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Estimating habitat suitability and potential population size for brown bears in the Eastern Alps

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ABSTRACT

According to the Habitats Directive of the European Union, a favorable conservation status for the brown bear (*Ursus arctos*) should be targeted at the population level in large contiguous habitats such as the Alps, the largest mountain range in Europe. However, in most of the Alps brown bears are extinct and habitat suitability in these areas is often questionable. For this paper, radio-tracking data from four projects with 42 individual bears was compiled to assess habitat suitability. Discrete-choice models with random bear effects were fitted and compared to results obtained from compositional analysis and logistic regression. Sound definition of the available area in the discrete-choice model turned out to be essential. Brown bears showed a preference for forested and steep habitats and an avoidance of roads.

Results from the three approaches were used to predict habitat suitability across the entire range of the Eastern Alps. Minimum potential population size was projected based on observed densities in Trentino and Central Austria, and ranged from 1228 to 1625 individuals, with 518–686 mature bears. This would satisfy a favorable conservation status. The developed methodology also has wide applicability to quantification of habitat suitability and potential population size in other cases where species are at risk.

1. Introduction

One fundamental prerequisite for species conservation is the identification of suitable habitats (e.g. Manly et al., 2002). There are several very different approaches researchers can use to model habitat suitability based on radio-telemetry studies (Thomas and Taylor, 2006). Compositional analysis (Aebischer et al., 1993) is one basic approach that compares proportions of used habitat types to proportions of available habitat types (e.g. used by Simcharoen et al. (2008)). However, it does not allow for investigating either the role of animal or habitat-specific covariates on the selection process. The more widely used logistic regression (i.e. Balbontin, 2005; Johnson et al., 2006; Oakleaf et al., 2006) models the probability of habitat use by using covariates to develop resource selection functions (RSFs). This allows identification of covariates that influence the selection process and estimation of the magnitude and direction of their influence. Unbalanced designs and individual heterogeneity can be examined by using individual specific random intercepts and slopes (Gillies et al., 2006) in mixed modeling approaches. Recent criticism of the use of logistic regression in use-availability studies, however, has raised questions about the fact that information regarding unused points is not available in radio-telemetry studies (Keating and Cherry, 2004). This problem can be avoided by using discrete-choice models. In recent years, the use of discrete-choice models for generating RSFs has increased (McCracken et al., 1998; Cooper and Millspaugh, 1999; McDonald et al., 2006; Thomas et al., 2006; Kneib et al., 2009). They allow resources available to change throughout the study period and help ensure that resources defined as available were accessible to the animal (Arthur et al., 1996; Cooper and Millspaugh, 1999). Discrete choice models can also be used to estimate magnitude and

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direction of the influence of covariates in the selection process and inclusion of random individual effects is possible (Thomas et al., 2006; Kneib et al., 2009).

Habitat suitability models are of particular importance when a species becomes locally extinct and recovery programs aim to return the species to its former, possibly since then altered, range. Brown bear (*Ursus arctos*) recovery has been a major issue in the Eastern Alps since the late 1980s when WWF-Austria started a re-introduction program for brown bears in the Lower Limestone Alps of Central Austria (Rauer and Gutleb, 1997). Concurrently, Slovenia, where the Dinaric Mountains meet the Alps, allowed a natural expansion of the bear population from the northern Dinaric Mountains to the south-eastern Alps (Adamic et al., 2004). Furthermore, in the late 1990s the Italian province of Trentino developed and implemented a recovery program for the last autochthonous bears of the Alps (Dupré et al., 1998).

Despite these restoration efforts, the situation of the brown bear in the Eastern Alps remains critical. The Trentino recovery program seems promising (Dalpiaz et al., 2008), but the expansion of bears from Slovenia has been largely restricted to single male bears (Jerina and Adamič, 2008; Krofel et al., 2010) and the Austrian re-introduction failed (Kruckenhauser et al., 2009). Although this failure was attributed to illegal killings which had a significant effect on the small founder population (IUCN/WWF Workshop, 2009), the availability of suitable habitat for bears in the Eastern Alps has been repeatedly questioned (Market Institute, 2008).

Habitat selection by brown bears has been intensely studied and, in Europe where brown bears live in rather densely settled multi-use landscapes, they seem to select primarily for cover and against human infrastructure. In the Abruzzo Mountains of Central Italy, bears prefer deciduous forests and high altitude areas and avoid open scrub lands (Posillico et al., 2004). Re-introduced bears in Trentino, Italy select for deciduous forests and avoid areas with anthropogenic disturbance (Preatoni et al., 2005). In Spain, bears prefer beech and oak dominated forests and show an avoidance of roads and villages (Clevenger et al., 1992). In Norway the presence of bears is associated with rugged forested areas at lower elevations (May et al., 2008). In Sweden, bears show an avoidance of human infrastructure and a preference for rough terrain (Nellemann et al., 2007). On a fine scale female bears in Sweden were shown to select for abundant food sources and minimal disturbances both on a spatial and temporal scale (Martin et al., 2010).

