitation of the Alpine Convention © Réseau Alpin des Espaces Protégés

Figure 8.1. Reference area in the Alps. The black and grey dots represent radio fixes and kill sites from the Swiss Alps and the Jura Mountains, respectively, used to build and/or to validate the habitat suitability map. The thick line delimits the area of the Alpine Convention. Medium and thin lines show the national borders and the administrative units, respectively. Horizontally shaped = large lakes.

We divided the presence data (N = 3,271) into cross-validation groups following a k-fold partitioning design. Huberty's rule of thumb was used to determine the model training to testing ratio:

$$t = \frac{1}{1 + \sqrt{(p-1)}}$$

where *t* and *p* are the proportion for test data and the number of environmental predictors, respectively. Predictions have been divided into 10 equal-interval bins, scaled between 0 and 100. Base on this rule, a testing ratio of 29% was determined and a k-fold partition of four groups considered. Using cross-validation procedures, we trained our model iteratively on three of the four data sets using ENFA analyses. Validation was based on the remaining testing set. A Spearman-rank correlation between area-adjusted frequencies of cross-validation points within individual bins and the bin rank was calculated for each cross-validated model as described in Boyce *et al*. (2002). Area-adjusted frequencies were simply the frequency of presence cells lying within a bin divided by the frequency of locations belonging to that bin across the study area. An area-adjusted frequency of 1.0 indicates that cross-validated testing presence cells occur at rates expected by chance.

8.3.2. Potential distribution and population size

The cut of value of the habitat suitability map was fixed arbitrary in a way that 80% of the presence cells were included in the boundaries of the potential distribution map. We defined patches based on individual home ranges requirements (see Theobald & Hobbs 2002). We used only the predefined cells of the potential distribution map and calculated the frequency of more cells of that type in a circular window of 5 kilometres radius, which corresponds approximately to the size of a female home range in the Alps (Breitenmoser-Würsten *et al*. 2001). The resulting map depicts a gradient of values, or proportion of a cell that contributes to habitat. To identify contiguous habitat adequate for an individual, we set the threshold so that 70% of the presence cells were included in the boundaries of the distribution map. We used our knowledge of the land tenure system of resident lynx (Breitenmoser *et al*. 1993; Breitenmoser-Würsten *et al*. 2001; Breitenmoser-Würsten *et al*. subm.) to estimate the size of the lynx sub-populations in the Alps. All estimation of the population size have been done under the assumption that the number of lynx is proportional to the amount of good lynx habitat, and that the prey base is not a limiting factor for the lynx in this mountain range. The distribution map was then overlaid with the barriers map (highways, main roads, and railways less than one kilometre apart from highways, elevation above 2,500 meters, settlements, and lakes) in order to identify sub-units of habitat. The terminology of the European Lynx Online Information System (ELOIS) was used for the identification of the lynx populations (see von Arx *et al*. 2004).

8.3.3. Connectivity

The land use and land cover type at any given location influences the relative ease or difficulty of a species to move through the habitat matrix. Ferreras (2001) showed that connectivity – in this case defined as the proportion of the dispersing animal going out from a given sub-population reaching a specific distinct sub-population – was significantly related to the effective distance measured as the least effort in moving over a friction surface. Using the CORINE data set, we specified the relative resistance to movement for each land use category in the GIS using values based on (i) our own expert opinion and (ii) combining expert knowledge with statistical estimates where the later relative resistance to movement was inversely related to the score of the selection index specific to the habitat in each cell (Table 8.3). The higher the value, the higher the resistance to movements. All agricultural areas were pooled in one category enclosing permanent crops, arable land and heterogeneous agricultural areas. Finally, six habitat types remained for the analyses: (1) forest; (2) shrubs and/or herbaceous vegetation; (3) pastures; (4) open spaces; and (5) agricultural areas.

Jacobs' index (Jacobs 1974), which varies from +1 for maximum preference to −1 for maximum avoidance, with radio-tracking data was used to study the habitat selection of dispersing lynx. This index compares the use (u) and the availability (a) of a resource through the formula

$$\text{Jacobs' Selection Index} = \frac{u - a}{u + a - 2 \times u \times p}$$

Habitat composition within areas used by dispersing lynx (later called "home range" although by definition a true home range cannot be considered for dispersing animals) was calculated in the GIS using the minimum convex polygon method (Hayne 1949). Availability was defined as the proportion of each habitat type within the home range. The sampling unit was the individual. Each habitat type was considered to be significantly preferred or avoided if its mean value on the Jacobs' index was significantly different from zero. Statistical significance was obtained comparing alternative hypotheses, where the null hypothesis corresponds to a Jacobs' index equal to zero (habitat used as available). The obtained value were compared with t-distribution (with n-1 degrees of freedom, where n is the number of individuals used in the analysis). Habitat with a low proportion within home ranges may have very high or low Jacobs' index and probably do not represent the true habitat use. To avoid this, only individuals for which a given habitat type make up >5% of its home range were considered for the calculation of the selection index of that habitat type. The forest was the preferred habitat type by dispersing lynx (Jacobs' index = 0.64), and agricultural areas the most avoided habitat (Jacobs' index = – 0.72), other habitat having intermediate values (Fig. 8.2). An arbitrary scale of friction from 1 to 30 was chosen, where the lowest value (1) is assigned to the preferred habitat (forest), and the highest value (30) is assigned to the most avoided habitat (agricultural areas, Fig. 8.3). The reduced spatial extension of the land use category inland wetland and crops did not allow us to calculate the Jacob's index. In this case we had to recourse on an expert opinion and set the friction value to the same value as the most avoided habitat.

Settlements, industrial, mining, and "artificial non-agricultural vegetated areas" (e.g. green urban areas, sport and leisure facilities), lakes, elevation above 2,500 were considered as insurmountable barriers for lynx and their value was set to 1,000 points (very high resistance).

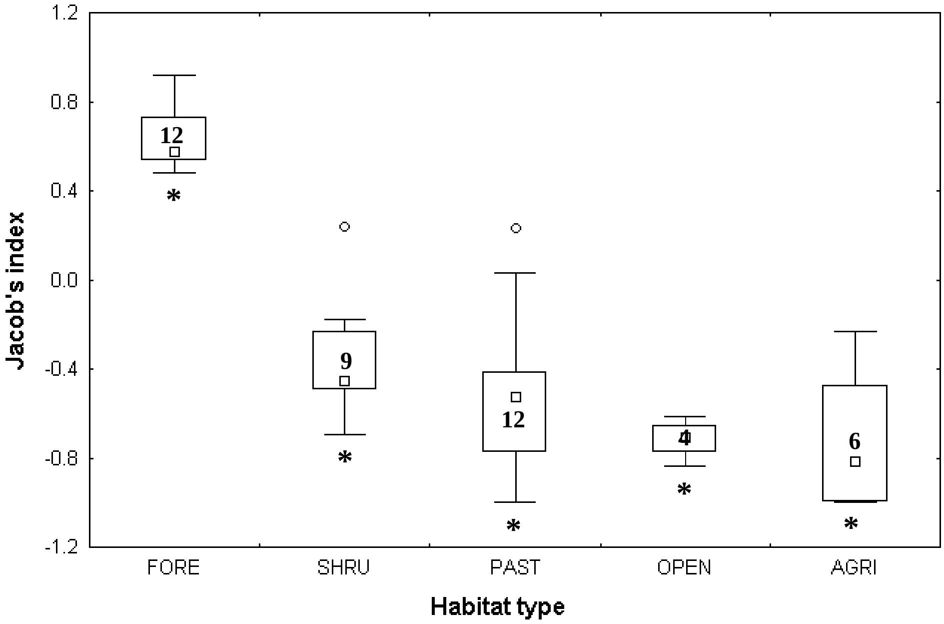


Figure 8.2. Jacobs index for each habitat used by 12 subadult lynx in the Swiss Alps and the Jura Mountains. Positive and negative values indicate preference and avoidance, respectively. Boxes indicate the 25-75th percentile range and contain the median line. Whisker caps represent the 10th and 90th percentile values. Asterisks indicate that the mean is significantly different from zero. Numbers indicate sample size, the number of individuals for which availability of that habitat type was higher than 5% within MCP100 home range. (FORE: forest; SHRU: shrubs and/or herbaceous vegetation; PAST: pastures; OPEN: open areas; AGRI: agricultural areas).

