

The challenge posed by newly discovered cryptic species: Exploring the environmental niches of long-eared bats in Switzerland

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1. SUMMARY

(1) The discovery of cryptic species poses new challenges for species conservation. First, species distribution and status have to be re-evaluated. Second, the ecological requirements of species so far confused have to be clearly recognized before suggesting conservation guidelines. In 2002, a new cryptic bat species, *Plecotus macrobullaris*, was discovered in Switzerland, which called for a re-assessment of the distribution and conservation status of all three *Plecotus* species occurring in Switzerland.

(2) We investigated the ecological niches of the three long-eared bat species and built preliminary habitat suitability maps. Records of bats and roost locations (species DNA identification) were used for constructing a landscape-scale model. Local-scale models were also built based on locations of foraging bats obtained from radio-tracking. Niche characteristics were investigated with Ecological Niche Factor Analysis (ENFA) and discriminant analysis.

(3) The occurrence of all three species was mainly explained by the proximity to rural settlements and warm summer temperature. The distribution of *P. auritus* was positively associated with the presence of arboreal structures, whilst *P. macrobullaris* depended on deciduous woodland. *P. austriacus* showed a preference for orchards and vineyards. *P. auritus* had a relative broad niche, with occurrence predicted in most forested regions of Switzerland. The predictive distribution of *P. macrobullaris* was mostly in the southern part of the Alpine arch. In contrast, *P. austriacus* showed a very narrow niche and was predicted to occur mainly in the lowlands, with habitat requirements strongly overlapping with those of *P. macrobullaris*. The species may present a parapatric distribution, indicative for interspecific competition. The currently projected distribution of *P. auritus* matches previous views (forest bat exclusively). Our results shed new light on the distribution of *P.*

austriacus, which is very much restricted to intensively cultivated lowlands and may thus suffer from recent major land-use changes at low elevation. This requires its reclassification as species of high conservation concern. *P. macrobullaris* seems to be quite widespread and common in the southern part of the Alpine arch. Further studies are necessary to refine our knowledge of species' ecological requirements so as to provide sound conservation guidelines.

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KEYWORDS: Chiroptera, conservation status, Ecological niche factor analysis (ENFA), habitat suitability, Plecotus, presence only

2. INTRODUCTION

The global species diversity is highly underestimated (Ceballos & Ehrlich 2008) and still new many species are discovered. For instance, it has been shown recently that even in a popular and well-studied taxon as mammals, discoveries increased the worldwide number of known species by ten percent within the last 15 years (Ceballos & Ehrlich 2009). Of the 408 newly detected mammal species, 60% were classified as “cryptic species”, a main reason for the discovery of new species (Ceballos and Ehrlich 2009). Cryptic species were not distinguished originally from their sibling species due to high morphological similarities (Bickford *et al.* 2006) and they often became discovered only due to the application of molecular genetic techniques (Ceballos & Ehrlich 2009; Mayer, Dietz & Kiefer 2007). With the discovery of new cryptic species the knowledge about whole cryptic species complex has to be questioned. A main problem is that a species listed already as endangered might in reality be much rarer (Schönrogge *et al.* 2001). In order to decide if conservation action is necessary, the ecology and potential distribution of the new species has to be re-evaluated. Due to the high number of species worldwide (Ceballos & Ehrlich 2009) and the increasing pressure on a growing amount of them (Brook *et al.* 2006, Novacek & Cleland 2001), methods to gain basic information have to be efficient, transferable (Elith & Leathwick 2007) and, given the limited funding, should preferably be able to deal with limited and incomplete data in order to make use of existing data sets (Elith & Leathwick 2007). Spatial distribution models became increasingly popular (e.g. Reutter *et al.* 2003, Rowe 2005) in this context. These multivariate models evaluate the ecogeographic conditions at proved species' locations to assess species-specific habitat requirements and to predict areas of potential occurrence (Guisan & Zimmermann 2000). Among these models, presence-only methods, such as the Ecological Niche Factor Analysis (ENFA Hirzel *et al.* 2002), can be advantageous

when reliable absence data are difficult to obtain, e.g. in secretive living species or when exploring species distribution patterns over large areas (Hirzel *et al.* 2002). In addition, these methods are beneficial as they allow interpreting already available museum samples (Reutter *et al.* 2003) and even using small sample sizes (Pearson *et al.* 2007). In conservation, predictive distribution models were for instance used to compare the influence of climate vs. topography on reptile distribution (Guisan & Hofer 2003), to determine areas for the reintroduction of an eradicated species (Hirzel *et al.* 2004), to predict the impact of climate change on species spread (Estrada-Peña & Venzal 2007), to predict the distribution of rare species (Engler, Guisan & Rechsteiner 2004) or to set conservation priorities for species and habitats (Chefaoui & Lobe (2008). In addition, they have been used to discriminate niche requirements and distributions of sympatric sibling species (Sattler *et al.* 2007).

Within mammals many new discoveries of cryptic species occurred in the order of bats (Chiroptera) (Arlettaz *et al.* 1997, Ceballosa and Ehrlich 2009; Mayer & von Helversen 2002; Patterson 2000). Chiroptera species represent a 21% of the 5487 known mammalian species (Schipper *et al.* 2008). Worldwide 94 new species have been described since 1993 (Ceballos & Ehrlich 2007). Even in a well studied area as Europe many new species – often cryptic ones - were identified since the introduction of DNA sequencing and still more discoveries are expected (Mayer, Dietz & Kiefer 2007). One of the recently discovered cryptic bat species is *Plecotus macrobullaris*, a long-eared bat species (Kiefer & Veith 2001; Spitzenberger *et al.* 2003). The morphological characteristics of this species are overlapping with its sibling species, *P. auritus* and *P. austriacus* (Kiefer & Veith 2001; Pavlinić & Tvrtković 2004), it was only recognised in 2001 (Kiefer & Veith 2001). All three species were observed in Switzerland and for *P. macrobullaris* and *P. auritus* a mixed colony was reported by means of 15 DNA verified roosts (Ashrafi *et al.*, in prep.). *P. auritus* was known to occur in woodlands all over Switzerland up to the

timber line (Beck, Güttinger & Lutz 1995) and *P. austriacus* was known to occur mainly in the lowlands (Beck 1995). Due to the discovery of *P. macrobullaris* the distributions of all three *Plecotus* species, especially in the Alps, has to be newly investigated.

The aim of this study was to explore and predict the potential distributions as a basis for a reassessment of the conservation statuses of all three sibling species in Switzerland. As absence is *per se* unreliable in cryptic species complexes (Hirzel *et al.* 2001), we applied with ENFA a presence-only approach using the already available museum data, supplemented by additionally verified records. We identified (a) differences in the three species' realised niches by determining the most important eco-geographical predictors for occurrence at two spatial scales; at the landscape level using casual records and at the local level using foraging observations and (b) determined areas of potential occurrence in Switzerland in order to prioritize further research and conservation actions.

3. MATERIALS AND METHODS

An Ecological Niche Factor Analysis (ENFA, Hirzel *et al.* 2002) was applied to investigate the species' environmental niches at two spatial scales ("landscape" and "local" scale, as defined below) and to predict potentially suitable areas for the three species in Switzerland. ENFA is based on Hutchinson's (1957) concept of the ecological niche as a multi-dimensional space of environmental variables. ENFA requires two types of input data. First, it requires presence data of the three species, and second, a set of independent eco-geographical variables (EGV) covering the whole study area (Hirzel *et al.* 2002).

STUDY SITES

Landscape model: The study was carried out in Switzerland (Central Europe). The country covers a total area of 41,293 km² and incorporates a variety of different landscapes, which are divided into six biogeographical regions based on fauna and flora (Gonseth *et al.* 2001) (Figure 1).