The Habitats Directive of the European Union (EU) requires all member states to work towards a "favorable conservation status" for selected species, including the brown bear (92/43/ECC). This should be based on a population approach that considers contiguous habitats as management units, irrespective of national borders (Linnell et al., 2008) and requires the identification of potential habitat. There have been several past attempts to assess habitat suitability in the Alps, or parts of the Alps, for brown bears (e.g. Boitani et al., 1999; Knauer, 2000), but meanwhile new habitat and bear data,as well as new analysis techniques, have become available.

In this study we analyzed radio-tracking data from 42 bears in Italy, Austria and Slovenia using discrete-choice models to obtain RSFs. Since the definition of which habitat features are available to an animal can affect the results of the analysis (Johnson, 1980; McClean et al., 1998; Boyce et al., 2003), we compared different definitions of availability (Supplementary materials Appendix A). Subsequently, we spatially extrapolated model predictions to (1) evaluate the Eastern Alps as brown bear habitat, (2) identify suitable areas, and (3) assess the potential of the Alps to support a bear population in a "favorable conservation status" according to the EU habitats directive. We checked the robustness of our habitat suitability predictions by additionally applying logistic regression and compositional analysis models.

2. Methods

2.1. Study area

The Alps are the largest mountain range in Europe. Our study area, the Eastern Alps, covers about 90 000 km^2 and, in descending order of size, includes parts of Austria, Italy, Switzerland, Germany, Slovenia and Liechtenstein. However, we excluded Switzerland and Liechtenstein because no comparable land use data were available. On the other hand, we included all of Slovenia because all data from radio collared bears in Slovenia came from the adjacent Dinaric Mountain range. This added another 11 500 km^2, technically outside the Eastern Alps, to our study area (Fig. 1). Hereafter, the two areas are called Eastern Alps (Eastern Alps including alpine Slovenia) and Dinaric Mountains (in Slovenia).

The highest peak (La Spalla) in the Eastern Alps, located in Italy on the Swiss border, reaches more than 4000 m a.s.l., however

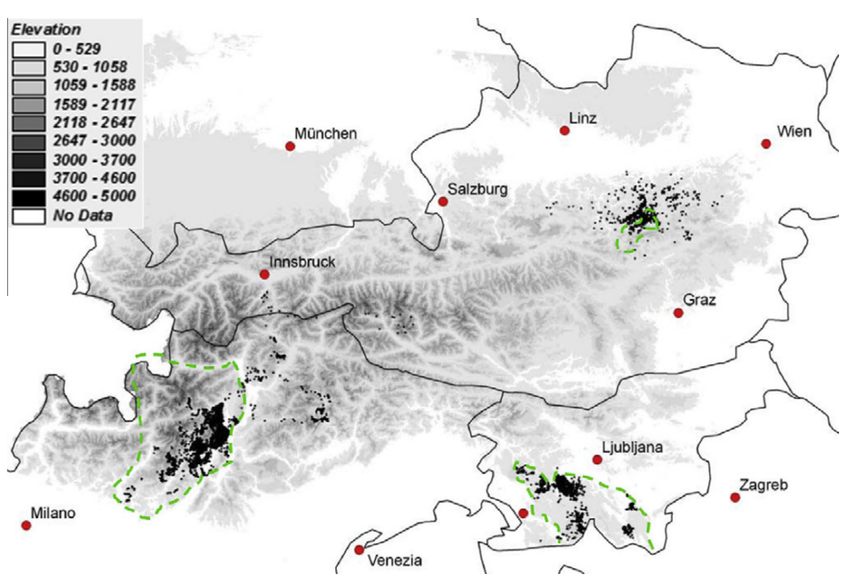

Fig. 1. Distribution of the radio-tracking data (black points) in the study area and current bear occurrence (dashed lines). The gray shadings darken with increasing altitudes.

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most mountain ranges do not exceed 3000 m. Timberline is at about 1800 m a.s.l. in the northern part of the Eastern Alps and about 2100 m in the southern part. Almost all settlements are at the valley floors. The Alps are probably the most heavily touristically used high mountain range in the world (Bätzing, 2003). Agricultural production is mostly limited to livestock husbandry, whereas arable fields are rare and restricted to low elevations. The Eastern Alps are dominated by coniferous forests, followed by mixed and broad-leaved forests. Forest cover is about 54%.

In Slovenia, the areas outside the Eastern Alps are the Dinaric mountains and the Pannonian basin. The Dinaric Mountains are densely forested, whereas the Pannonian basin in the east consists mostly of arable fields. Forest cover in the Dinaric Mountains is about 60% and is dominated by mixed and broad-leaved forest followed by coniferous forests. The highest mountain is Snežnik at 1796 m. The Dinaric Mountains have a long history of bear-human coexistence (Simonic 1994). Within the 5200 km^2 bear core area, Slovenia houses a bear population of 400–500 individuals, which corresponds to a density of roughly 9 bears/100 km^2 (Skrbinšek et al., 2008).