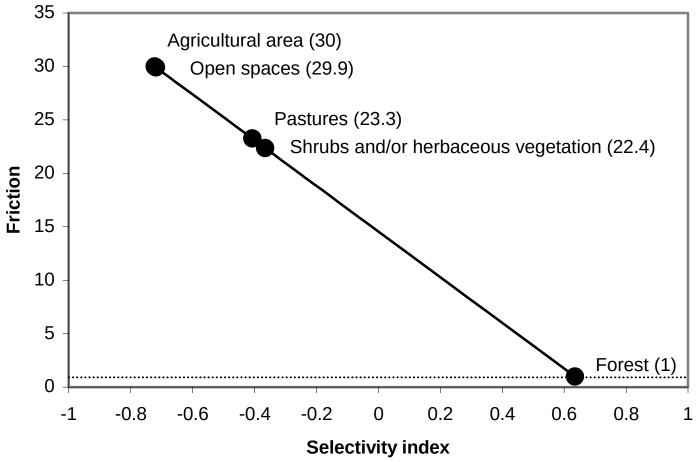


Figure 8.3. Function linking habitat selectivity index (Jacobs 1974) during dispersal and proposed values of friction to movement employed to calculate the cost-distance between subpopulations. The dotted line indicates the minim value arbitrarily assigned to the friction scale.

We also incorporate the influence of linear barriers such as highways, main roads, railways, and rivers in our model. Several observations showed that lynx swam across rivers of 30 meter (P. Molinari, pers. comm.; A. Ryser pers. comm.) and still waters of up to 200 meter (J.M. Vandel, pers. comm.). In the study areas in the Jura Mountains and the Alps, radio-tagged animals used to cross (fenced) highways. A value of 120 points was set to highways and large rivers; 40 to medium rivers, railways and main roads (Table 8.3). The distance was then calculated based on matrix quality using the Cost Distance Matrix 2.1 extension written by Nicolas Ray in the GIS ArcView, where the patches resulting from the distribution model are the source patches for the cost-distance-function to assess the possible corridors between the different habitat patches. If the costs are below a threshold related to dispersal ability, then the patches are considered connected. Dispersing lynx are not supposed to find the optimal connexion between two patches, as indicated by the cost-path analysis (Schadt *et al.* 2002). However the cost-path analyses delivers a relative measure for comparing the connectivity between different patches (e.g. two patches that are connected by a low-cost optimal path will also be connected by many alternative low-cost paths with slightly higher cost than the optimal one). The corridors were evaluated by comparing them with the characteristics (length, barriers and costs) of known passages used by radio-collard lynx when roaming outside their prime habitat.

Table 8.3. Friction value of the environmental variables for the four grids used in the cost-distance analyses. *Grid 1* = expert estimation without linear barriers, *Grid 2* = combination between expert and statistical estimation without linear barriers, *Grid 3* = expert estimation including linear barriers, *Grid 4* = combination between expert and statistical estimation including linear barriers.

Category	**Environmental variables**	**Friction values**			
		Grid 1	*Grid 2*	*Grid 3*	*Grid 4*
Land use	Forest	1	1	1	1
	Shrubs	5	22	5	22
	Permanent crops	10	30	10	30
	Pastures	10	23	10	23
	Inland wetland	10	30	10	30
	Open areas	10	30	10	30
	Arable land	30	30	30	30
	Heterogeneous agricultural areas	30	30	30	30
	Settlement	1,000	1,000	1,000	1,000
	Lakes	1,000	1,000	1,000	1,000
Topographic	Elevation > 2,500	1,000	1,000	1,000	1,000
Linear barriers	Medium rivers	-	-	40	40
	Main roads	-	-	40	40
	Railway	-	-	40	40
	Highway	-	-	120	120
	Large rivers	-	-	120	120

8.4. Results

By applying the ENFA method to the calibration sets, we got an overall marginality of 0.46 and an overall specialization value S of 1.53, indicating that lynx' habitat differs from the average condition in the study area (Alps, Jura Mountains and surround areas). According to the Mac-Arthur's Broken-Stick rule four factors (*M*, *S1*, *S2*, *S3*; Table 8.4) were retained, accounting 79.6% of the total specialization (Table 8.4). The *marginality* factor additionally accounted for 29% of the total *specialization* and showed that lynx were essentially linked to forest and shrubs and/or herbaceous vegetation. On the other end, lynx tended to avoid areas of heterogeneous agriculture. The second (20.6% of the total *specialization* explained), the third (19.5% of the total *specialization* explained) and the fourth (10.5% of the total *specialization* explained) factor accounted for more *specialization*, mostly regarding distance to large and medium town, heterogeneous agriculture, forest and open space frequencies.

Table 8.4. Result of the ENFA analyses. The response variable is the presence of lynx in each square kilometre. Radio fixes (n = 13,380) and locations of lynx kills (n = 1,611) were used to generate and validate the models. EP = Environmental predictor, factors: *M* = *Marginality*, *S1*, *S2* and *S3* = *Specialization*. Bold = EP with an absolute score ≥ 0.2. The amount of specialisation accounted for is given in each column heading.

EP	***M***	***S1***	***S2***	***S3***
% of the total *S* explained	29.0%	20.6%	19.5%	10.5%
Shrub and/or herbaceous vegetation	**+0.779**	**0.254**	0.117	0.09
Forest	**+0.476**	**0.284**	**0.333**	0.179
Distance to large and medium town	+0.134	0.135	**0.612**	**0.545**
Pastures	+0.082	0.019	0.022	0.3
Open spaces	-0.071	0.057	**0.621**	**0.741**
Roads	-0.149	0.016	0.045	0.019
Heterogeneous agricultural areas	**-0.339**	**0.913**	**0.337**	0.151

The habitat suitability map (Fig. 8.4) was computed using the species distribution on these factors.

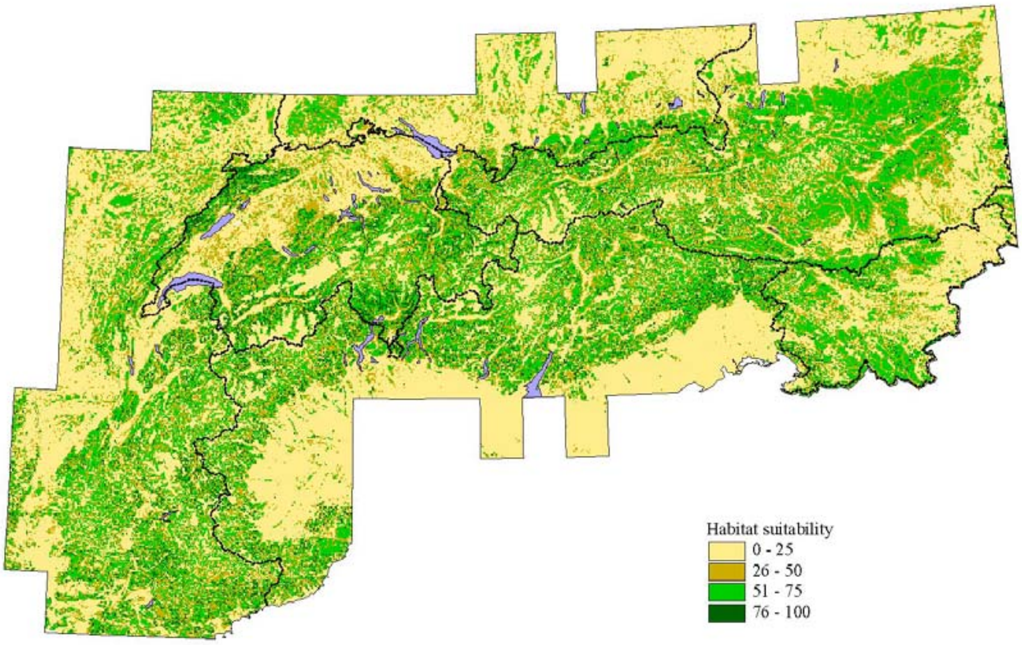


Figure 8.4. Map showing the predicted distribution of ENFA. Habitat suitability index (0 ≤ HS ≤ 100). The higher the value the suitable is the habitat.

Cross-validated Spearman-rank correlation (r_S) between RSF bin ranks and area-adjusted frequencies (Fig. 8.5) for individual and average model displayed significant positive rank values (r_S: 0.891-0.939, $p<0.001$), suggesting that model performance is good.