There are two main mountain ranges, the Jura and the Alps. Between them lies the low situated Midland, which is intensively cultivated and densely populated. Here forests are relatively small and isolated; whilst in the Alps and the Jura exist large woodlands. The Jura, a calcareous hill range, is composed of predominantly coniferous forests and pastures. The forest border line lies already at 1400-1500 m a.s.l. The Alps are the largest mountain range in Europe. In Switzerland they are divided into four bioregions. The Western and Eastern Central Alps have less precipitation than the rest of Switzerland. The Ticino (Southern Alps) is characterised by a mild, Mediterranean influenced climate. Forests in the valleys of the Ticino (Southern Alps) are mainly deciduous. Generally the low valley floors are cultivated; the higher situated valley floors are used as grassland and the slopes are covered with mainly coniferous forests up to 2300 m a.s.l.

Local model: We investigated individuals of *P. macrobullaris* and *P. auritus* in the Alpine Goms valley, because there the two species occur sympatrically. The Goms lies in the uppermost part of the Rhone valley in the Western Central Alps of Switzerland (Figure 7). The *P. macrobullaris* colony in Obergesteln (46°30'49" N, 8°19'27" W, 1355 m a.s.l.) lies at the upper end of the Rhone valley. The *P. auritus* colony in Blitzingen (46°13'17" N, 8°12'9" W, 1297 m a. s. l.) is situated 12 kilometres downstream. The study area for the local analysis was delimited first by applying a circular buffer with a radius of 12 km around each colony. Within this range all areas where the landscape model predicted presence of either one or both of the two species formed the final study area.

SPECIES DATA

Landscape model: As presence data we used DNA-verified species records, assembling data from the literature (Ashrafi *in prep.*; Juste *et al.* 2004), and already available data from A. Kiefer and M. Mattei-Roesli (Centro protezione chirotteri Ticino). Additionally we collected DNA samples (faeces and tissues) from regional bat conservation experts, which were determined by the A. Kiefer group, Germany (protocol in Ashrafi *et al.*, *in prep.*). Because the current distribution patterns are of major importance for conservation issues we focussed our analysis on specimens sampled within the last 25 years (till 1984 (Figure 1)). Due to the rareness of *P. austriacus* we obtained only a small sample size of this species. To enlarge the data set of *P. austriacus* we included one radio tracking location randomly chosen from each of the two colonies investigated by Ashrafi *et al.* (*in prep.*) and additionally added 11 skull-measured specimens from 1948-1992, resulting in a total sample size of N=21 for *P. austriacus*. The very reliable skull determination was done by I. Pavlinić, Croatia (I. Pavlinić *et al.*, *in prep.*). For *P. macrobullaris* and *P. auritus* only DNA-verified samples were applied throughout. Only locations with a spatial precision of ≤ 3 km were used. A minimum distance of 1300 m between the presence points of a species was chosen to avoid spatial

autocorrelation, as the frequency of eco-geographical variables (EGVs) in the latter analysis was calculated within this radius.

Local model: For the local model we used locations revealed by radio tracking of N=4 *P. auritus* and N=4 *P. macrobullaris*. Bats were caught by hand-netting in the roost or were mist netted at roost entrances. We studied only females due to their binding to maternity roosts and focussed on reproductive individuals as they are energetically more stressed and thus are expected to optimise foraging. Bats originated from DNA-verified roosts. They were determined by seven external morphological measurements according to Ashrafi *et al.* (in prep.). Then, radio transmitters (Holohill Systems Ltd, BD-2M, 0.43g or Biotrack, Pip Ag317, 0.45 g, light potting) were glued (Torbot Cement) on a trimmed spot on the neck of the individuals. Additionally bats were ringed (ring size 2.9 according to Eurobats recommendations, Anonymous 2003) to avoid a repeated tracking of an individual. To achieve locations of the bats within their foraging habitats we tracked them applying the triangulation technique (White & Garrott 1990). We used Australis (26k Scanning Receiver, Titley Electronics, Australia) and Wildlife receivers (TRX-1000S, Wildlife Materials, USA) together with hand-held Yagi-antennae (Titley Electronics, Australia). The team coordinated their work by walkie-talkies and timer watches (Casio 2575) to record data in 5 min intervals. Every interval we recorded time, our positions, bearing and an accuracy estimate of the location. We categorised each location into three categories of accuracy, with an error range smaller than 50, 100 and 250m, respectively (classes high, medium and low, according to Bontadina & Naef-Daenzer, 1996). For the analysis we kept only locations of high and medium accuracy, so that the error polygon was smaller than one hectare.

ECO-GEOGRAPHICAL VARIABLES (EGV)

LANDSCAPE MODEL

Based on a literature review on the ecological requirements of the three *Plecotus* species (e.g. Entwistle *et al.* 1996; Flückinger & Beck 1995; Fuhrmann & Seitz 1992; Kiefer & Veith 1998; Swift & Racey 1983) and on information won during the radio tracking season (Ashrafi *et al.* in prep.), variables which were supposed to be relevant for at least one of the three species were preselected for the ENFA (Table 1). All variables were prepared as raster maps with a 100 x 100m resolution.

Table 1: Eco-geographical variables (EGVs) used in the Swiss-wide analysis. Original resolution is given as side length of a square area (metres). Either the frequency within a radius of 1300m (fq) or the distance (dist) to the respective feature was used.

Category	EGVs	Description	Data source	Survey period
Closed habitats	Coniferous forest (fq)	90-100% conifers	Geostat	1990/92
	Mixed forest (fq)	10-90% conifers	Geostat	1990/92
	Deciduous forest (fq)	90-100% deciduous trees	Geostat	1990/92
Semiopen habitats	Alpine bushy forest (fq)*		Geostat	1990-2001
	Forest edges (fq/dist)*		Geostat	1990-2001
	Open forest (fq)		Geostat	1990-2001
	Small woods (dist)	Hedges, bushes and tree groups (on agricultural areas)	Geostat	1990-2001
Open habitat	Orchards & vineyards (fq)		Geostat	1990-2001
	Meadows (fq)		Geostat	1990-2001
Anthropogenic structures	Towns (dist)	Urban settlements	Geostat	1990-2001
	Single buildings & villages (dist)	Rural settlements	Geostat	1990-2001
Climate	Traffic (dist)*		Geostat	1990-2001
	Average summer temperature (°C)	May to August	WSL	1961-1990
Topography	Elevation*		Geostat	

*) Variables which were highly intercorrelated or unimportant and not included in the final model.

Binary land cover data were made quantitative either through calculation of the minimum distance (module DistAn in Biomapper 4.0, Hirzel *et al.* 2008) to the particular type of EGV or by calculating the frequency of the EGV type within a 1300m circular moving window (module CircAn in Biomapper 4.0, Hirzel *et al.* 2008). This radius resembles the average radius of the foraging range from the roost, as measured for all three species by means of 12 radio-tracked individuals (Ashrafi *et al.* in prep.). Additionally we compared the altitudinal distribution of the locations of the

three species.

LOCAL MODEL

For the local analysis we used eco-geographical variables with a higher resolution (cell size 25x25 m), except for meadows, which had to be converted from a 100x100m resolution (Table 2). Boolean data were made quantitative by calculating the minimum distance to or the frequency of the particular EGV type within a radius of 50 metres. This radius corresponds to the radio tracking accuracy.

Table 2: The 13 eco-geographical variables (EGVs) applied for the local analysis. Original resolution is given as side length of a square area (m). Either the frequency within a radius of 50m (fq) or the distance (dist) to the respective feature was used.