2.2. Bear data

The data on brown bears used for this study were obtained from four different studies in Slovenia, Austria and Italy. In each study area, bears were captured and radio-tagged following methods described in Kaczensky et al. (2002). In Austria, six bears were radio-tracked between 1989 and 1998, in Slovenia 26 bears between 1994 and 2004, and in Italy 10 bears between 1999 and 2003. From these 42 bears (25 females and 17 males), there are 10 626 locations available, 819 from Austria, 2375 from Slovenia and 7432 from Italy. Each bear was located daily, however, some bears, especially those dispersing, were tracked less often; other bears had multiple locations per day. For our analysis we used only the first location per day, which resulted in 3335 locations being discarded. Bears were also radio-tracked during winter months when they mostly hibernate. For analysis, we used only the first location for each bear and consequently removed a total of 657 consecutive locations with identical x and y coordinates. Some of the Slovenian bears moved south into Croatia. As we did not have habitat data at these locations, we excluded 33 locations from five individuals. A total of 6558 locations were used for analysis, 789 from Austria, 2144 from Slovenia and 3625 from Italy. The number of locations per bear varied greatly, ranging from 6 to 712 locations.

2.3. Habitat data

We used the Corine Land Cover database from 1990 (CLC1990) to identify habitat type at each bear location. The database represents the most consistent information on land use in the European Union, comprising 44 habitat classes. The 44 CLC1990 classes were combined into 11 habitat types: settlements, artificial surfaces, agricultural surfaces, broad-leaved forest, coniferous forest, mixed forest, scrub and/or herbaceous vegetation, open spaces with little or no vegetation, wetlands, water bodies, and sea/ocean. We did not use habitat types with few locations, as their inclusion caused convergence problems in the estimation of random effects variances of the discrete-choice model. Hence, only six habitat types remained for analysis: agricultural surfaces, broad-leaved forest, coniferous forest, mixed forest, scrub and/or herbaceous vegetation, and open spaces. We used additional information on roads and altitude to obtain covariates for each grid cell on a 250 m resolution: Euclidean distance to the nearest road and settlement in m, mean elevation in km and mean slope in degrees. The data was processed using the Geographical Information System (GIS) ArcGIS 9.2 (ESRI, Environmental Systems Research Institute, Inc., Redlands, California, USA).

2.4. Habitat models

All statistical computations were done using the statistical program R (R Development Core Team, 2007).

2.4.1. Discrete-choice model

Discrete-choice models are multinomial logit models (Fahrmeir and Tutz, 2001). We fitted a mixed effects discrete-choice model to the nominal response variable habitat type *r*, chosen by animal *i*, at time *t*. The choice set was defined by the six habitat types. The observed locations were used to form the choices the bears actually made. We defined availability separately for each bear location as a circle centered on the bear's position. We chose the radius of the circle a priori to be 10 km, because 97.5% of the daily straight line distance covered did not exceed this threshold. Ideally, it is best to center the location circle on the bear's previous location (as for example used by Arthur et al. (1996)). However, for this definition of availability, locations must be from consecutive days, whereas in our data 27% were not consecutive. Hence, we chose to use two different definitions of availability: (1) the circle centered on the location itself to avoid losing a crucial number of observations, which we called "main-model", and (2) the circle centered on the location of the previous day, only applicable for locations on consecutive days, which we called "previous-day model". Further, we compared different radii and choice sets. Details of the comparison can be found in the methods, results and discussion sections of Appendix A (Supplementary materials).

The proportion of each habitat type within the circle was calculated and included in the model via the offset term $A^{(r)}$. Coniferous forest was treated as reference habitat type (*k*) as it was available for all bears at all times.

We distinguished two types of explanatory variables: animal specific variables, i.e. sex, and habitat-specific variables, e.g. elevation. We calculated habitat-specific variables as the mean of the variable in habitat patch $(r)_{it}$. Hence, habitat-specific variables differed among our different models. We fitted a discrete-choice model of the form:

$$\pi_{it}^{(r)} = \frac{A_{it}^{(r)}\ \exp\ (\beta^{(r)} + x_{it}'\gamma^{(r)} + (z_{it}^{(r)} - z_{it}^{(k)})'\delta + b_i^{(r)})}{1 + \sum_{s=1}^{q} A_{it}^{(s)}\ \exp\ (\beta^{(s)} + x_{it}'\gamma^{(s)} + (z_{it}^{(s)} - z_{it}^{(k)})'\delta + b_i^{(r)})}$$
$$r = 1, \ldots, q. \qquad (1)$$

for each of the models. $\pi_{it}^{(r)}$ was the probability of bear *i*, choosing habitat type *r*, at time *t*. The other parameters were defined as follows:

$A_{it}^{(r)}$ accounts for the varying availability of habitat types. Setting $A_{it}^{(r)} = 0$ for some habitat types *r* makes it possible to exclude these habitat types from the choice set for animal *i* at time *t*.
$\beta^{(r)}$ indicates overall preference of habitat type *r* after accounting for possible covariate effects and availability. Preference for habitat *r* compared to reference habitat *k* is indicated by a positive parameter value ($\beta^{(r)} > 0$).
$b_i^{(r)}$ animal-specific random effects that indicate the preference of habitat type *r* by animal *i*. This allows for animal-specific deviations in selection preferences from the overall pattern. Random effects are assumed to be a random sample of the Gaussian distribution with category-specific variances τ_r^2, i.e. $b_i^{(r)} \sim N(0, \tau_r^2)$. Hence, τ_r^2 measures between animal heterogeneity in the preference of habitat type *r* compared to the reference.
$\gamma^{(r)}$ are category-specific parameters that indicate the effect of animal-specific covariates x_{it}.
δ are global parameters that indicate the effect of habitat-specific variables $z_{it}^{(r)}$.