The cut of value of the habitat suitability map was fixed arbitrary in a way that 80% of the presence cells were included in the boundaries of the potential distribution map (Fig. 8.6a). The resulting map has been smoothened in order to remove small isolated patches (Fig. 8.6b) and the threshold was set in a way that 70% of the presence cells were included in the boundaries of the final distribution map (Fig. 8.6c). This map was then overlaid with the barriers map (Fig. 8.6d) in order to identify sub-units of habitat. When all patches smaller than 50 km^2 were ignored, the model divided the lynx habitat into 59 suitable patches, of which 37 are within the boundaries of the Alpine Convention (Fig. 8.7). 16 patches in the Alps were larger than 380 km^2 and up to 18,711 km^2. Even within some patches (e. g. patch no. 6 between the north-western Alps, the Valais north and the Valais south) there were larger plots of suitable habitat connected through small bands of habitats only, which may act as bottlenecks and impede movements of lynx.

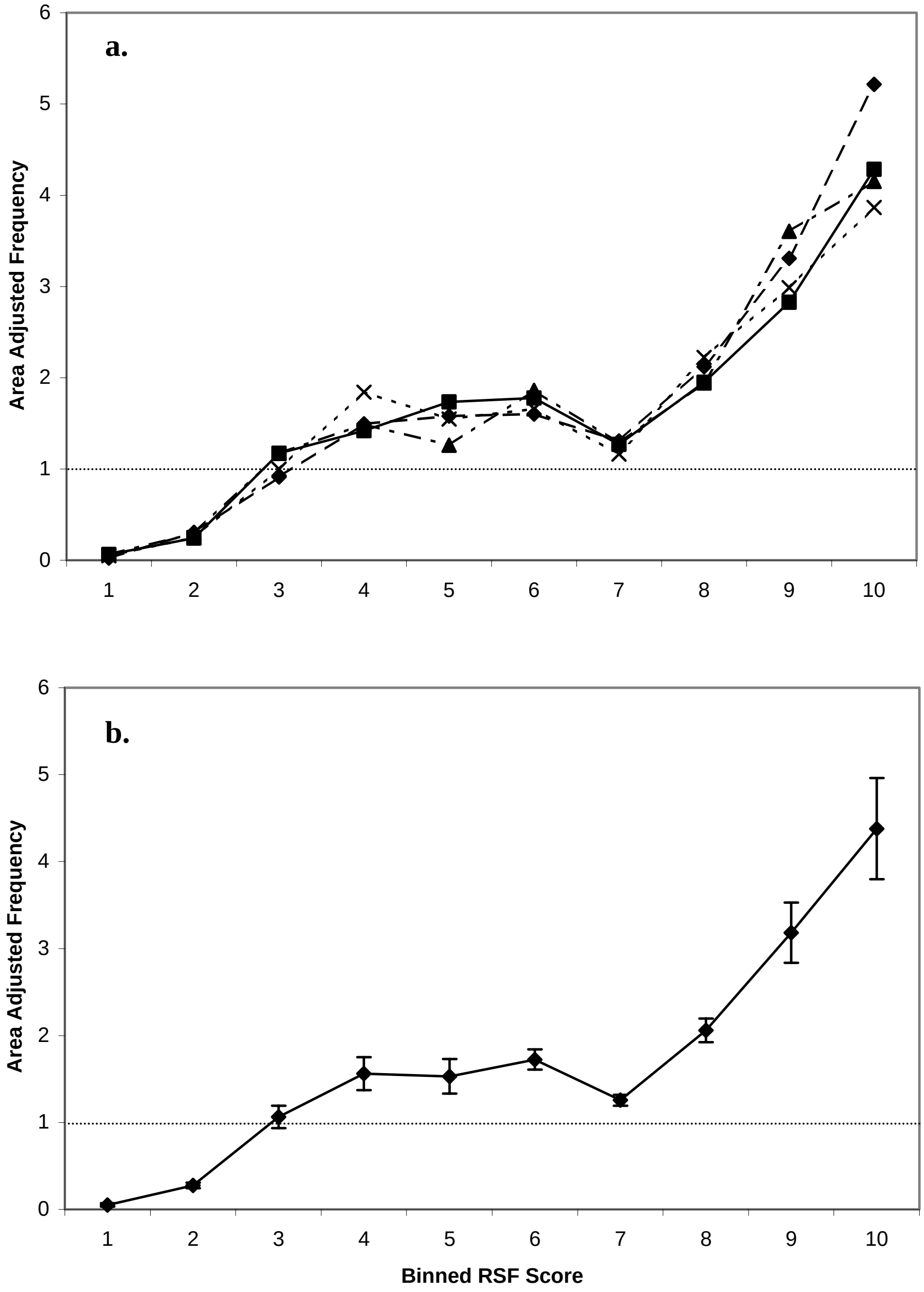


Figure 8.5. Area-adjusted frequency of binned crossed-validated use locations for RSF model. Frequency for individual cross-validation sets (n = 4) are depicted with unique symbols (graph a). Mean (± S.D.) frequency values by bin are illustrated in graph b. A Spearman-rank coefficient for mean frequency values by bins (r_s = 0.915, p < 0.001) indicates that the model predicted cross-validated presence well. Values close to one (dotted line) indicate that the observed frequency is not different from random expectation; values smaller than one indicate avoidance and greater than one preference.