Category	EGV	Description	Data source	Survey period
Closed habitats	Coniferous forrest (fq)	90-100% conifers	Geostat	1990/92
	Mixed forest (fq)	10-90% conifers	Geostat	1990/92
	Deciduous forest (fq)	90-100% deciduous trees	Geostat	1990/92
	Forest edges (fq)		Swisstopo	2004
Semiopen habitats	Hedges & Single trees (fq)		Swisstopo	2004
Open habitats	Intensive meadows (fq)		Geostat	1995
	Extensive meadows (fq)		Geostat	1995
Hydrology	Water (dist)		Swisstopo	2004
Anthropogenic structures	Roads (dist)		Swisstopo	2004
	Ways (dist)		Swisstopo	2004
	Buildings & villages (dist)		Swisstopo	2004
Topography	Elevation		Swisstopo	
	Slope		Swisstopo	

DATA ANALYSIS

LANDSCAPE MODEL

Ecological Niche Factor Analysis (ENFA): Before applying the ENFA, all variables were normalised by Box-Cox transformation. ENFA converts these correlated variables into the same number of uncorrelated factors, which summarize the niche information into two main components, marginality and specialisation (Table 3) (Hirzel *et al.* 2002). Marginality, as

maximised by the first factor, describes the deviation between the mean environmental conditions at the species' locations (species distribution) and those in the study area (global distribution), thus indicating the niche position. Specialisation, as maximised by the second and all subsequent factors, describes the ratio of species' variance to global variance and indicates the niche breadth (Hirzel *et al.* 2002).

For each species, we first ran an analysis including all EGV. In order to simplify the models, we subsequently discarded highly intercorrelated variables (correlation threshold $k > 0.8$), as well as irrelevant variables, for which contribution to marginality and specialisation fell below 0.1 for all three species.

Habitat suitability map: Based on the resulting predictor set, habitat suitability (HS) maps were calculated to show potentially suitable and non-suitable areas for the three species (Table 2). Maps were computed applying derivatives of the median algorithm (Hirzel *et al.* 2002, Braunisch *et al.* 2008) on the significant factors, as determined according to MacArthur's broken stick heuristics (Hirzel *et al.* 2002). The "pure" Median algorithm (M, Hirzel *et al.* 2002) assumes the median of the species' frequency distribution along each factor to be the optimal approximation of the species' environmental optimum. However, as global availability is not taken into account, this can be misleading when the species is investigated in marginal habitats, or shows a preference for extreme conditions (Braunisch *et al.* 2008). As in our study the ratio between the species and the global distribution was skewed towards extreme values in all three species, the best results were obtained by derivatives of the median algorithm, generated to account for these problems (Braunisch *et al.* 2008). For *P. austriacus* and *P. macrobullaris* we applied the median algorithm with an extreme optimum on the marginality factor (M_e), using the additionally area-adjusted (M_{ae}) for *P. auritus* (Braunisch *et al.* 2008).

Model validation: The habitat suitability models were evaluated by means of a five-fold cross-validation (integrated in BIOMAPPER 4.0, Hirzel *et al.*

2007). Thereby the presence data set was randomly subdivided into 5 subsets, with iteratively 4 partitions pooled to compute a habitat suitability model and the respective left-out partition used for validation. We computed two presence-only evaluation measures: the Boyce index (4 bins, Boyce *et al.* 2002) and the continuous Boyce index (Hirzel *et al.* 2006). The Boyce indices range both from -1 to 1, with 0 indicating a random model (Sattler *et al.* 2007).

Niche differentiation: The species' niches were compared by discriminant analyses (Legendre & Legendre 1998) based on the same set of variables. The resulting factors maximise the partitioning of the species distributions by minimising their variance and can be used to determine on which EGV the three species discriminate most.

An analysis of the species' frequency distributions along the discriminant factor allows comparing niche breadths and niche overlaps between species. The Standardised Levins' index (B') measures niche breadth (Colwell and Futuyma 1971) with a value close to 0 indicating a narrow niche and values close to 1 a broad niche. To analyse the niche overlaps we applied Lloyd's asymmetric overlap index (Hurlbert 1978). This directional measure accounts for the fact that the niche overlap between two species is often nonreciprocal. All applications are integrated in BIOMAPPER 4.0 (Hirzel *et al.* 2007).

LOCAL MODEL

For the local-scale analyses, individual differences in sample size of radio tracking locations (Table 7) were normalised by weighting the individual sample size over the total species' sample size. Furthermore we accounted for multiple observations in each grid cell. This resulted in quantitative instead of binary maps of species presence. Predictor selection, habitat suitability calculation and niche comparison were performed as for the landscape model. Due to the larger sample size we could apply more partitions (k=10) for cross-validation. Habitat suitability maps for both

species were calculated using the median algorithm that accounted for extreme optima (M_e) (Braunisch *et al.* 2008).

4. RESULTS

LANDSCAPE MODEL

PRESENCE DATA

We obtained N=45 samples of *P. auritus* distributed over all six bioregions in Switzerland (Figures 1 & 2). Data from *P. austriacus* (N=21) stemmed from north of the largest mountain range (Western and Eastern Central Alps, Southern Alps) in the low situated Midland and the Jura, plus one low-altitude location from the Western Central Alps (Figures 1 & 3). *P. macrobullaris* locations (N=49) stemmed from south of the largest mountain range plus a few samples from the edge of the Northern Alps (Figures 1 & 3).

HABITAT SUITABILITY MODELS

The landscape model revealed an overall marginality of 0.92 and a tolerance of 0.66 for *P. auritus*, indicating that it is the most generalist among the three species (Table 4). Among the predictors kept for all three models (Table 1) the three best explaining EGVs for the distribution of *P. auritus* were the distance to single buildings and villages (contribution to marginality: -0.795; to explained specialisation: 0.349), high average summer temperature (0.296; 0.275) and coniferous forest (0.266; 0.273) (Table 3). This species was positively related to all variables. The habitat suitability map for *P. auritus* was computed using the first five factors, which accounted for 94% of the explained information. The species finds potentially suitable habitats in all bioregions of Switzerland (Figures 1 & 2), but was not predicted above the timberline.

The *P. austriacus* model revealed an overall marginality of 1.40 and a very low tolerance of 0.20 for this species (Table 4). The high marginality indicates that the occurrence of this species depends on environmental

conditions that largely deviate from the average conditions in the study area. The very low tolerance value illustrates a high sensitivity to deviations from the optimum in comparison to the other species. The marginality of the distribution of *P. austriacus* indicated preference for proximity to single buildings and villages (-0.557, negative correlation with distance), high average summer temperatures (0.448) and a high frequency of orchards and vineyards (0.397). The species was also highly specialised concerning these variables (contribution to explained specialisation: 0.49, 0.45, and 0.36 respectively). In contrast to *P. auritus*, *P. austriacus* avoided coniferous and open forest. Small woods and mixed forest were irrelevant for explaining the species' distribution (Table 3). Habitat suitability for *P. austriacus* was computed based on four factors explaining 99% of the information. The model shows potentially suitable habitats in large areas of the low Midland and Jura as well as in the low situated alpine valleys including the Ticino (Southern Alps). Areas of high suitability are scattered and sparsely connected (Figures 1 & 3).

For *P. macrobullaris* we obtained an overall marginality of 1.39 and a tolerance of 0.50 (Table 4). The high marginality, almost the same as in *P. austriacus*, showed that this species selected habitats different from the average global conditions. The low tolerance value, situated between those of the other two species, showed its sensitivity to deviations from optimal conditions. Like in the other two species, the distribution of *P. macrobullaris* was mostly correlated with proximity to single buildings and villages (contribution to marginality: -0.680 for distance; to explained specialisation: 0.394) and high average summer temperature (0.449; 0.277); but additionally the frequency of deciduous forest (0.362; 0.231) was highly explicative. This species' distribution in the study area was not related to coniferous and mixed forest, meadows and proximity to towns (Table 3).