For a detailed description of the discrete-choice model see Kneib et al. (2009). Backward-forward selection based on Akaike's Information Criterion (AIC, Akaike, 1973) was performed to identify the relevant subset of covariates listed in Table 1.

Preference ratios $\text{pr} = \pi^{(r)}/\pi^{(k)} = \exp(\hat{\beta}^{(r)})$ were calculated for the main-model. They are a simple tool used to clarify the effect of the estimated preferences. If, for example, the preference of coniferous forest is taken to be one, the preference of all other habitats is their preference ratio.

We wrote a function in R that allowed estimation of multinomial logit models with random effects to fit the discrete-choice model. The source code of the function, and a description of its usage, can be found in the Supplementary materials Appendix C.

2.5. Compositional analysis

We carried out compositional analysis, a preference ranking of habitat classes, as proposed by Aebischer et al. (1993). Further, we used the extension proposed by Hansbauer et al. (2010) to obtain preference values. For each individual i and each habitat type r preference was calculated as $\text{d}_i^{(r)} = \log\left(u_i^{(r)}/u_i^{(k)}\right) - \log\left(a_i^{(r)}/a_i^{(k)}\right)$ based on use (u), the proportion of an individual's radio locations, and proportional availability (a). To define the available area we calculated the minimum convex polygon for each bear and buffered this with the mean distance between consecutive observations, i.e. 2600 m. Proportional availability of habitat r was calculated as the proportion of habitat r within the home range. For each habitat type the individual preference values were weighted (by the square root of the number of observations) and averaged.

We used the function `compana` in the R package `adehabitat` (Calenge, 2006) to carry out compositional analysis. For missing proportions of habitat use, Aebischer et al. (1993) suggest replacement with a value smaller than the smallest proportion of used habitat. We chose a replacement value of 0.0001 as the smallest observed value was 0.0039. A randomization test was carried out using 1000 replicates.

2.6. Logistic regression model

We fitted a mixed effects logistic regression with random intercepts to account for the unbalanced design (different sample sizes for each individual bear), and random coefficients for the variable habitat type to allow individual habitat preferences (as suggested by Gillies et al. (2006)). Fixed effects included habitat type (with coniferous forest as reference) and the covariates listed in Table 1. Hence, probability of presence (π_{it}) for bear i at time r was modeled as:

$$\log\left(\frac{\pi_{it}}{1-\pi_{it}}\right) = \beta_0 + v'_{it}\beta_1 + x'_{it}\gamma + b_{1i} + v'_{it}b_{2i}, \quad (2)$$

where v_{it} indicates habitat type chosen by animal i at time t (with $i = 1,\ldots,n$ and $t = 1,\ldots,T_i$). Therefore, β_1 is the vector of estimated overall habitat preferences and b_{2i} is the vector of individual habitat preference of animal i. Further, b_{1i} is the random intercept of animal i, x_{it} is the vector of covariate values of animal i at time t, and γ is the vector of estimated effects of covariates.

Maximum distance to the nearest road and settlement was set to 2000 m, as we expected no effect of greater distances on bear behavior. Covariates were centered by subtraction of their mean (elevation: 1097 m, distance to roads: 1.735 km, distance to settlements: 1.774 km and slope: 17 degrees) to keep main effects biologically interpretable (compare Schielzeth, 2010). We checked for spatial autocorrelation by visual examination of Anscombe residuals that are based on a transformation that avoids (or at least reduces) skewness (compare Pierce and Schafer, 1986). The residuals did not show an indication of spatial autocorrelation present in our data.

We defined used as observed bear locations. To obtain a sample of available habitat we used random samples from the buffered home range of each bear. Random points were generated in ArcGis with a density of points in each home range of 3 points/km^2. A maximum of three times the number of locations in the respective home range was used.

We calculated the odds ratio (OR) = exp(β) or exp(γ), which approximates the preference ratio for a case-control design when availability over the years is constant (Keating and Cherry, 2004). We had basically a case-control design as the probability of contamination (probability of random points falling on observed bear locations) was negligibly small (Keating and Cherry, 2004).

In a stepwise procedure we tested whether inclusion of an interaction term between habitat type and the other covariates, or dropping a covariate, improved the model fit based on AIC. Estimation was carried out using the function `lmer` in the R software package `lme4` (Bates, 2007).

2.7. Prediction of suitable habitat

We predicted and mapped habitat suitability for the entire Eastern Alps using estimates obtained from the three model approaches. For predictions from discrete-choice models, we used the results of the "main-model" and "previous-day model" and Eq. (1) with equal availability, i.e. $A_{it}^{r} = 1$, and the actual value of covariates at each grid cell (not the differences of means in the available circles that were used for model fitting purposes). To predict from the logistic regression we centered the covariate layers as described in the previous section and calculated habitat suitability for each cell. To map the results from compositional analysis we used preference values with coniferous forest as reference category and a linear transformation to obtain relative probabilities.

