Potential distribution and population size of the Eurasian lynx Lynx lynx in the jura Mountains and possible corridors to adjacent ranges

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Fridolin Zimmermann & Urs Breitenmoser

To estimate the potential population size of the Eurasian lynx *Lynx lynx* in the Jura Mountains and to assess possible corridors between this population and adjacent areas (the Vosges Mountains, the Black Forest and the 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 of 74-101 individuals and 51-79 individuals when continuous habitat patches of < 50 km^2 are disregarded. The Jura population lies within the range of a viable population if only demographic aspects are taken into account, but is rather small from a genetic point of view. Genetic viability would be assured if the Jura lynx population were part of a larger metapopulation. Potential corridors exist from the Jura Mountains to the Vosges Mountains, the Black Forest and the Alps (Chartreuse and Salève, respectively). The length of these corridors range within 7.3-37.3 km, and their costs are all within the range of radio-collared lynx roaming outside their prime habitat. The best corridor leads south to the Chartreuse, an isolated part of the French Alps, which is itself connected to the rest of the Alps by two corridors of 4.5 and 6.5 km, respectively. 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 species has not yet completely occupied this area. 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 good surveillance would allow the necessary conservation measures to be initiated in time.

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Eurasian lynx *Lynx lynx* were reintroduced to the Swiss Alps and the Swiss Jura Mountains in the 1970s (Breitenmoser et al. 1998). Although the Swiss reintroductions were considered rare examples of successful translocations of large predators (Yalden 1993), these still small populations cannot yet be considered viable. The expansion is, from an anthropogenic point of view, very slow; the population in the Jura Mountains has, after almost 30 years, not yet occupied the entire mountain range (Capt 2007). The reasons for the slow spread may include ecological, anthropogenic and intrinsic (demographic or genetic) factors. For the conservation of a large carnivore species in a limited living space, such as in the Jura Mountains which extend over approximately 14,000 km^2 (Breitenmoser et al. 2007), 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 to 1) estimate the population size based on knowledge of the land tenure system of resident lynx (Breitenmoser et al. 1993, Breitenmoser-Würsten et al. 2007b), and 2) assess possible corridors between the Jura Mountains and adjacent 'lynx areas' (the Vosges Mountains, the Black Forest and the Alps).

Material and methods

Study area
Our study was performed in the Jura Mountains, a secondary limestone mountain chain forming the northwestern border between Switzerland and France (Fig. 1) in which altitude varies from 372 m a.s.l. (Lake of Geneva) to 1,718 m a.s.l. (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. 2007). Roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* are the main prey of lynx in the Jura Mountains (Jobin et al. 2000, Molinari-Jobin et al. 2002). The main sheep *Ovis aries* breeding area is located in France (Stahl et al. 2001), along the southwestern foothills of the mountain chain, at elevations of 400-700 m a.s.l.

Data sets
We used a total of 6,282 radio fixes accurate to either the ha or the km^2 from 11 resident lynx followed during 1988-1998 to generate and/or validate the model. The response variable was presence/absence of lynx in each 1×1 km cell. Lynx was con-
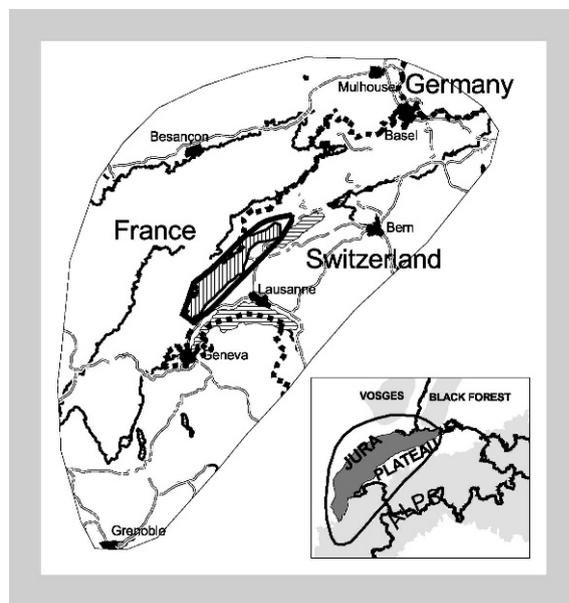
Figure 1. Reference areas in the Jura Mountains. The polygon in the large map shows the intensive study area of the 'Swiss Lynx Project' (SLP) in the Swiss part of the Jura Mountains, where the radio fixes for the calibration of the model were obtained. Vertically hatched areas were used for the calibration of 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 inserted map) according to the definition in Breitenmoser et al. 2007. Horizontally hatched areas show lakes, simple lines show rivers, double lines show highways, broken lines show international borders, and black patches show major human agglomerations.