For *P. macrobullaris* we computed habitat suitability on four factors explaining 94% of the information. The potentially most suitable areas for

this species were situated in the Western Central Alps and Ticino (Southern Alps) of Switzerland, but occurrence was also predicted for the lower alpine valleys and in some low connected areas in the Jura and the Midland (Figures 1 & 4).

MODEL EVALUATION

The model evaluation indices for the habitat suitability model of *P. auritus* and *P. macrobullaris* showed a high predictive power. For *P. auritus* the Boyce index with four bins ($B_4 = 0.96 \pm 0.08$, mean \pm standard deviation) and the corresponding continuous Boyce index ($B_{\text{cont}(0.25)} = 0.75 \pm 0.23$) were close to one and had small standard deviations. The model of *P. macrobullaris* ($B_4 = 0.88 \pm 0.24$, $B_{\text{cont}(0.25)} = 0.84 \pm 0.19$) gave an almost equally good result. Due to the small sample size the model of *P. austriacus* ($B_4 = 0.41 \pm 0.34$, $B_{\text{cont}(0.25)} = 0.20 \pm 0.57$) fitted less well and has to be interpreted with cautiousness.

NICHE DIFFERENTIATION

The two discriminant factors accounted for 77% of the total variance (first factor: 45%, second factor: 32%) indicating a good discrimination between the species. The discriminant analyses showed that the niches of all species were overlapping (Figure 5). Along the first discriminant axis, species were most discriminated by summer temperature and deciduous forest (Table 6). *P. austriacus* and *P. macrobullaris* could only hardly be drawn apart. Their maxima lied apart from the maxima of the global distribution, whilst the maximum of the *P. auritus* distribution corresponded largely to the maximum of the global distribution. The species' frequency distribution along the second discriminant axis showed that the habitats of *P. auritus* were well separated against the other two species, *P. macrobullaris* and *P. austriacus*, which are largely overlapping. Along this axis, species were mostly discriminated by mixed and coniferous forest. The standardised Levin index (B') on the first discriminant factor indicated that the niches of *P. austriacus* was narrower

($B' = 0.180$) than those of the other two species. *P. auritus* ($B' = 0.284$) and *P. macrobullaris* ($B' = 0.247$) showed a similar niche breadth. The standardized Levin index on the second discriminant factor showed again a small niche breadth for *P. austriacus* ($B' = 0.180$), but this time the niche of *P. macrobullaris* ($B' = 0.365$) was broader than the one of *P. auritus* (0.223).

The trends of Lloyd's asymmetric niche overlaps were the same for both discriminant factors. The ecological niche of *P. austriacus* was to a larger part encompassed in the niches of the two other species than *vice versa* (Table 5). It highly overlapped with the niche of *P. macrobullaris*, which was more overlapping with *P. auritus*. The niches of the latter two species were integrated in each other's niche about equally.

Altitudinal distribution: The differences in the three species were also illustrated by their observed distribution along the altitudinal gradient (One-way ANOVA, total $df = 114$, $p < 0.0001$). Locations of *P. auritus* were on average at 936 ± 65 m a.s.l. ($N=45$, median \pm SE), of *P. austriacus* ($N=21$) at 437 ± 12 m a.s.l. and of *P. macrobullaris* ($N=49$) at 708 ± 46 m a.s.l. There was no record above the timberline at 1800 m a.s.l. (Figure 6).

LOCAL MODEL

HABITAT SUITABILITY

In the local model *P. auritus* showed an overall marginality of 1.18 and tolerance of 0.49. Its distribution was mostly explained by low distances to villages and buildings (contribution to: marginality -0.529; explained specialisation 0.394), the frequency of intensive meadows (0.427; 0.320), and low elevation (-0.409; 0.394) within the study area. Moreover, presence was negatively affected by the frequency of coniferous forest and extensive meadows (Table 9). The habitat suitability map was computed using the first 10 factors, which accounted for 96.5% of the information.

For *P. macrobullaris* the local model revealed an overall marginality of 1.26 indicating that optimal conditions for this species deviate stronger from the global average than in *P. auritus*. *P. macrobullaris* was also less tolerant (0.35) to deviations from this optimum. Frequency of intensive meadows (0.529), low slope (-0.438) and low elevation (-0.315) were the three most important factors determining the marginality, whilst the specialisation was mostly associated with the frequency of intensive meadows (0.372), elevation (0.334), and the frequency of coniferous forest (0.176). Habitat suitability was negatively affected by the frequency of deciduous and mixed forest, of forest edges and of extensive meadows (Table 9) and was computed based on the first two factors explaining 89% of the information.

Generally the suitable habitats of the two species were highly overlapping. The areas of highest suitability were situated at the valley floor or close-by.

EVALUATION

The evaluation indices for the local habitat suitability model of *P. auritus* ($B_4 = 1 \pm 0$, $B_{\text{cont}(0.25)} = 0.89 \pm 0.12$) showed a very high fit and the model for *P. macrobullaris* fitted well too ($B_4 = 0.71 \pm 0.49$, $B_{\text{cont}(0.25)} = 0.64 \pm 0.47$).

NICHE DIFFERENTIATION

The niches of the two species were hardly separable at the local scale (Figure 8). The discriminant factor accounted for 44% of the variance and was mostly associated with extensive meadows, which were less frequently selected by *P. macrobullaris*, same applied to coniferous forests and water (Table 6). Again *P. auritus* ($B' = 0.368$) displayed a broader niche than *P. macrobullaris* ($B' = 0.287$). Llody's asymmetric niche overlap index showed that its niche overlaps slightly more with *P. macrobullaris* ($Z_{x(y)} = 6.506$) than *vice versa* ($Z_{x(y)} = 6.274$).

5. DISCUSSION

We showed that the two most important eco-geographical predictors for the landscape model in all three species were proximity to rural settlements and high summer temperature, but further relevant predictors were different. In *P. auritus*, the frequency of coniferous forest was additionally important. The third relevant factor explaining the distribution of *P. austriacus* was the proximity to orchards and vineyards. This species had a very narrow niche and records originated mostly from the Midland and the Jura, whilst potentially suitable areas were additionally found in lower situated alpine valleys, especially in those of the Ticino (Southern Alps). For *P. macrobullaris* the third important predictor of presence was the frequency of deciduous forest. The niche of *P. macrobullaris* was almost as broad as in *P. auritus*. The species was recorded and predicted mainly in the Ticino (Southern Alps), the Western and the Eastern Central Alps as well as for alpine valleys. In the discriminant analysis it was difficult to disentangle *P. austriacus* and *P. macrobullaris*.

ECOGEOGRAPHICAL VARIABLES

Rural settlements: The high attraction of all three species to villages and single buildings on the landscape scale reflected their local roost preference, in Switzerland usually in attics (Beck 1995; Beck, Güttinger & Lutz 1995) or house walls (Arlettaz, pers. communication), but *P. auritus* has is known to roost also in tree cavities and bat boxes (Beck, Güttinger & Lutz 1995; Fuhrmann & Seitz 1992). During summer *P. austriacus* is roosting in buildings, evidences from three cavities are missing (Beck 1995). Buildings like barns and machine halls were even used as foraging areas (Kiefer and Veith 1998). Up to now *P. macrobullaris* has been observed to roost exclusively in buildings (Kiefer & von Helversen 2004) with the exception of one radio tracked individual (Ashrafi *et al.*, in prep.). However, as presence data were not sampled systematically, our results may also be affected by a sampling bias, as bats are more easily found in

higher populated areas.