2.8. Potential bear population size

To estimate potential bear population size in the Eastern Alps we used observed bear densities of populations in Central Austria and Trentino as reference and projected these densities over the entire Eastern Alps after adjusting for habitat suitability, and calculated from this projection absolute population numbers. The bear population in Central Austria peaked in 1999 with 12 bears occupying an area of 543 km^2 (minimum convex polygon of all reliable bear observations, Kruckenhauser et al., 2009). For the Trentino bear population we used the population size of the resident bears (17 bears in 2007) which occupied an area of 1109 km^2. We calculated the proportion of mature individuals in the total population

Table 1
Covariates for habitat models.

Variables	Description	Label
Habitat-specific		
Distance to road	Euclidean distance to the nearest road in km	Street
Distance to settlement	Euclidean distance to the nearest settlement in km	Settlement
Slope	Slope in degrees	Slope
	Slope squared	Slope2
Elevation	Elevation in km	Elevation
	Elevation squared	Elevation2
Bear-specific		
Sex	Sex of each bear	Sex

by using a deterministic, stage structured population model (see Supplementary materials Appendix B). In the model we used demographic parameter values derived from data on both populations (Trentino: Dalpiaz, pers. comm., Austria: own data). The area of the entire Eastern Alps is 89635 km^2.

3. Results

83% of all bear locations used for analysis were from forested areas. Within the forest layer by far the most locations were within coniferous forest (N = 2542), followed by mixed forest (N = 1808) and broad-leaved forest (N = 1114). The remaining locations fell into scrub and/or herbaceous vegetation (N = 691), agricultural areas (N = 217) and open spaces (N = 186).

3.1. Habitat models

3.1.1. Discrete-choice model

Main-model. Backward-forward selection resulted in a model with four significant covariates: slope, distance to road, elevation and squared elevation (AIC: 15044.66). Discarding both elevation and the quadratic term for elevation, led to a model with a slightly lower AIC (15043.47). Hence, for our final model, we used only the variables slope and distance to roads, both of which were significant at the 5% level.

Estimates of habitat preferences $\hat{\beta}$ given in Table 2 show that the reference habitat, coniferous forest, was preferred over all other habitat types.

Preference ratios (pr) showed that within forest habitat, the reference habitat type coniferous forest was preferred over mixed forest (pr = 0.748), which was preferred over broad-leaved forest (pr = 0.655). Open spaces (pr = 0.120) and agricultural surfaces (pr = 0.149) were clearly the least preferred habitat types and scrub and/or herbaceous vegetation was intermediate in preference (pr = 0.309).

3.1.2. Compositional analysis

The randomization test for the 42 bears and the six habitat types revealed that the habitat types are used significantly different from random Λ = 0.165 and p = 0.001. The resulting ranking was:

Conifer > Mixed > Broadleaf > Scrub > Agricultural > Open.

There was no detectable difference in use of coniferous and mixed forest (d = −0.12), however, both habitat types were used significantly more than all other habitat types. Furthermore, broad-leaved forest (d = −0.64) was preferred over scrub and/or herbaceous vegetation (d = −2.29), agricultural surfaces (d = −2.70) and open spaces (d = −2.31). Preference ranks of the later three habitats were interchangeable.

3.1.3. Logistic regression model

In the model selection process only the animal specific variable sex and the habitat-specific variable quadratic term for slope were excluded. Interactions of all other variables with habitat type remained in the stepwise selection. The estimated coefficients, standard deviations, p-values, odds ratios and deviance reduction for this complex model are given in Table 3.

Estimates for habitat type show that, again, forested habitat types were significantly preferred over all other habitat types. There was no difference in the preference of the reference habitat type coniferous forest, broad-leaved (OR = 0.985) and mixed forest (OR = 0.963). Open spaces (OR = 0.276) and scrub and/or herbaceous vegetation (OR = 0.289) were the least preferred habitat types. Agricultural surfaces (OR = 0.455) had moderate preference. The model suggested for all habitat types an increasing probability of use with increasing distance to roads; this effect was significantly larger in agricultural surfaces and open spaces than in the reference. Further, the model suggested an overall increasing use with increasing distance to settlements. Here, the effect was significantly smaller for mixed forest and scrub and/or herbaceous vegetation. Slope had a significant positive effect in the habitats agricultural surfaces, broad-leaved and mixed forest and scrub and/or herbaceous vegetation. The quadratic effect of elevation predicted the highest probability of use at 1060 m (compare Fig. 2). It was significantly higher for agricultural surfaces, broad-leaved forest and scrub and/or herbaceous vegetation and lower for open spaces.

3.2. Prediction of suitable habitat

All habitat suitability maps (Fig. 3) predicted that the northern, eastern, and southern parts of the Eastern Alps had more suitable habitat than the central part (areas along the western part of the Austrian–Italian border). Distribution of habitat suitability largely

Table 2
Estimated habitat preferences $\hat{\beta}^{(r)}$, covariate effects $\hat{\delta}$, corresponding standard deviations (SD), 95% confidence intervals, p-values, preference ratios ($\exp(\hat{\beta}/\hat{\delta})$), and estimated variances of the random effects $\hat{\tau}_r^2$ in the discrete-choice "main-model".