sidered to be present in each cell containing ≥ 1 telemetry fix. A data set of highly reliable monitoring records (Capt 2007), independent from the radio-telemetry data, and presence data from two subadult female lynx (F_{NADA}, F_{WINA}; Swiss Lynx Project, unpubl. data) dispersing to France, were subsequently used to evaluate the model.

The 13 environmental predictors (Table 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 databases had an accuracy of 250×250 m and approximately 1×1 km (grid spacing 30-arc seconds), respectively. Both were in digital form and ready to be analysed using the GIS Arc-View (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 250×250 m information and the 1×1 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; see Table 1).

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 General Linear Models (GLM) were calibrated in the S-Plus software (Mathsoft

Table 1. The 13 predictors used in the logistic regression analysis. The sources are: CORINE LAND COVER database (ETC/LC 1997; resolution 250×250 m) and GTOPO30 (EROS Data Center 1993; resolution 1×1 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	Metre	GTOPO30
13) Slope	Degree	GTOPO30

Inc.) by using a binomial distribution and a stepwise variable selection procedure. Because of the high sensitivity of the stepwise process, which eliminates part of the input predictors and retains only the most relevant input predictors, to the input order of the predictors, we tested several sequences and retained the model explaining the highest proportion of variance.

Potential distribution and population size

The potential distribution area of lynx was estimated for each threshold value ranging within 0-1. In the first step, we considered every raster of the grid. Consecutive areas of < 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 such that false presence predictions and false absence predictions had the same probability of occurring (P_{fair}). In a second approach (here called the 'ratio method'), we plotted the ratio of the area of lynx distribution predicted by the model to the 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} and F_{WINA}) dispersing to France to estimate the optimistic cut of value ($Thres_{opt}$). This value was fixed in such 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. 2007b) 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 (Zimmermann 2004). Molinari-Jobin et al. (2002) estimated a number of six adults (four females and two

males) and one subadult lynx in a study area of 710 km^2 (see Fig. 1). All estimations of the population size were 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 et al. 2007).

Corridors

The land use and land cover type at any given location influences the relative ease or difficulty with which a species is able 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 (Zimmermann 2004). The higher the value, the higher the resistance to movements. Lynx principally used vegetation cover when roaming through the landscape and never moved > 400-500 m away from the closest vegetation cover. Several observations showed that lynx swam across rivers up to 30 m wide (P. Molinari, pers. comm.) and still waters up to 200 m wide (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 arbitrarily set 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 and 1 to forests and shrubs. We then calculated the distance based on matrix quality using the cost-distance extension in the GIS ArcView, where the patches resulting from the distribution model with the threshold fixed at 0.35 (P$_{opt}$) considering only uninterrupted areas of ≥ 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-collared lynx when roaming outside their prime habitat.