Temperature and elevation: All three species showed a high dependency on warm temperature. Especially *P. austriacus* has been reported as thermophilic species before (Horáček, Bogdanowicz & Đublić 2004; Beck 1995). However, it has to be taken into account that the collection of records might be biased to more accessible sites (Elith & Leathwick 2007), so as low situated, warm areas. We found *P. macrobullaris* (N=49) on average at 710 m a.s.l. as a majority of data stemmed from the well investigated Ticino (Southern Alps). These findings are in strong contrast to the suggested allocation of *P. macrobullaris* as strongly alpine species and to first DNA verified locations, which were all derived from above 800 m a.s.l. (Kiefer *et al.* 2002). However, recent findings from Croatia (average at 700-800 m a.s.l.; Pavlinić & Tvrtković 2004) and from Northern Italy (average at 700 m a.s.l.; Trizio *et al.* 2005) support our outcome. Furthermore it has to be considered that in the Swiss Alps *P. macrobullaris* is at the northernmost and consequently coldest part of its currently known distribution.

Foraging areas: To a certain degree our landscape models also reflect foraging habitat preferences of the bats. The known feeding sites of *P. auritus*, a gleaning species (Beck 1987; Anderson & Racey 1991) are either associated with woodland or individual trees (Entwistle *et al.* 1996; Fuhrmann & Seitz 1992; Swift & Racey 1983). Our results (Table 2) from the landscape model suggest a preference for all tree related habitats but also weakly for open meadows, where *P. auritus* was almost never observed foraging (Entwistle *et al.* 1996; Fuhrmann & Seitz 1992; Swift & Racey 1983). The preference of *P. auritus* for intensive meadows in the local model is therefore surprising. We attribute this to the lower resolution of the meadow maps and to survey period of the forest maps which is dating back to 1990/92 (Table 2). Thus, the habitat preferences of radio-tracked individuals which were observed in semi-open areas of expanding forests, where often misclassified as meadows. The evidence

from the landscape model for a preference of *P. austriacus* for orchards and vineyards is in accordance with foraging observations from orchards (Ashrafi *et al.* in prep.; Flückinger & Beck 1995; Kiefer & Veith 1998). Although *P. austriacus* has been described as avoiding large woodlands, it recently has been shown to forage also at forest edges (Flückinger & Beck 1995), in deciduous forests (Kiefer & Veith 1998) and was observed foraging within a single tree (K. Märki, pers. communication).

The preference of *P. macrobullaris* for deciduous forests in our data might be influenced by the many records derived from the Ticino (Southern Alps). In the local model *P. macrobullaris* showed a preference for extensive meadows what is congruent with the observations in the field (Ashrafi *et al.*, in prep.). Radio tracking observations from two colonies in Switzerland are not showing a preference for deciduous forests (Ashrafi *et al.*, in prep.). But in Croatia this species covers the range from areas of deciduous forests at the lower slopes to the subalpine belt of deciduous or coniferous forests (Pavlinić & Tvrtković 2004).

ARE *P. AUSTRIACUS* AND *P. MACROBULLARIS* PARAPATRIC IN SWITZERLAND?

On the basis of the current state of knowledge, distributions of *P. austriacus* and *P. macrobullaris* are excluding each other in Switzerland, even though their broad-scale areas of habitat potential are overlapping. For instance we predicted *P. austriacus* for the lowlands in the Ticino (Southern Alps), but there the species was not recorded by recent broad surveys (Mattei-Roesli, pers. communication). Such a distribution where not all suitable regions are occupied is referred to as “non-equilibrium distribution” (Chefaoui & Lobo 2007). There are three possible explanations for this situation. First, the two species might be separated by the Alps due to historical reasons. In Austria *P. austriacus* was only recorded northeastern of the Alps (Spitzenberger 2001) and no records were found in Lombardy, Northern Italy (Trizio *et al.* 2005). The second explanation is competitive exclusion, which is supported by the strong similarities between the two species environmental niches’ as shown in

the discriminant analysis and by parallels in their feeding and foraging niches (Ashrafi *et al.*, in prep.). A third option is, that even though the two species highly overlap in their dietary requirements (Ashrafi *et al.*, in prep.) and most likely in their foraging habitats (Ashrafi *et al.*, in prep.), the two species might depend on different small-scale habitat variables which were not sufficiently detected by the model.

SAMPLING DESIGN

Nowadays, many Natural History Museums are digitalizing their specimen data and giving open access to researchers, an opportunity for making good use of this large datasets with spatial analyses (Rowe 2005). Key benefits are that such data are rapidly disposable, cover large areas and thus allow for a first prioritisation of areas for systematical investigations. However, it has to be considered that the collection of records lack a systematic sampling design and data thus may be biased towards more accessible (Elith & Leathwick 2007), densely populated and better-surveyed areas (Hausser *et al.* 1995).

Another possibility to gain information about habitat preferences was shown in the local model. Foraging data are highly accurate and up to date. However, for the analysis of such data, maps of high resolution are needed as *Plecotus* species are foraging in small, restricted areas. In the local model it seems that features relating to the natural foraging habitat were not sufficiently captured by the available geo-data and additional habitat mappings might be necessary.

CONCLUDING REMARKS & IMPLICATIONS FOR CONSERVATION

In the Swiss red list (Duelli 1994) *P. auritus* is categorized as “endangered” what implicates stable populations in some areas whilst decreasing populations in others. *P. auritus* is able to exploit a broad range of environmental conditions and based on our predictions the species is distributed all over Switzerland. *P. austriacus* is categorised as “potentially endangered with uncertainties in taxonomy or occurrence”

(Duelli 1994). Due to determination uncertainties in *P. austriacus* (e.g. Arlettaz *et al.* 1997, Beck 1995), missing systematic surveys of this species (Beck 1995), and the expected rareness, *P. austriacus* is a candidate for a typical case for the conservation-related problems, Schönrogge *et al.* (2001) described for cryptic species: This species was already rare in Switzerland (Beck 1995) and now after the new discovery of *P. macrobullaris* might be much rarer than it was realized beforehand due to confusions with the other two species. As this species is mainly restricted to the lowlands, the most intensified region in Switzerland, it is additionally prone to suffer from landscape transformations and intensifications in agricultural and silvicultural practices. We highly recommend emphasizing further systematic research and conservation action here. Due to its recent discovery, *P. macrobullaris* is not yet allocated to a red list status in Switzerland. It seems quite common south of the alpine arch, but more investigations in the alpine areas are needed. Missing information on fine-scale habitat selection and the lack of systematic long-term observations of the population trends of all three species still impede a final allocation of their conservation statuses. Like other studies (e.g. Sattler *et al.* 2007, Schönrogge *et al.* 2002) this study stresses the importance for conservation management to recognize cryptic species and their habitat requirements, as they can differ considerably between sibling species and, as a consequence, species might turn out to be more threatened as previously realized. Our results can contribute to further investigations by providing a spatially explicit framework for focusing fine-scale habitat selection analyses and conducting systematic surveys of distribution and population trends.

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8. APPENDIX

TABLES

LANDSCAPE MODEL

Table 3: Coefficient values for the eco-geographical variables (EGV) included in the models for *P. auritus* (N=45), *P. austriacus* (N=21) and *P. macrobullaris* (N=49) on the significant ecological niche factors (out of ten). The first factor explains 100% of the marginality, the contribution to the explained specialisation of each factor is given in brackets. Positive coefficient values on the marginality factor (M) indicate preference for a certain variable. In the last two columns the variables' contribution to overall explained specialisation (S.) and explained information ($I = (M. + S)/2$) over the significant factors are stated for each variable.