Variable	$\hat{\beta}/\hat{\delta}$	SD	95% CI		p-value	$\exp(\hat{\beta}/\hat{\delta})$	$\hat{\tau}_r{}^2$
Agricultural	−1.963	0.246	−2.444	−1.481	<0.001	0.140	1.51
Broadleaf	−0.424	0.239	−0.893	0.045	0.077	0.655	1.86
Mixed	−0.290	0.110	−0.506	−0.075	0.008	0.748	0.39
Scrub	−1.176	0.228	−1.622	−0.730	<0.001	0.309	1.21
Open	−2.119	0.352	−2.809	−1.429	<0.001	0.120	1.40
Street	0.043	0.021	0.002	0.084	0.039	1.044	
Slope	0.045	0.012	0.021	0.069	<0.001	1.046	

Table 3
Estimated coefficients, standard deviations, p-values, odds ratios (OR) and the reduction in deviance (RD) for the logistic regression model.

Variable	Coef.	SD	p-value	OR	RD
Intercept	−0.724	0.101	<0.001	0.484	
Agricultural	−0.787	0.183	<0.001	0.455	34
Broadleaf	−0.015	0.193	0.940	0.985	
Mixed	−0.066	0.115	0.568	0.963	
Scrub	−1.243	0.239	<0.001	0.289	
Open	−1.287	0.457	0.005	0.276	
Street	0.448	0.063	<0.001	1.565	0
Settlement	0.684	0.078	<0.001	1.983	0
Slope	0.003	0.003	0.287	1.003	0
Elevation	−0.045	0.105	0.670	–[a]	140
Elevation̂2	−1.224	0.106	<0.001	–[a]	See above
*Agricultural*Street*	0.533	0.200	0.008	1.705	172
*Broadleaf*Street*	−0.284	0.164	0.083	0.753	
*Mixed*Street*	0.098	0.109	0.372	1.103	
*Scrub*Street*	−0.047	0.206	0.819	0.954	
*Open*Street*	1.448	0.623	0.020	4.256	
*Agricultural*Elevation*	1.275	0.270	<0.001	–	151
*Broadleaf*Elevation*	0.896	0.198	<0.001	–	
*Mixed*Elevation*	0.191	0.156	0.219	–	
*Scrub*Elevation*	0.863	0.193	<0.001	–	
*Open*Elevation*	−1.214	0.316	<0.001	–	
*Agricultural*Settlement*	−0.143	0.166	0.388	0.867	201
*Broadleaf*Settlement*	0.247	0.162	0.127	1.281	
*Mixed*Settlement*	−0.417	0.110	<0.001	0.659	
*Scrub*Settlement*	−0.516	0.189	0.006	0.597	
*Open*Settlement*	0.676	0.745	0.365	1.965	
*Agricultural*Slope*	0.021	0.009	0.020	1.021	137
*Broadleaf*Slope*	0.020	0.006	<0.001	1.020	
*Mixed*Slope*	0.018	0.004	<0.001	1.018	
*Scrub*Slope*	0.017	0.005	<0.001	1.017	
*Open*Slope*	0.012	0.008	0.134	1.012	

[a] The odds-ratio of *Elevation*+*Elevation̂2* is given in Fig. 2.

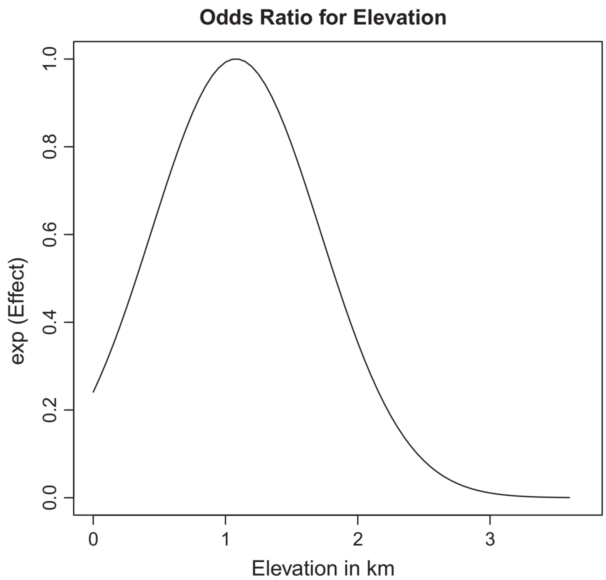

Fig. 2. Effect and odds ratio for the variable elevation in kilometers.

corresponded with forest distribution, the preferred habitat type in all models. As a result of forest distribution, suitable habitat was more fragmented in the southern part than in the northern and eastern parts of the Eastern Alps.

The "main-model" predicted an intermediate suitability in high altitude regions of the central area and high suitability in most other areas, except the densely settled valleys and regions.

In comparison, the "previous-day model" predicted lower suitability in high altitude areas, but differentiated less between all other areas. Suitability of the Vienna forest in the northeast, an area with high levels of human disturbance, was predicted to be higher than in the "main-model". This was difficult to evaluate, however, since no bear data were available from such disturbed areas.

The compositional model largely agreed with both discrete-choice models, but clearly differentiated less than the former ones. In this model, the six habitat types were the only information used.