Results

Distribution model

For our final model, four out of 13 predictors were selected. 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:

$$
\begin{aligned}
LP = \ & {-}4.5391 + (0.0152 \times \text{shrub}) \\
& + (0.0016 \times \text{altitude}) \\
& + (0.1337 \times \text{declivity}) \\
& + (0.0472 \times \text{forest})
\end{aligned}
$$

where each coefficient is multiplied with its related predictor variable (e.g. shrub; Guisan et al. 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-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 exactly fitted the curve of percent presence cells within the main study area, but the classification of the presence cells of the two subadult females were less accurate (Fig. 2). For the threshold fixed at 0.5 (see Fig. 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%).
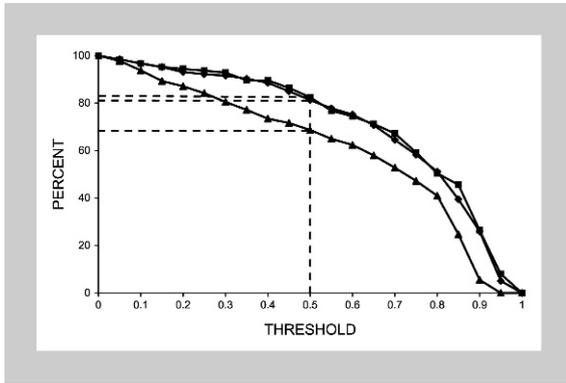
Figure 2. Percentage of correctly classified cells in relation to the threshold. The two upper curves show presence cells in the main study area (◆) and monitoring data from the Swiss Jura Mountains (■). The ▲ shows presence data from two subadult females (F_{NADA} and, F_{WINA}) that dispersed towards France.

Potential distribution and population size

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 of the area is considered good lynx habitat) is shown in Figure 3. In the optimistic approach (P_{opt}; maximum proportion of correctly classified cases), the threshold was 0.35 and in the pessimistic approach it was 0.54 (P_{fair}; same probability for false presence and false absence predictions; Fig. 4). With the threshold of 0.35, 89.6% (monitoring data Swiss Jura), 90.2% (telemetry data study area), and 77.1% (dispersing females) of presence cells were correctly classified. 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 were
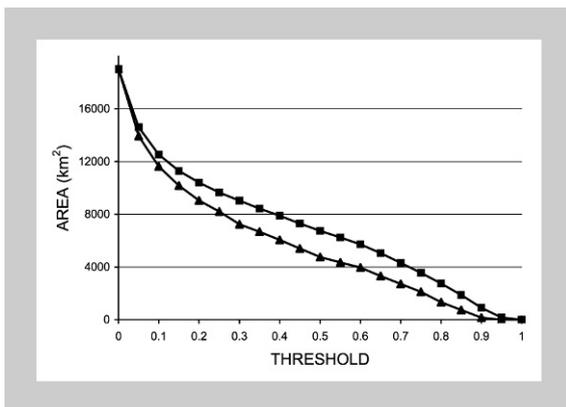

Figure 3. Potential lynx distribution area (in km^2) in relation to the threshold value. In the upper curve (■), every cell was considered, whereas in the lower curve (▲), only consecutive areas of ≥ 50 km^2 were considered.
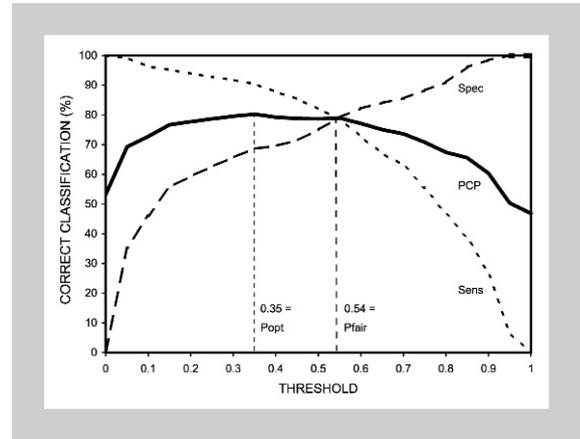

Figure 4. Estimation of the cut-off values based on P_{opt} (0.35) and P_{fair} (0.54). Percentage of correct prognoses (PCP) of the total model, sensitivity (Sens) and specificity (Spec) classifications are shown in relation to the threshold.

used instead of presence cells. 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.