<i>P. auritus</i>									
EGV	M + 1. F (33%)	2. F (25 %)	3. F (14%)	4. F (11%)	5. F (6%)	Expl. (87%)	S.	Expl. (94%)	I.
Coniferous forest (fq)	0.27	0.49	-0.07	-0.27	0.46	0.27		0.25	
Mixed forest (fq)	0.15	0.68	0.04	-0.12	0.63	0.27		0.20	
Deciduous forest (fq)	0.17	0.15	-0.40	-0.26	-0.23	0.19		0.17	
Open forest (fq)	0.24	-0.33	-0.22	-0.50	0.10	0.25		0.23	
Small woods (dist)	-0.18	0.22	-0.55	0.12	-0.09	0.21		0.18	
Orchards and vineyards (fq)	0.20	-0.09	-0.46	-0.38	-0.34	0.21		0.19	
Meadows (fq)	0.11	0.15	0.11	-0.37	-0.26	0.14		0.11	
Towns (dist)	-0.13	-0.05	0.01	0.03	-0.21	0.07		0.09	
Single buildings & villages (dist)	-0.80	0.25	0.05	-0.12	-0.20	0.35		0.55	
Average summer temperature	0.30	0.16	0.51	0.53	-0.22	0.27		0.27	

<i>P. austriacus</i>									
EGV	M + 1. F (85%)	2. F (6 %)	3. F (4%)	4. F (2%)		Expl. (97%)	S.	Expl. I. (99%)	
Coniferous forest (fq)	-0.34	0.21	0.42	-0.55		0.33		0.33	
Mixed forest (fq)	-0.09	0.03	-0.27	0.46		0.10		0.22	
Deciduous forest (fq)	0.15	0.01	0.05	-0.28		0.14		0.24	
Open forest (fq)	0.28	0.74	-0.16	0.54		0.30		0.32	
Small woods (dist)	0.00	-0.00	-0.05	0.17		0.01		0.17	
Orchards and vineyards (fq)	0.40	-0.10	0.25	0.26		0.36		0.34	
Meadows (fq)	0.11	-0.03	-0.46	-0.14		0.11		0.22	
Towns (dist)	-0.31	-0.02	-0.14	-0.04		0.27		0.30	
Single buildings & villages (dist)	-0.56	-0.07	-0.38	-0.01		0.49		0.41	
Average summer temperature	0.45	0.62	0.54	0.12		0.44		0.38	

<i>P. macrobullaris</i>									
EGV	M + 1. F (48%)	2. F (23 %)	3. F (11%)	4. F (6%)		Expl. (88%)	S.	Expl. I.(94%)	
Coniferous forest (fq)	-0.02	0.28	-0.11	0.08		0.09		0.05	
Mixed forest (fq)	0.03	0.85	0.17	0.22		0.24		0.12	
Deciduous forest (fq)	0.36	0.14	0.09	-0.24		0.23		0.28	
Open forest (fq)	0.22	-0.02	0.66	0.04		0.19		0.19	
Small woods (dist)	-0.26	-0.05	-0.14	0.70		0.20		0.22	
Orchards and vineyards (fq)	0.27	0.22	-0.21	-0.36		0.23		0.24	
Meadows (fq)	-0.08	0.31	-0.39	-0.19		0.16		0.11	
Towns (dist)	-0.07	-0.12	-0.46	-0.18		0.12		0.09	
Single buildings & villages (dist)	-0.68	0.15	0.18	-0.24		0.39		0.51	
Average summer temperature	0.45	-0.06	-0.24	0.37		0.28		0.35	

Table 4: Marginality, specialisation and tolerance (1/specialisation) for the three *Plecotus* species in Switzerland.

	<i>P. auritus</i> (N=45)	<i>P. austriacus</i> (N=21)	<i>P. macrobullaris</i> (N=49)
Marginality	0.92	1.40	1.39
Specialisation	1.51	4.91	2.02
Tolerance (1/S)	0.66	0.20	0.50

Table 5: Lloyd's asymmetric niche overlap of species X with species Y ($Z_{x(y)}$) between the three species in Switzerland on the first (a) and second (b) factor of the discriminant analysis.

(a)

X	Y		
	<i>P. auritus</i>	<i>P. austriacus</i>	<i>P. macrobullaris</i>
<i>P. auritus</i>	—	0.93	1.96
<i>P. austriacus</i>	1.95	—	2.48
<i>P. macrobullaris</i>	1.75	1.06	—

(b)

X	Y		
	<i>P. auritus</i>	<i>P. austriacus</i>	<i>P. macrobullaris</i>
<i>P. auritus</i>	—	0.37	1.59
<i>P. austriacus</i>	0.81	—	1.74
<i>P. macrobullaris</i>	1.43	0.735	—

Table 6: Discriminant analysis for the three species. The discriminant factor's contribution to the explained variance are given in brackets. Correlations of the eco-geographical variables (EGV's) with the first and second discriminant factor (DF1 and DF2) as well as to overall explained variance are indicated.

EGVs	Contribution to		Total explained variance (77%)
	DF 1 (45%)	DF 2 (32%)	
Coniferous forest (fq)	-0.01	-0.42	0.14
Mixed forest (fq)	-0.21	-0.66	0.31
Deciduous forest (fq)	-0.55	0.29	0.34
Open forest (fq)	-0.15	-0.09	0.10
Small woods (dist)	0.30	-0.13	0.18
Orchards and vineyards (fq)	-0.09	0.23	0.11
Meadows (fq)	-0.20	-0.40	0.22
Towns (dist)	0.16	0.25	0.15
Single buildings & villages (dist)	0.31	-0.09	0.17
Average summer temperature (May to August)	-0.61	0.03	0.28

LOCAL MODEL

Table 7: Reproductive state, total number of observation-nights and locations, average distance to roost ($m \pm$ standard deviation) and maximum distance to roost (m) of $N=8$ radio tracked females in 2008.

	Individual	Reproductive state	Season	N of nights	N of bearings	Mean distance	\pm SD	Max. distance
<i>P. auritus</i> (Blitzingen)	Aur 01	Lactating	July	3	44	481	41	1343
	Aur 28	Non-lactating	July	3	44	629	51	1595
	Aur 27	Post-lactating	August	2	57	1651	69	2309
	Aur 25	Lactating	July	3	31	359	19	732
	4 females			11	176	780	181	1495
<i>P. macrobullaris</i> (Obergestein)	Mac 04	Non-lactating	July	4	62	896	35	1650
	Mac 17	Non-lactating	July	5	30	635	42	1202
	Mac 03	Non-lactating	July	5	32	815	85	1502
	Mac 35	Non-lactating	August	2	53	606	37	1091
	4 females			16	177	588	198	5445

Table 8: Marginality, specialisation and tolerance ($1/\text{specialisation}$) of radio tracked *P. auritus* ($N=4$ individuals) and *P. macrobullaris* ($N=4$) in the local model.

	<i>P. auritus</i>	<i>P. macrobullaris</i>
Marginality	1.178	1.258
Specialisation	2.023	2.832
Tolerance ($1/S$)	0.494	0.353

Table 9: Coefficient values for the most important eco-geographical variables (EGV) included in the local models for (*P. auritus*) or two (*P. macrobullaris*) on the significant ecological niche factors (out of 13). The first factor explains 100% of the marginality, the contribution to the explained specialisation of each factor is given in brackets. Positive coefficient values on the marginality factor (M) indicate a preference for a certain variable. In the last two columns the variables' contribution to total explained specialisation (S.) or explained information ($I = (M. + S)/2$) the average of the absolute values of marginality and explained specialisation) over the significant factors are stated for each variable.