Finally, of the four models the logistic model resulted in the highest differentiation between good and poor habitat. Infrastructure in valleys and other settled areas, and also high altitude areas, reduced predicted habitat suitability.

3.3. Projection of potential brown bear population size and evaluation of conservation potential

The proportion of mature individuals estimated with the population model was 42.2% in Austria and 44.9% in Italy.

Projected bear numbers ranged from about 1200 to 1600 bears for the Austrian dataset and from 1300 to 1400 for the Italian dataset (see Table 4 for exact values), with resulting numbers of mature individuals ranging from 520 to 690 and from 570 to 630, respectively. Projected numbers based on the Austrian dataset differed

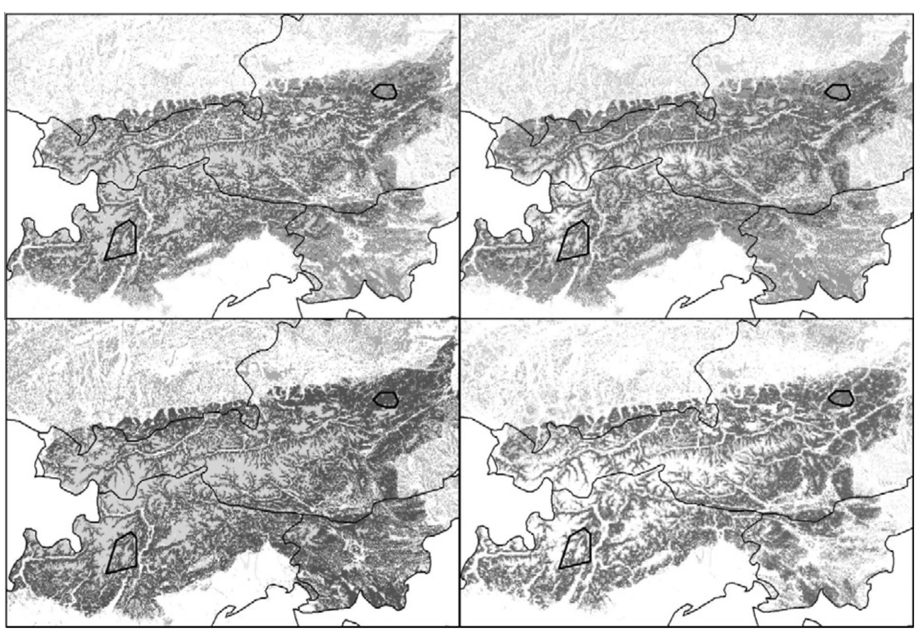

Fig. 3. Habitat suitability maps predicted from different models: Top left: discrete-choice "main-model", right: discrete-choice "previous-day model", below left: compositional analysis and right: logistic regression. The darker the gray the higher is the predicted suitability. The gray tones are on different scales.

Table 4
Mean habitat suitability in the reference areas (hab_{pop}) and in the entire Eastern Alps (hab_{alp}), and projected population size of all bears and only mature bears.

Pop. used for projection	hab_{pop}		hab_{alp}	All bears		Mature bears	
	Austrian	Italian		Austrian	Italian	Austrian	Italian
Main-model	0.6944	0.6117	0.5698	1625	1280	686	575
Previous-day model	0.8617	0.7138	0.6962	1600	1340	675	602
Logistic regression	0.6147	0.3751	0.3812	1228	1396	518	627
Compositional analysis	0.9098	0.6762	0.6918	1506	1406	636	631

more among habitat models than the numbers based on the Italian dataset.

Projected values for bear population size in the Eastern Alps easily exceed the number demanded by the habitats directive (250 mature bears) by at least factor 2 in all models. Based on this analysis, a favorable conservation status of brown bears in the Eastern Alps, with respect to habitat suitability, is possible.

4. Discussion

4.1. Habitat selection models

We used discrete-choice models to analyze radio-tracking data of 42 brown bears in the Eastern Alps region. One large advantage of discrete-choice models is that they do not need absence data, but rather use a choice set and definition of available area. The definition of the choice set and availability, however, is essential (Baasch et al., 2010). In resource selection studies there have been quite different definitions of the choice set and availability. Some studies divide the study area into small patches of land to form the choice set and use all patches (Thomas et al., 2006; Carter et al., 2010), others define as available a subset dependent on the individuals' locations (Cooper and Millspaugh, 1999; Baasch, 2008; Baasch et al., 2010) or a subset dependent on the individuals' annual home ranges (McCracken et al., 1998). Some of these definitions lead to a nonfinite choice set, which is problematic. The idea of the discrete-choice approach, first used for consumer choice studies, is to have a fixed, finite set of choices (McFadden, 1974). Further, if resource units are small geographical areas and are rarely selected more than once, then the discrete-choice model is equivalent to logistic regression (McCracken et al., 1998; McDonald et al., 2006). In our approach, we used the variable habitat type as a response variable to form the choice set (e.g. used by Kneib et al. (2009)). We believe that this definition is a more straightforward definition. Kneib et al. (2009) define availability separately for each animal based on its home range, but not separately for each location. Hence, the available habitat for each animal does not change over time and all variables in Eq. (1), including the habitat-specific covariates, are constant across all observations of one individual. As a result, the estimated effects of habitat-specific variables do not reflect choices made by the animals with regard to what is available to them at the moment of choice, but are instead an artifact of the combination of individual preference of habitat type and differences of habitat-specific variables in the individuals' home ranges.

