

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

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The lynx (*Lynx lynx*) populations of western and southern Europe disappeared during the eighteenth and nineteenth centuries as a consequence of direct persecution, alteration of the ecosystem (forest destruction and expansion of cultivated land), and 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 et al. 1998). Although the Swiss reintroductions 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 reintroduction programs.

The purpose of this study is to assess small-scale habitat variables and their importance to lynx recolonization 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 and Zimmermann [2000] for a review). The model was built using data from adult, resident lynx that were followed by means of radiotelemetry 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.

Study Area

The study was performed in the Jura Mountains, a secondary limestone mountain chain forming the northwestern border of Switzerland with France (Fig. 58.1). The altitude varies from 372 meters (Lake of Geneva) to 1,679 meters (Mont Tendre). The main study area (680 square kilometers) 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

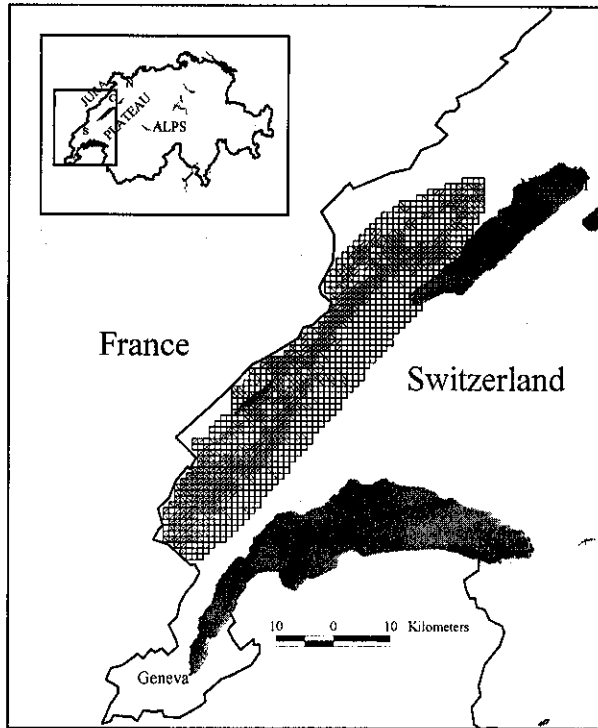


Figure 58.1. Situation of the study area in the Jura Mountains of Switzerland (small map) and France. The grid (large map) shows the 1,085 quadrats where the predictor and response variables have been sampled. Cells are hatched as follows: \ = cells visited by female lynx; / = visited by male lynx; X = visited by both sexes. In addition, S = southern, C = central, and N = northern part of the Swiss Jura Mountains.

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 and Haller 1987; Haller 1992), Western roe deer (*Capreolus capreolus*), and chamois (*Rupicapra rupicapra*) are the main prey of lynx in the Jura Mountains (Jobin et al. 2000).

Method

From April 1988 to June 1998 a total of twenty-nine lynx were surveyed by means of radiotelemetry 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 1×1-kilometer quadrat. The sampling area was restricted to all the quadrats intercepted by the minimum convex polygon (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. 58.1). 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 and Zimmermann 2000).

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. From this set of quadrats, three sets were prepared (Fig. 58.1), using radio fixes of (1) all lynx (females and males), (2) females only, and (3) males only.

The eighteen predictor variables (Table 58.1) 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 and 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 Federal Office of Statistics 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 58.1]).

General linear models (GLM; McCullagh and 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 et al. (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 χ^2 -test (p -value ≤ 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, Chapter 21), 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, Chapter 21). 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: (1) total (both sexes combined) minus female, (2) total minus male, and (3) 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.

Results

The proportion of deviance significantly explained ($\text{adj-}D^2$) in the models ranged from 0.39 to 0.44 , corresponding to a medium fit of the models (both sexes

TABLE 58.1.

Sources of the eighteen predictors used in the logistic regression analysis.

Predictor ^a	Units	Sources ^b
Forest areas	ha/km ²	GEOSTAT
Other wooded areas	ha/km ²	GEOSTAT
Fringe length	meter	FOT
Horticulture, viticulture	ha/km ²	GEOSTAT
Arable land, meadows	ha/km ²	GEOSTAT
Pastures	ha/km ²	GEOSTAT
Pastures in mountain areas	ha/km ²	GEOSTAT
Lakes and rivers	ha/km ²	GEOSTAT
Nonproductive vegetation	ha/km ²	GEOSTAT
Areas without vegetation	ha/km ²	GEOSTAT
Built-up areas	ha/km ²	GEOSTAT
Rest areas, parks	ha/km ²	GEOSTAT
Roads and railways	ha/km ²	GEOSTAT
Elevation	meter	GEOSTAT
Slope	degree	GEOSTAT
Eastness	(cosinus)	GEOSTAT
Northness	(sinus)	GEOSTAT
Human population density	ind./ha	GEOSTAT

^aPredictors had an accuracy of 1 hectare.

^bGEOSTAT database of the Federal Office of Statistics and FOT = Vector 200 database of the Federal Office of Topography.

TABLE 58.2.

Results of the GLM analyses with the three different sets of response variables.

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

pooled, females, males). The AUC at calibration and evaluation ranged between 0.84 and 0.90 (Table 58.2). 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,

TABLE 58.3.

Survival of subadult lynx (F = females, M = males) according to their habitat use.

Model ^a	Lynx	Probability class ^b					Destiny
		1	2	3	4	5	
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

^aThe 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.

^bProbability class: 1: 0–0.2; 2: 0.2–0.4; 3: 0.4–0.6; 4: 0.6–0.8; 5: 0.8–1.

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 .