The threshold values of 0.35 and 0.54 (see Fig. 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 of ≥ 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. 5). From the lynx followed by means of radio-telemetry in the study area (Breitenmoser et al. 1993, Breitenmoser-Würsten et al. 2007b), 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 of ≥ 50 km^2.

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 permanent lynx occurrence (Vandel & Stahl 2005), whereas from the Black Forest, only occasional observations of lynx of unknown origin have been reported (T. Kaphegyi, pers. comm.). Four possible corridors (A, B, C, D in Fig. 6 and Table 2) connect the Jura Mountains to the adja-
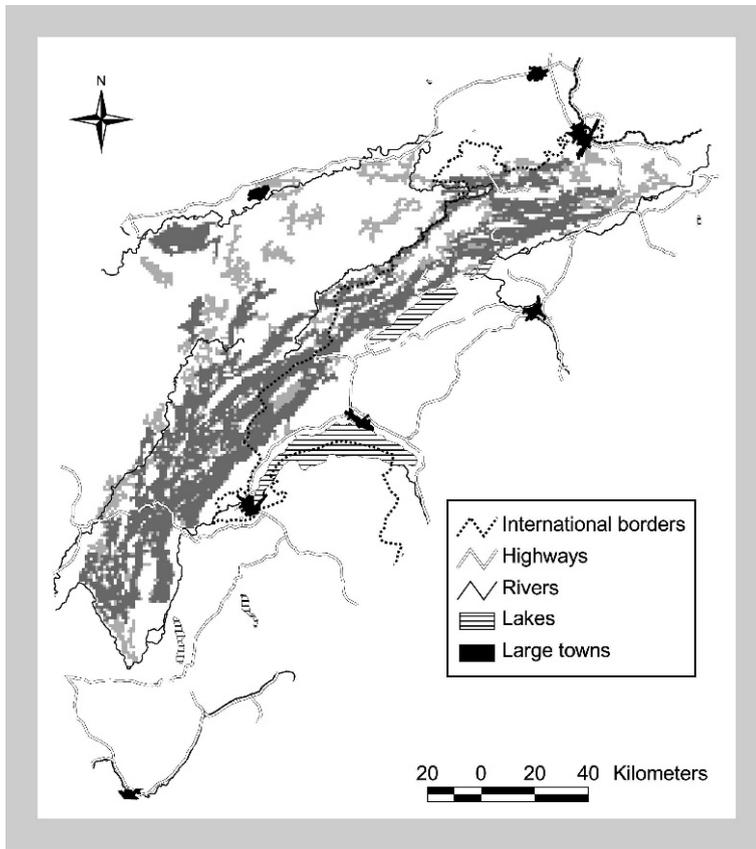
Figure 5. Optimistic and pessimistic estimation of good lynx habitat in the Jura Mountains considering all continuous areas of ≥ 50 km^2. Dark grey shows the pessimistic estimation (P$_{fair}$ threshold 0.54) and light plus dark grey show the optimistic estimation (P$_{opt}$ threshold 0.35).