<i>P. auritus</i>												
EGV	M ⁺ + 1. F* (53%)	2. F* (12%)	3. F* (6%)	4. F* (6%)	5. F* (5%)	6. F* (4%)	7. F* (5%)	8. F* (3%)	9. F* (2%)	10. F* (2%)	Expl. S. (97%)	Expl. I. (98%)
Coniferous forrest (fq)	-0.11	-0.07	-0.01	-0.41	-0.56	0.09	0.32	-0.14	0.24	-0.36	0.15	0.11
Mixed forest (fq)	0.05	0.08	-0.82	0.12	0.10	0.04	-0.19	-0.03	-0.38	0.19	0.12	0.07
Deciduous forest (fq)	0.20	0.07	0.11	-0.12	0.04	-0.27	0.35	-0.15	-0.02	-0.06	0.16	0.25
Forest edges (fq)	0.05	0.08	-0.82	0.12	0.10	0.04	-0.19	-0.03	-0.38	0.19	0.20	0.30
Hedges & single trees (fq)	0.23	0.02	0.32	0.11	-0.15	0.08	-0.52	0.09	0.45	0.29	0.08	0.05
Intensive meadows (fq)	0.43	-0.11	0.09	-0.36	-0.15	-0.34	-0.20	-0.61	0.15	0.22	0.32	0.74
Extensive meadows (fq)	-0.12	0.20	0.28	0.10	-0.07	-0.31	-0.19	0.12	0.05	-0.24	0.14	0.16
Water (dist)	0.05	0.11	-0.10	-0.02	-0.43	-0.39	-0.08	0.18	-0.27	-0.06	0.10	0.07
Roads (dist)	-0.28	-0.01	0.11	0.49	-0.27	-0.07	0.44	-0.01	0.19	0.47	0.23	0.29
Ways (dist)	-0.26	-0.24	0.21	0.23	-0.13	0.25	-0.27	-0.07	-0.44	0.03	0.23	0.28
Buildings & villages (dist)	-0.53	-0.36	-0.15	-0.39	0.40	-0.18	-0.10	0.19	0.30	0.41	0.41	0.62
Elevation	-0.41	0.79	-0.06	-0.28	-0.42	0.22	-0.32	-0.65	0.01	-0.22	0.39	0.47
Slope	-0.33	-0.33	0.20	0.07	0.10	-0.62	-0.10	-0.24	0.03	-0.18	0.27	0.37

<i>P. macrobullaris</i>				
EGV	M ⁺ + 1. F* (60%)	2. F* (18%)	Expl. S. (77%)	Expl. I. (89%)
Coniferous forrest (fq)	-0.26	0.12	0.18	0.33
Mixed forest (fq)	-0.03	0.00	0.05	0.24
Deciduous forest (fq)	-0.24	0.18	0.01	0.03
Forest edges (fq)	-0.25	-0.25	0.07	0.26
Hedges & single trees (fq)	0.18	0.06	0.02	0.18
Intensive meadows (fq)	0.53	0.31	0.37	0.82
Extensive meadows (fq)	-0.23	-0.04	0.10	0.27
Water (dist)	0.12	0.02	0.04	0.13
Roads (dist)	-0.30	-0.02	0.08	0.31
Ways (dist)	-0.10	0.05	0.03	0.10
Buildings & villages (dist)	-0.20	0.02	0.02	0.20
Elevation	-0.32	0.86	0.33	0.32
Slope	-0.44	-0.23	0.01	0.44

Table 10: Discriminant analysis for *P. auritus* and *P. macrobullaris*. Correlations of eco-geographical variables (EGV's) with the discriminant factor are indicated, which explains 42% of the variance.

EGVs	Coefficients
Coniferous forest (fq)	0.475
Mixed forest (fq)	-0.215
Deciduous forest (fq)	-0.250
Forest edges (fq)	0.123
Hedges & Single trees (fq)	0.100
Intensive meadows (fq)	-0.074
Extensive meadows (fq)	-0.723
Water (dist)	0.269
Roads (dist)	0.103
Ways (dist)	0.099
Buildings & villages (dist)	-0.050
Elevation	-0.018
Slope	-0.125

FIGURES

LANDSCAPE MODEL

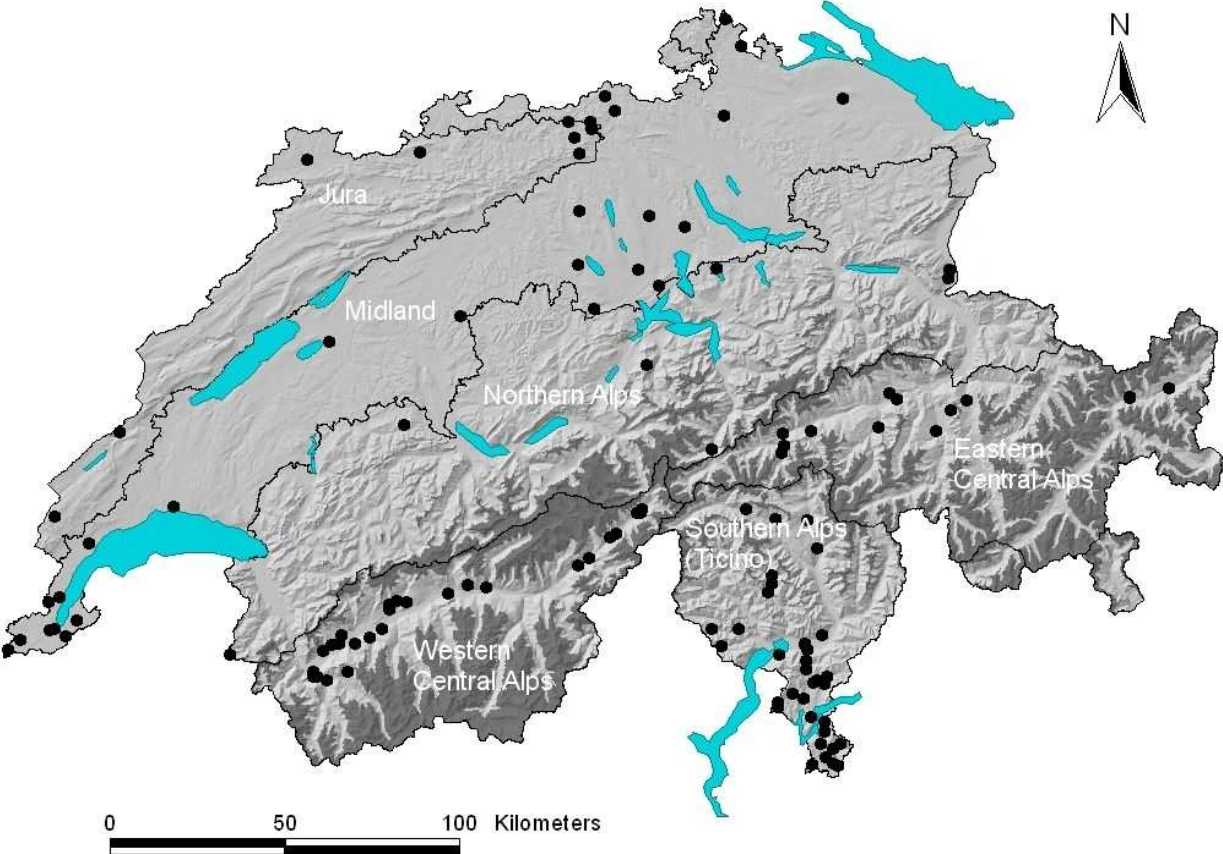


Figure 1: Map with six biogeographical regions of Switzerland according to Gonseth et al. (2001). Biogeographical regions are delimited by black lines. Data records of *Plecotus* (N=115, black circles) in Switzerland. The dark-grey shaded area represents zones above the forest border line (2300m a.s.l.).