We then extrapolated the outcome of the three distribution probabilities over the entire Swiss Jura Mountains (see Fig. 58.2 in color section). 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. 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). One can predict that subadult lynx can only establish a permanent home range if they find free space; otherwise, they would be driven into suboptimal 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. 58.2) dispersed north from our study area into the still-unoccupied part of the Jura Mountains (Breitenmoser and Baettig 1992; Capt et al. 1998). They traveled along the corridors predicted from the habitat model (Fig. 58.2), and both settled in good-quality habitat (Table 58.3). 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 58.3). 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 suboptimal habitat (Table 58.3). Both lynx died from a natural death during the dispersal—F13 after she had left a temporary home range in marginal habitat (Fig. 58.2).

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 and 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 and Cuicci 1993; Mladenoff et al. 1995; Corsi et al. 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. 58.2). Failure to incorporate such spot-like or linear, but critical, habitat features or ecological factors such as prey availability, competition, predation (Pearce et al., Chapter 32) 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, Chapter 21). 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 et al. 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 and 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. 58.1, 58.2). Our model confirms that the central part, especially for males, seems to be a suboptimal habitat (Fig. 58.2). 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. 58.1, 58.2). 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 58.2) 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, Chapter 21). 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.

Acknowledgments

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ways and forest, VECTOR 200, Federal Office of Topography; rivers, BFS GEOSTAT, Federal Office of Topography; land use 1992–1997, BFS GEOSTAT; digital terrain model RIMINI, BFS GEOSTAT.

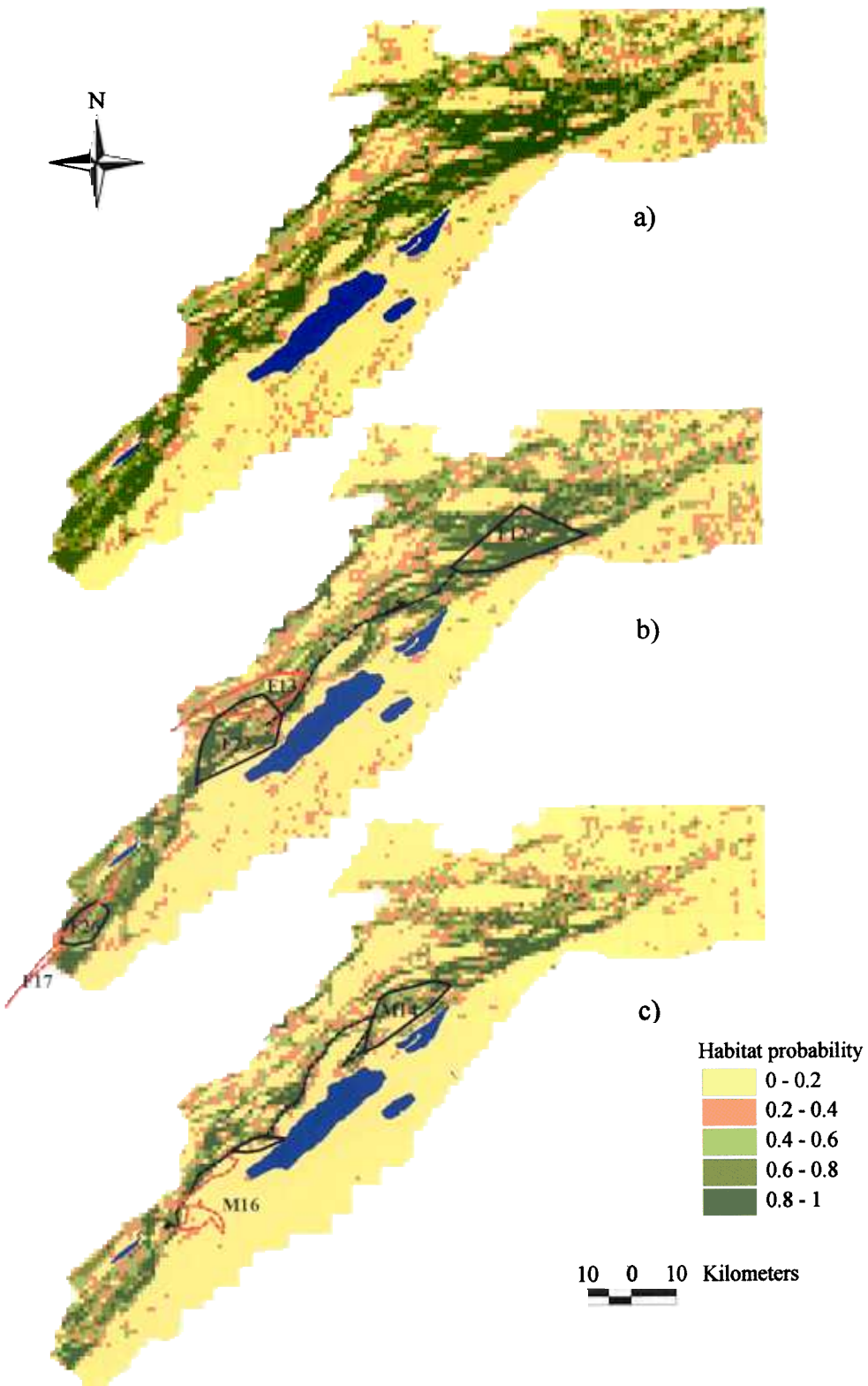


Figure 58.2. Potential distribution of the lynx in the Swiss Jura Mountains according to the model derived from the three sets of response variables (a = both sexes combined, b = females alone, and c = males alone). Lines represent the dispersal route of subadult lynx (F = females, M = males); polygons 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.