cent ranges. Corridor A connects the Jura Mountains with the Vosges Mountains. This 23.9-km long corridor crosses 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 in corridor B are the river Rhine, three main roads and the proximity to human settlements (see Fig. 6 and Table 2). 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 in Fig. 6 and Table 2). Two other connections exist between the Jura Mountains and the French Alps (Corridors C1-C2 and C1-C3 in Fig. 6 and Table 2). Corridor C1 connects the Jura Mountains to the Salève, a 5 km^2 wooded mount south of Geneva (see Fig. 6 and Table 2). 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; see Fig. 6 and Table 2). 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 (see Fig. 6 and Table 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 44/km and 62/km, respectively. Only 25% of corridor E and 57% 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, and one was followed in the Jura Mountains. One dispersing young male, who spent most of his 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 his prime habitat (< 20% of the corridor was within the forest and shrub category) with a total cost of 1,163 (55.6/km), but did not survive (Zimmermann & Breitenmoser 2002). The
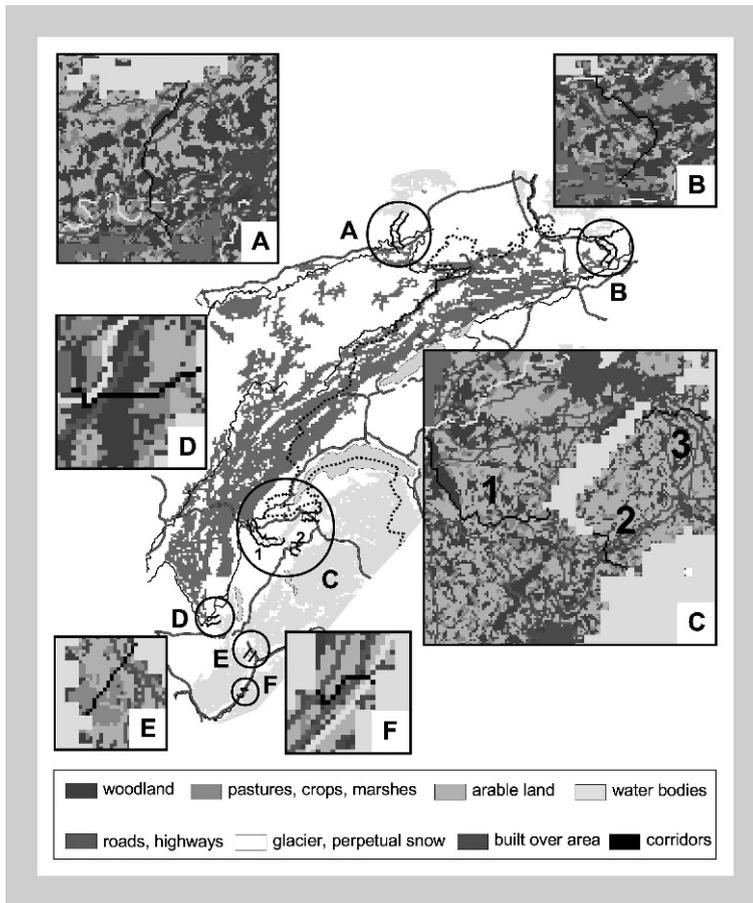
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Figure 6. Potential corridors between the Jura Mountains and the adjoining areas Vosges Mountains (A), Black Forest (B) and French Alps (C-F). Continuous areas of ≥ 50 km^2 with habitat probability greater than 0.35 (P_{opt}) are shown in dark grey for the Jura Mountains and light grey for the adjacent areas (1 × 1 km grid). The 250 × 250 m grid in the small maps shows the environmental variable categories used for the computation of the friction grid and the resulting potential corridors.

other three were successful, i.e. surviving, dispersers using corridors 18.8 (total costs 264; average cost 14/km), 60.6 (828; 13.7/km), and 2.2 km long (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 within 40-75.9%. One lynx crossed a medium river as wide as 30 m. On the other hand, highways were important barriers to dispersal. Three out of the four dispersing lynx did not cross high-

ways and turned back after they spent a few days in their vicinity (Breitenmoser-Würsten et al. 2001b; Zimmermann 2004). One adult male, however, crossed 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, four times. 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

Table 2. Characteristics of the corridors from the Jura Mountains to the Black Forest, the French Alps and the Vosges Mountains. No refers to the number of detail map in Figure 6. Costs represent 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$_{Chartreuse}$/Alps	6.5	286	44.0	One highway, passes close to human settlements
F	Alps$_{Chartreuse}$/Alps	4.5	279	62.0	One highway, 500 m in arable land

the costs of the corridors A-F (see Fig. 6 and Tables 2 and 3) or even more expensive.