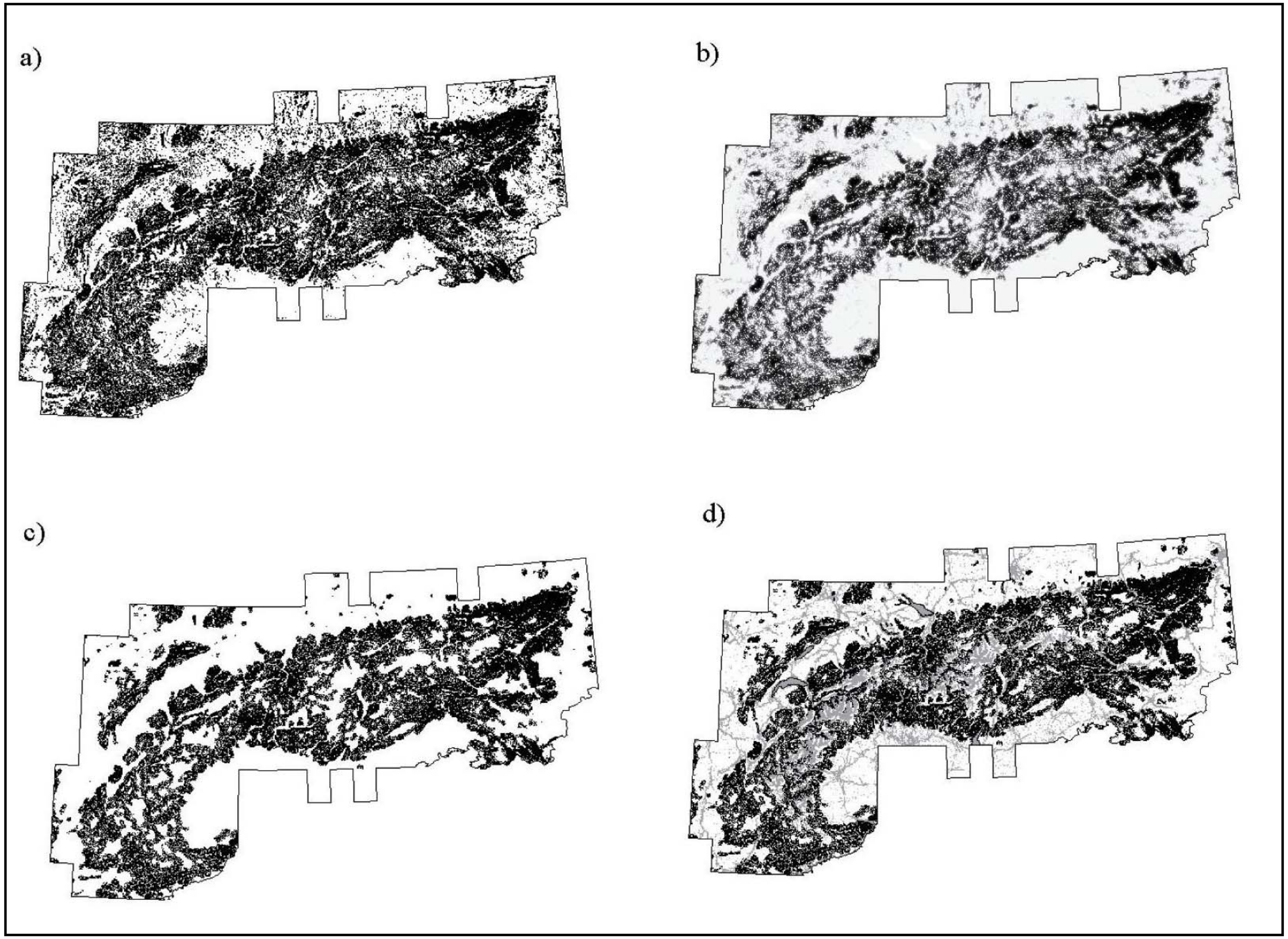
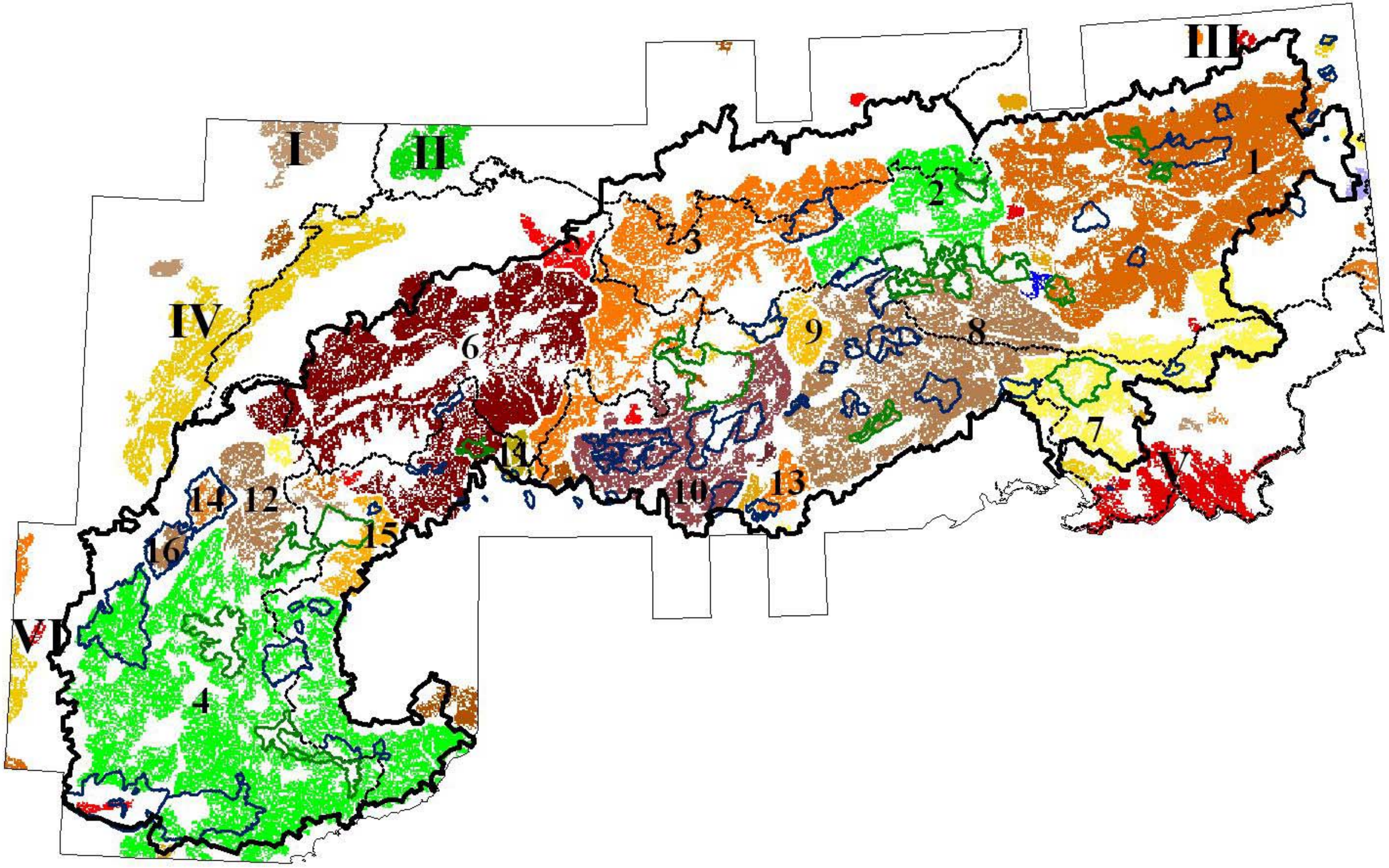


Figure 8.6. Smoothing process and identification of sub-units of habitat of the range map: a) cut of value of the habitat suitability map set in a way that 80% of the presence cells are within the boundaries of the distribution map, b) only the predefined cells of the distribution map are used and the frequency of more cells of that type in a circular window of 5 kilometres radius is calculated, c) the threshold was set in a way that 70% of the presence cells were included in the boundaries of the final distribution map, and this map was then d) overlaid with the barrier-map in grey (highways, main roads, and railways less than one kilometre apart from highways, elevation above 2,500 meters, settlements, and lakes) in order to identify sub-units of habitat.



Delimitation of the Alpine Convention and borders of the national and natural reserves © Réseau Alpin des Espaces Protégés

Figure 8.7. Suitable lynx habitat and fragmentation in the Alps and the adjoining regions (I = Vosges; II = Black Forest; III = Bohemian-Bavarian Mountains; IV = Jura Mountains; V = Dinaric Mountains; VI = Massif Central). The different coloured areas represent distinct patches separated by barriers. Labelled (1-16) are all patches > 380 km^2 located within the zone defined by the Alpine Convention (thick line). The dark green and blue thick lines delimit the national and regional parks, respectively.

The total area of suitable habitat in the Alps is about 93,600 km^2, of which less than 11% are located within national parks and natural reserves (Fig. 8.7). More than 70% of the area of national park consist of unsuitable habitat, mainly represented by high mountain habitat, and no single national park contains more than 522 km^2 of suitable habitat. Natural reserves are small in size too, but contain about 50% of suitable habitat. The largest natural reserve consist of 1,200 km^2 of suitable habitat. Using the moderate lynx population density found in the Jura Mountains (Breitenmoser *et al.* 1993, Breitenmoser-Würsten *et al.* subm.) or the higher density found in the north-western Alps (Breitenmoser-Würsten *et al.* 2001), we estimated that the Alps could host a population of 961 to 1,827 resident lynx (Table 8.5).

Table 8.5. Patch size and estimation of the number of self provisioning lynx (adults and independent subadults) in each sub-population of the Alps. Low and high = lynx densities from the Jura Mountains (Breitenmoser *et al.* 1993, Breitenmoser-Würsten *et al.* subm.) and from the north-western Swiss Alps (Breitenmoser-Würsten *et al.* 2001) have been used for the calculation, respectively. Remaining = all patches smaller than 381 km^2.

		Lynx density estimates					
			Low			**High**	
Patch no.	**Area [km^2]**	**♀**	**♂**	**Sef provisioning**	**♀**	**♂**	**Self provisioning**
1	17,239	112-127	65-72	202-242	208-216	112-120	441-473
2	3,824	25-28	14-16	45-54	46-48	25-27	98-105
3	9,931	64-73	38-41	117-140	120-125	65-69	254-272
4	18,711	121-138	71-78	220-263	226-235	122-130	478-513
5	723	5	3	8-10	9	5	18-20
6	12,385	80-91	47-52	145-174	150-155	81-86	317-340
7	6,560	43-48	25-27	77-92	79-82	43-46	168-180
8	10,487	68-77	40-44	123-147	127-132	68-73	268-288
9	1,000	6-7	4	12-14	12-13	7	26-27
10	5,685	37-42	22-24	67-80	69-71	37-40	145-156
11	405	3	2	5-6	5	3	10-11
12	1,735	11-13	7	20-24	21-22	11-12	44-48
13	663	4-5	3	8-9	8	4-5	17-18
14	381	2-3	1-2	4-5	5	2-3	10
15	1,062	7-8	4	12-15	13	7	27-29
16	444	3	2	5-6	5-6	3	11-12
remaining	2,344	15-18	7	29-31	29	15-17	59-62
Total	**93,579**	**606-689**	**355-388**	**1,099-1,312**	**1,132-1,174**	**610-653**	**2,391-2,564**

To migrate from one patch to a neighbouring one (Fig. 8.7), an animal has to overcome a certain "landscape resistance" (costs). This is not a fix value, but depends on the ability of a dispersing lynx. When we increase the maximum allowed costs a lynx can spend, patches merge into cluster (Fig. 8.8, using friction *Grid 4*).