Although we did not perform any model validation, such as cross validation, we assessed the robustness of our results from the discrete-choice models by reanalyzing the data with compositional analysis and logistic regression. All three approaches yielded similar results concerning preference order of habitat types. With regard to the covariates thought to be involved in the selection process, the three approaches were quite different. Compositional analysis is not capable of modeling covariates unrelated to the animals. The "main-model" included only distance to roads and slope. Both variables had positive estimates, suggesting that the further the distance to the road or the steeper the habitat in comparison to the reference habitat, the higher the probability of selection for the respective habitat. The "previous-day model" additionally suggested an influence of elevation, with an estimated quadratic effect. However, in the logistic approach, all covariates except sex were significant with p-values smaller than 0.001. A potential reason could be that pseudo-absences in the logistic approach that were randomly drawn from each animal's home range were too far away from the locations, which can yield an important overestimation of effects (Lobo et al., 2010).

Our modeling approaches did not account for serial correlation. We used a maximum of one location per day, hence temporal correlation is limited. We also presumed that the habitat a bear chose on one day does not depend on what the bear chose the previous day.

4.2. Estimation of potential brown bear population size

We estimated the potential bear population size in the Eastern Alps simply by extrapolating from observed densities in two areas after adjusting for habitat suitability. This approach has some shortcomings. Firstly, the two reference areas only cover 1.7% of the Eastern Alps and the reference populations are very small. However, it is somewhat reassuring that the estimates from two distant areas that are different in terrain (hills and low mountains in Austria and high mountains in Italy) produced similar estimates. The Italian reference area is larger and more heterogeneous than the Austrian reference area and might therefore be more representative of the entire Alps.

Secondly, our estimations are only extrapolations from reference areas without any estimate of uncertainty for the number of bears in the reference areas and their range covered. We believe that numbers of bears in the reference areas are reliable as the monitoring program is very extensive and well established (compare Rauer et al., 2005). However, the monitoring program may have missed bear signs outside their core range, which would lead to underestimation of the bears' range and hence an overestimation of population density. On the other hand, estimates of population density are based on populations, which we believe have not yet reached natural carrying capacity. The Austrian population declined after the peak in 1999 most likely due to illegal killings which had a significant effect on the small founder population (IUCN/WWF Workshop, 2009). The Trentino population has increased since 2007, reaching about 20–22 bears in the core area in 2009 (Dalpiaz et al., 2010). It is hard to believe that brown bears will ever reach natural carrying capacity in Central European landscapes due to arising bear-human conflicts. Therefore, we assume that our projected population numbers represent a minimum of what is currently possible. Considering all the shortcomings, we believe the results are robust enough to be useful estimates of a minimum bear population size, as long as they are understood as magnitudes and not as precise estimates.

4.3. Conservation and management implications

The co-operation between four bear research projects in the Eastern Alps and Dinaric Mountains has given us the opportunity to compile data from many radio-tagged bears, more than possible in small populations.

We analyzed this comprehensive dataset using three different statistical approaches to derive habitat suitability. Although the resulting models from the three approaches were somewhat different, habitat suitability maps and predictions of potential population were quite similar. Even logistic regression, which provides the most conservative prediction since it has the smallest risk of predicting large heavily disturbed areas as suitable, identified large areas as suitable. Our habitat suitability assessment of the Eastern Alps clearly showed that there are large patches of suitable and interconnected habitat well beyond the areas where bears presently occur.

The relevant reference population size for a favorable conservation status, based on guidelines developed by Linnell et al. (2008) is a minimum of 1000 mature individuals for isolated and 250 for interconnected populations. The bears in the Eastern Alps are interconnected with those in the Dinaric Mountains and our estimates of bear numbers in the Eastern Alps show that there is certainly the habitat potential for 250 mature bears. Even if the connection to the Dinaric population was cut and assuming a similar amount of additional suitable habitat in the Western Alps, which have not been evaluated here, it seems possible that the reference value of 1000 mature bears for isolated populations could also be reached.

Hence, this study showed that successful bear recovery in the Eastern Alps is unlike to be inhibited by a lack of suitable habitat. If bear conservation is stagnating or failing, the reasons will likely have to do with human-related factors such as unsolved human-bear conflicts including fear, damage compensation and prevention or hunting issues (Krystufek and Griffiths, 2003; Kaczensky et al., 2002). Falcucci et al. (2009) have already cautioned that habitat suitability models alone may fall short as conservation tools because they do not allow to distinguish between source and sink habitats. Based on bear mortality data, they estimated that as much as 43% of the area suitable for bears in the Appenine mountains of Italy is actually also associated with a high human caused mortality risk. The failure of the central Austrian bear re-introduction also highlights the importance of addressing the human-related habitat conditions. The fact that the Eastern Alps extend over four countries with different languages and administrational responsibilities makes bear conservation management even more challenging.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.03.010.

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