Discussion

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. 2007) to be incorporated into a GIS analysis. However, as ungulate distribution is habitat dependent by itself, we argue that the presence/absence data of lynx also reflect prey availability. It must also be stressed that ungulate abundance was not a limiting factor during our study period (Jobin et al. 2000, Stahl et al. 2001, Molinari-Jobin et al. 2002, 2007). In our model, we assume that disturbances are reflected by variables describing land use (e.g. urban fabric, industrial, artificial areas in Table 1).

Top predators are generally not very sensitive to a particular habitat structure, vegetation or ecosystem type (Mladenoff et al. 1995). However, 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. 2001b). Radio-tagged lynx stayed close to human settlements or main roads if they were able to find secure day resting places. It was not uncommon to locate lynx close to logging sites, 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 2007) are comparably well classified as the presence cells in the study area, from where data have been used to calibrate and validate our model (see Fig. 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. 1) and extrapolated over the rest of the mountain range, which, however, have the same habitat characteristics as the reference area.

Present distribution and viability of the population

Our model predicts that the breeding population in the Jura Mountains ranges within 74-101 individuals and within 51-79 individuals when continuous areas of < 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 estimate 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. 2007b: 0.7-0.8 individual/km^2, or 1.0-1.1 individual/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. 5), but also in the 'optimistic' areas (light grey area in Fig. 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 sub-adult 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. 2007b).

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 1987), 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, Sæther et al. (1998) estimated the minimum viable size for the brown bear *Ursus arctos* 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 2007), and preliminary genetic analysis (Breitenmoser-Würsten et al. 2001a) revealed that the population underwent genetic drift and has reduced genetic variability compared to the Slovakian source population. Genetic viability would be guaranteed if the Jura population were part of a larger metapopulation, allowing the exchange of individuals between neighbouring subpopulations. 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 (2007), we estimate that 92% of the potential distribution area in the Jura Mountains is actually occupied by lynx. The not yet occupied parts, however, lie in the north, where the corridors to the Vosges and the Black Forest originate. The recolonisation of an area by a large mammal species seems generally to be a long-lasting process, which requires several decades if not centuries. From an anthropogenic point of view, the spread of the Jura population might be slow, but it is probably not much different from other recolonisations, e.g. as observed in Scandinavia. Based on our habitat modelling approach we conclude that habitat fragmentation in the Jura Mountains plays only a marginal role compared to anthropogenic factors (e.g. illegal killing; see Breitenmoser-Würsten et al. 2007a) in regard to the spatial expansion of the population.

Lynx have been reintroduced in the Vosges Mountains (Stahl & Vandel 2002). According to Vandel & Stahl (2005), the southern edge of the population in the Vosges Mountains is about 40 km away 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. 6). Stahl & Vandel (2001) assume that lynx signs found in the Chartreuse ac-

tually came from immigrating lynx from the Jura Mountains. The Chartreuse occurrence, however, has so far been isolated from the Alpine lynx population. These corridors may be used often enough to ensure sufficient genetic exchange between existing populations, but such occasional migrations may seldom allow the initial recolonisation of unsettled areas. As an alternative to the spontaneous migration of lynx between adjacent subpopulations, 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, Ryser et al. 2004). If at some time the neighbouring areas of the Alps, the Jura and the Vosges Mountains and the Black Forest (the single subpopulations) will be occupied, the probability that individuals would disperse through the existing corridors and hence guarantee genetic exchange would increase considerably.

Conclusions

Our habitat and distribution model, together with MVP and metapopulation considerations, can help to develop concepts for the conservation and the management of the lynx population in the Jura Mountains and the adjacent ranges. In practice, the results of our model suggest that the size of the Jura population will always be in the lower range of viability. As a consequence, 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 subpopulations 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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