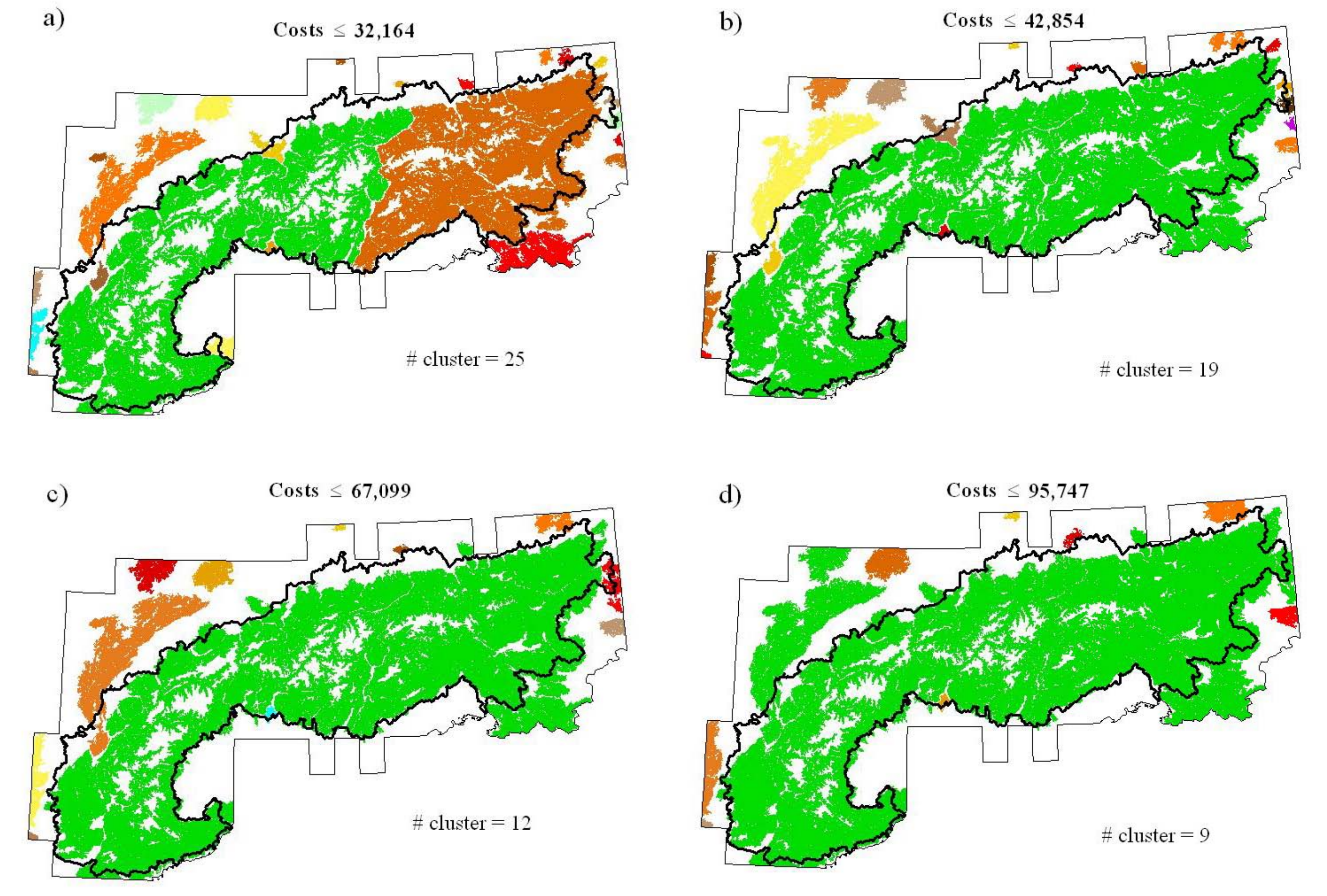


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Figure 8.8. Sensitivity of the landscape to dispersal ability for the Alps when *Grid 4* is used as friction gird for the calculation in the cost-distance analyses. The patches resulting from the distribution model (Fig. 8.7) are the source patches for the cost-distance function.

With costs ≤ 32,164, the patches situated within the area of the Alpine Convention (Fig. 8.7) form almost two large distinct cluster separated by the Brenner Valley and 4 more small, still isolated patches (Fig. 8.8a). The Alps form almost one distinct cluster when the cost are ≤ 42,854 (Fig. 8.8b) with the exception of the north-eastern part of Switzerland (patch 5 in Fig. 8.7), the Chartreuse (patch 16) and a small patch south to the lake of Como which are still isolated. The north-eastern part of Switzerland (5) is connected to the remaining Alps with costs at 58,135. The Chartreuse (16) is only weekly connected to the Alps (Fig. 8.8d; costs = 95,747). Connectivity between the Alps and the neighbouring populations according to the terminology of the ELOIS (von Arx *et al*. 2004) are subsequently described. The Dinaric (V in Fig. 8.7) and the Jura Mountains (IV) populations are connected to the Alps with costs at 41,561 and 67,099, respectively. The Vosges population (I), the Black Forest occurrence (II), the Bohemian-Bavarian population (III) and a potential population in the Massif Central (V in France) are relatively strongly isolated from the Alps and neighbouring populations (all costs > 103,000).

Figure 8.9 summaries how fragmentation (y-axis) varies with the costs (x-axis) for friction *Grid 1-4*. The patterns of the curves are quite similar when expert or mixed (expert and statistical) friction *Grids* are used to estimate the fragmentation of the landscape. There is a critical threshold value at about 12,500 for *Grid 1* and *2*. The connectivity of the landscape changes very rapidly below 12,500 (Fig. 8.9). Similarly there is a critical threshold of about 26,000 in the case of *Grid 3* and *4*. The results show furthermore that fragmentation is very sensitive to the friction value attributed to linear barriers (Fig. 8.9). The costs of known passages used by subadult lynx when dispersing outside their prime habitat revealed that all patches were within the range of maximal dispersal cost of subadult lynx moving through unfavourable habitat (Table 8.6).

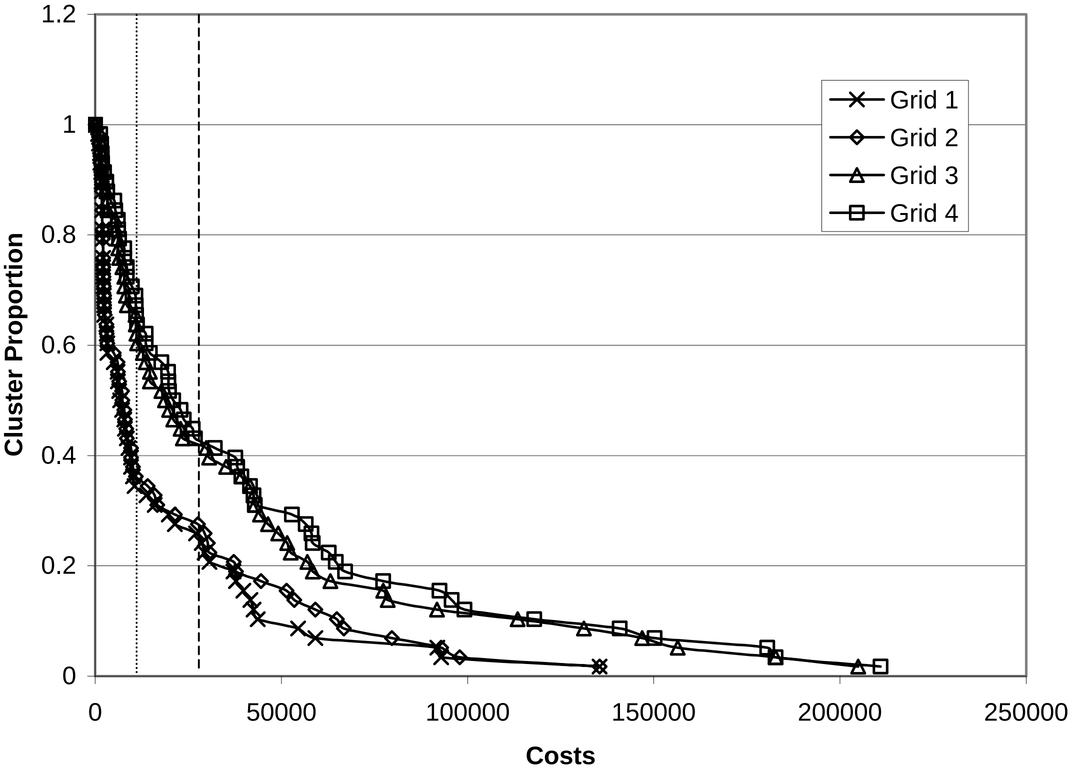

Figure 8.9. Cluster proportion (# clusters/ #patches) in relation to the costs for four different friction grids. #patches is equal to 59. Frictions values of the different land use variables of each grid have been set according to the values defined in Table 8.3. Linear barriers are not included in *Grid 1* and *2* whereas the are included in *Grid 3* and *4*. Critical thresholds for Grids 1 and 2 and Grids 3 and 4 are indicated by the dotted and dashed vertical lines, respectively.

Table 8.6. Characteristics of the paths used by subadult (M29, M24, M16 and M30) and adult lynx (M26) during their dispersal. Fate during dispersal: s = survived, d = died.

Lynx	Connection	Length (km)	*Costs*				Major Barriers	Fate
			Grid 1	*Grid 2*	*Grid 3*	*Grid 4*		
M29	North-western Swiss Alps/Rhone Valley	2.2	2,321	2,321	23,247	23,247	Crossed a river, a railway, stopped at the highway and turned back.	s
M26	North-western Swiss Alps/Central Alps	2.2	19,109	23,873	28,922	34,471	Crossed a railway, a highway and a medium river, covered a min. dist. of 600 m in arable land.	s
M24	North-western Swiss Alps/Plateau	18.8	22,619	22,619	120,672	208,774	Covered a min. dist. of 408 m in arable land, stopped at the highway and turned back.	s
M16	Jura/Plateau	20.9	286,115	398,427	390,343	487,663	Covered a min. dist. of 3,000 m in arable land, stopped at the highway and turned back, crossed three main roads	d
M30	North-western Swiss Alps/Plateau	60.6	233,397	416,007	387,574	608,358	Covered a min. dist. of 650 m in arable land, stopped at the highway and turned back, crossed one main roads	d

8.5. Discussion

The environmental variables came from the CORINE data set and from GEOSTAT for Switzerland. The later are only compatible with the second level of the CORINE Land Cover. Therefore, only 15 land use cover classes were available for the analyses. Some environmental layers have furthermore been removed because they were not continuous enough to be included in the ENFA analyses. Model predictions were quite good even with this limiting set of environmental predictors. Earlier investigations (Chapter 3) allowed us to select the most relevant variables. High accuracy and resolution of biophysical input maps are still considered the primary requirements for improving model predictions (Guisan & Zimmermann 2001). The problem of accuracy becomes even more important when models are developed for mountainous terrain with heterogeneous topography, where vegetation is distributed in mosaic-like pattern. In the future, an Alps-wide cooperation for the elaboration of cross boundary compatible biological relevant digital environmental variables should be established. Such digital environmental variables would also be useful for other large mammals. Additionally, analyses of recent satellite imaginaries in the GIS should be conducted if no adequate land use variables are available in digital form. Input data from distinct landscapes or habitats can considerably influence the results (Chapter 3). Although the model performs well in the Jura Mountains and the Swiss Alps as indicated by the significant positive Spearman rank coefficient, new validations should be conducted in the French, Italian and Austrian Alps once adequate lynx presence data are available.

Our results show furthermore that connectivity in the Alps is very sensitive to the friction values given to linear barriers, especially highways. The friction values of linear barriers in our study resulted from expert opinion, as only few empirical data were available to build statistical models (e.g. only four subadults radio-tracked in the north-western Swiss Alps left the prime habitat and moved through unsuitable habitat; three of them stopped at highways and turned back, Chapter 5). The limited spatial extension of linear barriers makes it particularly difficult to find appropriate statistical methods. New analytical tools should be developed in order to get more reliable estimates of friction values given to linear barriers, as connectivity largely depends upon it. Some studies (Ray, Lehmann & Joly 2002; Theobald 2002) used the maximal cost of dispersal defined as the maximal dispersal distance multiplied by the friction cost of the most favourable habitat (expressed in cost units per distance unit). When applying this definition to the dispersal data from the Jura Mountains and the north-western Swiss Alps by multiplying the respective maximal dispersal distances by 1,000, we obtain a maximal cost of dispersal of 97,000 and 56,000, respectively (maximal dispersal distance in the Jura Mountains: 97 km; in the north-western Swiss Alps: 56 km; Chapter 5). These costs are much smaller than the maximal cost of lynx moving outside their prime habitat (608,358; Table 8.7) and therefore would have led to an underestimation of the number of connected habitat patches. Only the future spread of the lynx population across the Alps will finally allow us to validate the predictions of our connectivity model.

Lynx were linked to shrubs and forest and avoided heterogeneous agricultural areas. The second and third factor accounted for more specialization mostly regarding distance to large and medium towns, heterogeneous agriculture areas, forest and open space frequencies. Both forest and shrubs are known to provide good shelter and food for roe deer and chamois, the staple prey of lynx in the Alps (Breitenmoser & Haller 1987).

The Alps consist of about 93,600 km^2 of suitable habitat and may host a viable population ranging from 1,000 up to 1,800 resident lynx. The estimation presented in the Pan-Alpine Conservation Strategy for the Lynx (PACS: Molinari-Jobin *et al*. 2003), which was rather conservative, was 90 to 120 resident lynx in three patches: the north-western Swiss Alps, the Valais and the central Swiss Alps (patch 6) and in the Tarvisiano and the Slovenian Alps (patch 7 and 8). Less than one eighth of the suitable habitat is occupied 30 years after the first re-introduction of lynx in the Alps, and there was no major change in the lynx distribution area in the past 10 years. Fragmentation through natural and artificial barriers is high and divides the Alps in 37 suitable habitat patches. According to the connectivity results of our model, lynx sub-populations once established in the different patches across the Alps would be connected through dispersal. The whole Alpine population could therefore ultimately be considered as a metapopulation according to the definition of Hanski & Simberloff (1997): “a group of interconnected populations that function as unit”.

Although most patches seemed to be connected, experience suggests that only few dispersers will cross unsuitable areas and barriers such as (fenced) highways. During a peak of the lynx population in the north-western Swiss Alps from 1997-2000, only four out of fourteen radio-tagged subadult lynx, all males, went beyond the edge of suitable habitat, but only one crossed a major barrier successfully (Chapter 5). Subadult lynx showed furthermore a rather conservative dispersal behaviour and tended to colonise areas close to occupied home ranges (Chapter 4). Peak lynx densities, which may provide an increased number of potential dispersers, are not likely to exist over prolonged periods. The combination of prey depression, increased attacks on livestock and emerging conflicts with hunters and sheep breeders result in a decreasing lynx abundance after a few year only (Zimmermann *et al*. 2004). Furthermore, there is good evidence that high lynx density is not correlated with a corresponding high dispersal rate (Chapter 5).

The Alps are connected to the Dinaric, the Jura Mountains, and Bohemian-Bavarian populations although only weakly to the last one. The Chartreuse (patch no. 16 in Fig. 8.7) is more connected to the Jura Mountains than to the remaining Alps. This is confirmed by the recent increase of signs of presence resulting from individuals that presumably migrated from the Jura Mountains (P. Stahl & J.M. Vandel, pers. comm.). Exchange between established neighbouring populations will likely be enough to maintain (sub)populations and genetic exchange, as resident adult lynx, especially males, show a higher propensity to cross barriers than subadults, particularly during mating season (Breitenmoser-Würsten *et al*. 2001; Ryser *et al*. 2004). The occasional crossing of barriers however seems not to be sufficient to initiate a new subpopulation in a still empty patch. To found a new population, several individuals arranged according to the specific land tenure system are needed. The Alps are the largest potential European population outside Fennoscandia and Russia and occupy a central position among the western-central European populations. They therefore play a key role for the maintenance of the metapopulation-compound and the recovery of the lynx in this part of the world.

8.5.1. Management and conservation implications

The main goal of the Pan-Alpine Conservation Strategy for the Lynx (PACS: Molinari-Jobin *et al*. 2003) is to re-establish and maintain, in co-existence with people, a vital lynx population covering the whole of the Alpine arc. Habitat restoration is of little concern for the conservation of the Eurasian lynx as forest and shrubs have continuously increased since the eradication of the species at the beginning of the 20 century, and seem to further increase as a consequence of the economic changes in the Alpine areas. Prey base is not a limiting factor either since roe deer and chamois, lynx’s main prey, have recolonized almost all suitable habitat in the Alps and are more abundant than ever.

Protected areas have been a central element in the conservation strategy for several large carnivores in Africa (Mills 1991), and most notably also for the tiger in India (Seidensticker 1997). The large home ranges of large carnivores make it difficult to maintain viable population only within isolated protected areas (Nowell & Jackson 1996). National and regional parks represent 10,146 km^2 or 11% of the suitable habitat in the Alps, and there are very few single areas that are large enough to host more than a few lynx considering the reported home range size (74–425 km^2 for males and 39–225 km^2 for females; 100% Minimum Convex Polygon; Haller & Breitenmoser 1986, Breitenmoser-Würsten *et al*. 2001). Therefore, protected areas play only a limited role in the conservation of lynx in the Alps, and lynx will always be a source of potential conflict with human activities, such as hunting and livestock breeding.

According to the PACS, the vitality of the Swiss and Slovenian populations should be maintained and must be helped to expand and to join through colonisation of the area in between (Austrian Alps, Germany, Italy and Liechtenstein). As an alternative to spontaneous dispersal, translocation of individual across the barriers should be considered. Such "management reproducing dispersal" (Macdonald, Mace & Rushton 2002) may be necessary when natural colonisation is hindered in a more and more human dominated landscape (Woodroffe & Ginsberg 2000). Patches 2, 3 and 8 (Fig. 8.7) may host some 45–54, 117–140 and 123–147 resident lynx, respectively, and have a central position between the Swiss and Slovenian population. They are furthermore connected to a large number of adjacent patches of which some are already occupied by lynx. This makes them particularly suitable for further re-introductions in order to join the Swiss and the Slovenian populations. Surplus individuals should be caught in high density (sub)populations to avoid the source (sub)populations to be weaken. This would accelerate the desired spread of the population and allow to locally reduce the "surplus" lynx. In addition, this helps reducing the conflicts with local people. For genetic reasons – all the re-introduced populations were founded with few and often close relatives (Breitenmoser *et al*. 2001) – individuals may furthermore be translocated from different source populations (e.g. Jura Mountains, Carpathians Mountains) to improve the genetic variability. Such a strategy would allow the lynx to settle all suitable habitat. These new releases should follow international guidelines (Council of Europe, IUCN/SSC Re-introduction specialist group 1998), have the support of the regional authorities, and involve local interest groups.

Our connectivity model furthermore provides the possibility to evaluate the impact of land use scenarios on landscapes (Vuillemier & Prélaz-Droux 2002) and assess management options. The model for instance allows planning an ecological network in order to improve the connections between different patches within the Alps (e.g. between patches 2, 3, and 8) and to neighbouring populations. Another possible application is the testing of management concepts such as zoning (Linnell *et al*. 1996), where either predators or livestock are excluded from certain areas. Such concepts basically change the distribution of "suitable" habitat and fragmentation of the whole area. This modelling approach is not restricted to lynx and can be extended to other large mammals to restore habitat, improve connectivity, and to develop conservation and management concepts.

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Chapter 9. General conclusions and perspectives

The analyses and results provided new insight into Eurasian lynx dispersal and habitat use, and allowed to predict potential species distribution over different central European mountain ranges. Some results have important consequences on the management of the species as well as for the modelling of population dynamics and expansion. The most relevant results and future perspectives are highlighted and discussed in the underlying sections.

9.1. Habitat suitability analyses

Management and conservation measures are often proposed but cannot be implemented. One reason is that (i) the indicator variables cannot be readily identified as they are often neither well defined nor measured adequately, then (ii) it might be too expensive to sample them over the whole area, and finally (iii) the chosen statistical methods do not allow identifying the most critical variables. Our habitat suitability analyses overcome these problems by providing easily identified environmental factors (e.g. frequency of forest, shrubs, pastures in mountainous areas, roads, intensive agricultural areas, fringe length, and population density; Chapters 2, 3, 7 and 8), which can be monitored in a cost efficient way allowing appropriate management actions to be conducted. Many applications can be derived from habitat suitability maps (HS) as for example (1) to predict the area that could potentially be invaded by an expanding species (Chapters 4, 5, 6 and 8); (2) to choose the best location for re-introductions (Chapter 8); (3) to improve the monitoring of elusive species by optimising the searching effort in areas with a high presence probability; (4) to estimate the potential size of a population based on the knowledge of the species’ land tenure system (Chapters 4 and 8); and (5) to analyse the effect of various management scenarios (habitat restoration, deforestation, road construction) on habitat suitability. The HS can furthermore be used as input maps for other models. Patches of suitable habitat can for instant be derived from habitat suitability maps and used as source patches in cost-distance analyses in the GIS to infer the ecological distances (Chapters 7 and 8) or to parameterise dynamical dispersal and population models (Hirzel 2001; Schadt 2002; Patthey 2003; Kramer-Schadt *et al*. 2004).

High accuracy and resolution of ecogeographical input maps are still considered the primary requirements for improving model predictions. The problem of accuracy becomes even more pronounced when models are developed for mountainous terrain with heterogeneous topography, where vegetation is distributed in a mosaic-like pattern (Guisan & Zimmermann 2000). Progress in GIS-modelling and in remote sensing in the past years may allow to obtain more accurate information.

ENFA analysis – a profile method that needs only presence data – was used to predict lynx habitat suitability over large and heterogeneous areas in Switzerland and across the whole Alps. Hirzel *et al*. (2001), using a virtual species with known absences in a real landscape, have shown that ENFA performs better than GLM in the case of invading species. GLM on the other hand performs significantly better than ENFA when estimating habitat suitability in an overabundance scenario i.e. the species occupy all optimal habitats but occupied secondary habitats at lower probabilities (Hirzel *et al*. 2001; Brotons *et al*. 2004). In such a scenario, absence data are useful to enhance model calibration. New techniques such as GLM analyses with ENFA-weighted pseudo-absences are a possible way to enhance the quality of GLM-based potential distributions for endangered species that have a limited spatial extension and where distribution data are scarce (Engler *et al*. 2003). It should not be concluded that one method performs always better than the other. The performance of each statistical method depends on the species modelled, on the environmental predictors as well as on the spatial grain considered (Engler *et al*. 2003). Lynx may serve as an excellent model for further investigations on model performance.

9.2. Dispersal

Both sexes in our lynx field study dispersed and our data did not reveal any male biased dispersal rate and distance as predicted in mammals (Greenwood 1980). We furthermore did not observe any body condition dependent dispersal in lynx. However, we have to be cautious as the residual value of the ratio of log body mass on log body length obtained in a reduced major axis regression may not be the appropriate measure of body condition. Disperser may encounter aggression from conspecifics (see Chapter 2) when they try to establish themselves in new territories (Holekamp & Smale 1998; Nunes *et al*. 1998). Thus, the acquisition of a sufficiently robust physical condition prior to natal dispersal probably plays a critical role in determining the timing and, perhaps, other aspects of natal dispersal by juvenile animals (Dufty & Belthoff 2001). Body condition dependent dispersal has been reported for different species, mostly birds (e.g. Ellsworth & Belthoff 1999; Mori & George 1978; Nilsson & Smith 1985).

Subadults that dispersed for long distances through unfamiliar landscape did generally not survive their first year of independence (Chapters 4 and 5). The process of searching for a suitable new habitat involves mortality costs, as a result of accidents, diseases, or starvation. Dispersal directions and distances were shaped by the surrounding habitat, topography, as well as linear barriers (e.g. highways). These outcomes have consequences for the calibration of individual based dispersal models: not only road mortality should be considered (see Kramer-Schadt *et al*. 2004), but habitat-type specific mortalities as well as the effect of linear barriers (e.g. highways) should furthermore be included.

Delayed dispersal was observed in the high lynx density situation and our results suggest furthermore that dispersal in lynx may be negatively density dependent. In our studies, few individuals moved for long distances, and the distances in the high density population were small compared to the few existing dispersal studies on Eurasian lynx. Many of the most important conservation consequences of dispersal depend on rates of long-distance movement, and on dispersal between rather than within populations (Waser *et al*. 2001). Such data are difficult to collect particularly in the case of re-introduced populations, where only few individuals are present. There are furthermore good reasons to suppose that the dispersal process between extant populations may look different compared to the colonization of unsettled areas (Chapter 4). The decision to settle down is based on the individual assessment of living space, which depends on intrinsic habitat quality perception and social requirements (Danchin *et al*. 2001). All subadult lynx settled in or close to areas already occupied by conspecifics. Thus, information on the presence of resident lynx is likely to be particularly valuable for the choice to settle, because it can be gathered at low costs and is reliable.

If, in an adaptive management approach, measures taken would be planned and carried out as real field experiments, they could provide opportunities to test hypotheses. This may e.g. allow to refine the question of density dependence in lynx dispersal as well as the respective importance of the population status, habitat, and landscape features (Chapters 4 and 5). Radio-telemetry studies in experimentally managed populations (removal of individuals through translocations or harvest) may for example allow to get more insight on the effect of density on dispersal.

For a small-scale assessment, we are presently not only limited through the accuracy and resolution of ecogeographical maps available, but also the precision of lynx field data. Lynx are mainly active at night (Bernhart 1990) and often move through difficult terrain, making it difficult to locate them accurately by means of VHF radio-telemetry. In the future, new generations of GPS/VHF collars may offer the possibility to track the animals around the clock at a very high precision. Such data would help to improve our qualitative and quantitative knowledge on animal movements and habitat use, and the significance of linear barriers (e.g. highways).

An indirect measure of dispersal distance may be provided by correlating pairwise individual genetic and spatial distances in relation with an estimate of the effective population size studied (e.g. Rousset 2000; Sumner *et al*. 2001, Wandeler in prep.) In addition, population genetic data can detect sex bias (Goudet *et al*. 2002) or even reveal some information on the direction of dispersal (Wandeler in prep.). Yet, such genetic methods have also their limitations based on numerous assumptions (see Rousset 2001 for a review). In addition, different genetic methods can give different results (Ross 2001). Furthermore, inferring dispersal patterns from genetic data might only be useful when for a given species good field data and further knowledge on its natural history are available (Ross 2001). Finally, numerous well-characterized and polymorphic genetic markers alongside an adequate sample size are essential. Regarding the Eurasian lynx, these conditions are fulfilled – good knowledge of the biology of the species is available and polymorphic genetic markers have currently been developed and tested (Breitenmoser-Würsten *et al*. 2003) – opening the door to a new field of investigations. These analyses, however can be quite costly as these re-introduced populations have a low genetic variability, and, as consequence, many genetic markers are needed.

9.3. Patch and network analyses

I provided a methodology to define suitable habitat patches based on species home range and habitat requirements. This allowed us to estimate the population size in different mountain ranges. The method is not specific for the Eurasian lynx and can thus be extended to other territorial species. The least cost path analysis in the GIS showed that the simulation of diffusive dispersal through the graph theory allows a straightforward design of ecological networks according to animal movement constraints in a fragmented landscape (Chapters 7 and 8). Some patches are more important than others, not because of size or habitat quality, but because of the position of a patch within the network. New approaches allowing to quantify more accurately landscape connectivity and the relative importance of each patch are currently being developed (e.g. Theobald 2002; Jordán 2003). The methodology proposed by Jordán (2003) takes into account both structure and function of the patches and corridors, respectively, and allows ranking the ecological significance of each patch. However, these static methods have some limitations. There is for example no obvious reason supposing that movement pathways are closely related to the theoretical optimum. Different pathways through the landscape may be feasible, producing variation among individuals in net dispersal distance (Wiens 2001).

A quite promising approach consist in modelling interpopulation connectivity through spatially explicit individual based models (DeAngelis & Gross 1992; Vuillemier 2003; Kramer-Schadt *et al.* 2004). Such models have several clear advantages: among others they force one to develop explicit hypothesis, to organize existing knowledge, and to estimate values for unknown parameters. Sensitivity analyses can furthermore be conducted in order to reveal which parameters are likely to be important and which relatively insignificant, and how much complexity and details had to be considered to understand dispersal and its consequences. However, there are also disadvantages and constraints to the application of such type of models. The results – as for any model – are largely a consequence of the model structure and assumptions, and a poorly structured or incomplete model will produce only incomplete or poor insights (Wiens 2001). In lynx for example, modelling results can lead to misleading conclusions if one failed to incorporate the effects of linear barriers or mixed up two different movement patterns (e.g. movement during dispersal, movement in temporary home ranges) during model calibration. Therefore, good knowledge and understanding of the dispersal process is needed before starting the modelling process. These kind of models are data-hungry and may require quantification of many parameters to describe the structure of landscapes and the responses of the animal to them. Furthermore, they may be especially sensitive to errors in the estimation of dispersal rates and survival (Ruckelshaus *et al.* 1997, 1999; South 1999), which may be strongly influenced by the landscape matrix disperser encounter. Besides, the lack of data does often not enable to validate such models with an independent data set in a new area. The results can therefore not be extrapolated to other areas and can only be used as qualitative hypothesis. With improved ecogeographical data sets and an advanced understanding of dispersal from field observations, spatially explicit individual based models will increasingly allow to develop realistic and applicable models.

Data on genetic differentiation has lately been used to validate ecological distances between habitat patches (e.g. Vuillemier 2003). Nevertheless, this approach is less suitable when applied on recently re-introduced populations. In this case, the observed level of genetic differentiation does not only reflect dispersal patterns alone but also genetic founder effects induced by the re-location. However, genetic data might be used in the future, when the natural expansion of the population has advanced sufficiently over time to wear any founder effects and thus resulting in a mutation-drift equilibrium.

Habitat suitability is not black or white, it is rather changing gradually and it is sometimes difficult to set an adequate cut-off value above which the habitat is suitable. This problem has particularly been encountered in the Alps, where large patches of suitable habitat are connected through small ribbons of suitable habitat. Analyses of the connectivity considering source patches within a matrix of unsuitable habitat might not be the ideal solution. In such cases a cellular automata model like the one developed by Hirzel (2001), merging demography and landscape information in a lattice of identical hexagonal cells, might be more appropriate. Beside spatial aspects this approach would allow to treat temporal aspects like for example when and how long a species would be spreading.

9.4. Conservation and management implications

Evidence is increasing that dispersal rates are negatively density-dependent (Lambin *et al.* 2001; Ims & Hjermann 2001). This may also be true for lynx (Chapter 5) as high lynx densities such as the one observed in the NWSA did not lead to the colonisation of unsettled areas. Peak lynx density lead however to conflicts with local people, and did not prevail long enough to allow for the colonisation of unsettled areas. It is impossible to maintain large carnivore populations in the present context in a cultivated landscape without a management offering compromises between conservation and exploitation (Breitenmoser & Breitenmoser-Würsten 2001). In the situation of the Alps, a metapopulation management in the form of translocating lynx from one patch to another may be an acceptable conservation tool (Chapters 5, 7 and 8). Such a management, reproducing dispersal, may be necessary when natural colonisation is hindered in a more and more human dominated landscapes

(Macdonald & Johnson 2001). The reduction of "surplus lynx" would also respect the needs, opinions, and feelings of local people who are not in favour of the presence of lynx (Breitenmoser *et al*. 1999). As our results suggest that lynx may use the presence of conspecifics as an indication for a suitable area to settle, translocations may in some circumstances increase the number of individuals that will later on settle within the given patch. Danchin *et al.* (2001) suggest to use strategically placed captive individuals, in order to increase aggregation in suitable habitats.

Habitat corridors have become popular in land use planning and conservation management despite of being supported by few empirical data only and being subject to controversial debates (Simberloff & Cox 1987; Noss 1987; Simberloff *et al*. 1992). Besides, it is very difficult to obtain data on corridor use (Hobbs 1992), and appropriate field experiments to reveal the biological importance of corridors are intensive and expensive (Inglis & Underwood 1992). One can argue that the maintenance of existing linkages should be an important point in any conservation plan as it is easier to protect them now than to restore them in the future. Riparian vegetation may serve as natural corridors as shown by the dispersal path of one subadult male (Chapter 5). Connectivity may be enhanced if corridors are established in the direction of predominant ridgelines or other landscape level features (e.g. forests, riparian vegetation) which may aid or direct dispersing lynx.

9.4.1. Concluding remarks

The work of the wildlife biologist usually ends with a list of general management implications telling resource managers what to do. However, these suggestions are only rarely implemented. One reason is probably that these implications are seldom providing instructions on how these goals can be reached or how to determine whether they have been reached (Morrison *et al*. 1998). Another reason might be that results cannot be adequately converted into management practice (e.g. wildlife researchers are usually preoccupied generating the best P-value rather than by determining the best result in relation to possible implementations in the field). Many wildlife biologists think that the implementation of their recommendations does not belong to their responsibility and that any failure to incorporate them is the fault of the managers. However, wildlife biologists can play a crucial role in developing adaptive management experiments to help managers learning by trial. The case of the lynx in Switzerland is so far a good example of a fruitful cooperation between wildlife biologists, managers, decision makers and politicians in an adaptive management process. This cooperation resulted in a Lynx Management Plan which was implemented in 2000 and updated in 2004 to give the cantons directives on how to handle lynx-related problems (SAEFL 2000, 2004). This plan did not end up in a drawer; almost all management implications and recommendations have currently been put into practice, including the translocation of lynx into unsettled areas. This would not have been possible without a strong political will, and a compromise between practical requirements and scientific understanding.

9.5. References

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