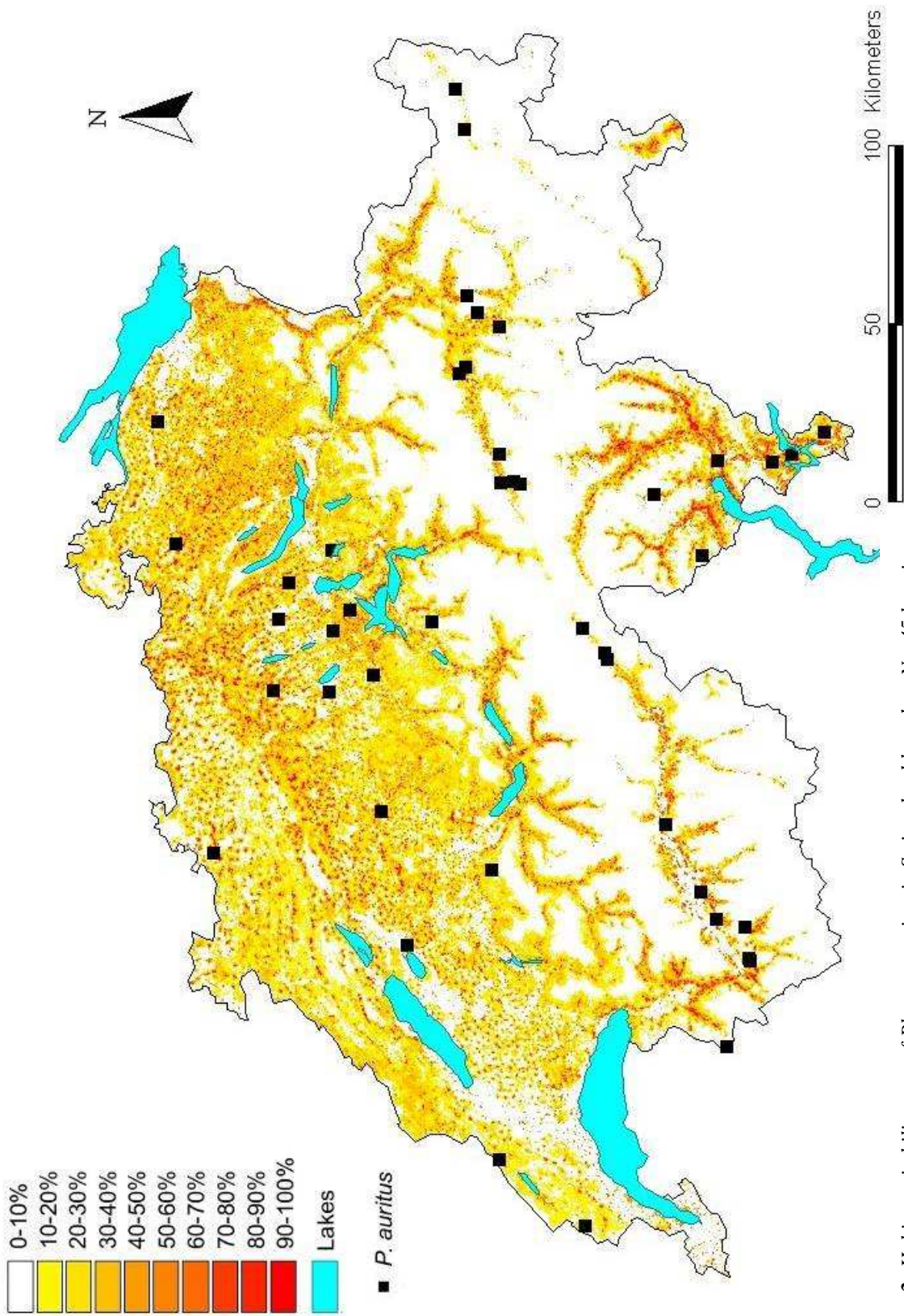


Figure 2: Habitat suitability map of *Plecotus auritus* in Switzerland based on N= 45 locations (black squares). HS-values range between 0 and 100 %.

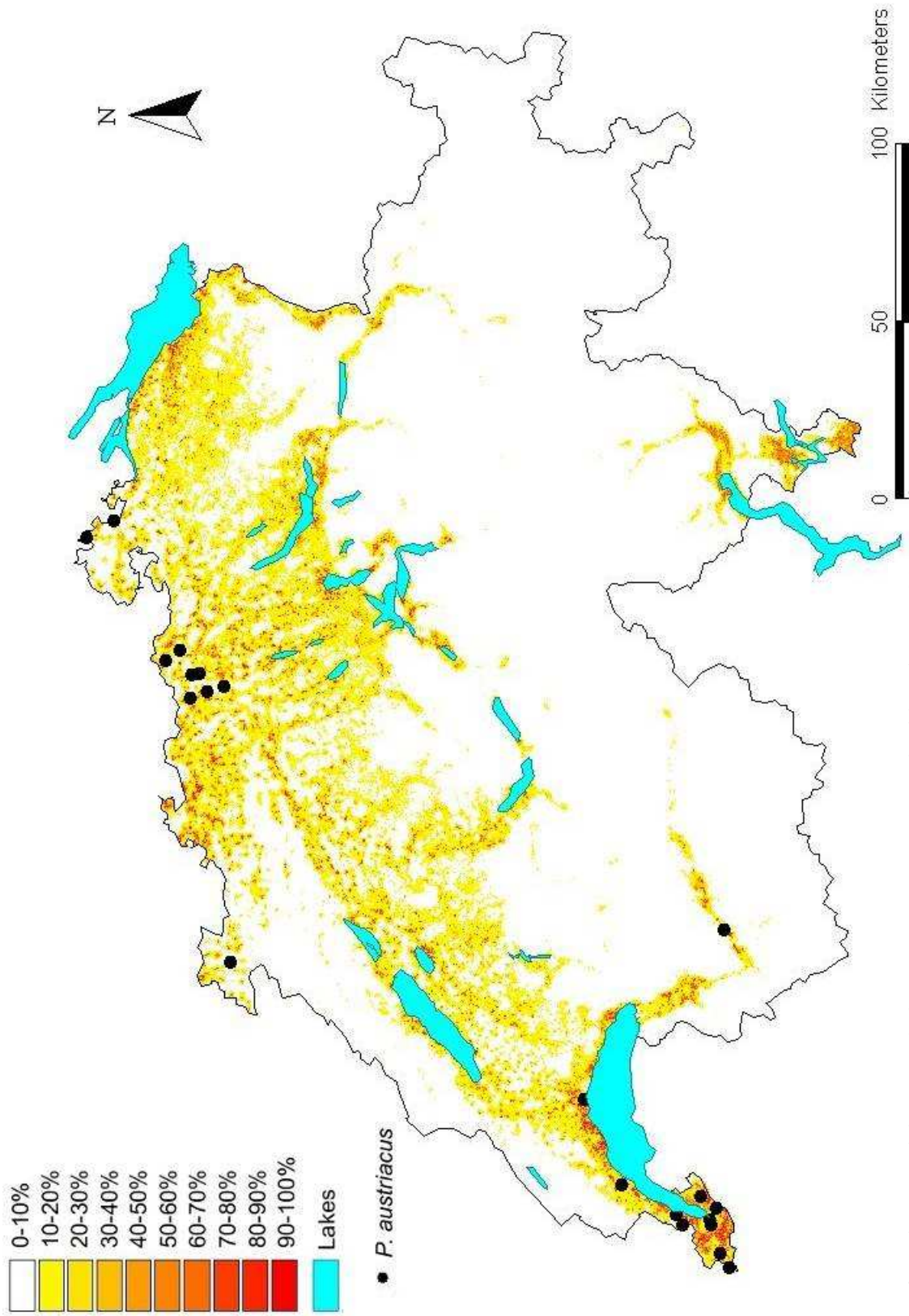


Figure 3: Habitat suitability map of *Plecotus austriacus* in Switzerland based on $N=21$ locations (black circles). HS-values range between 0 and 100 %.

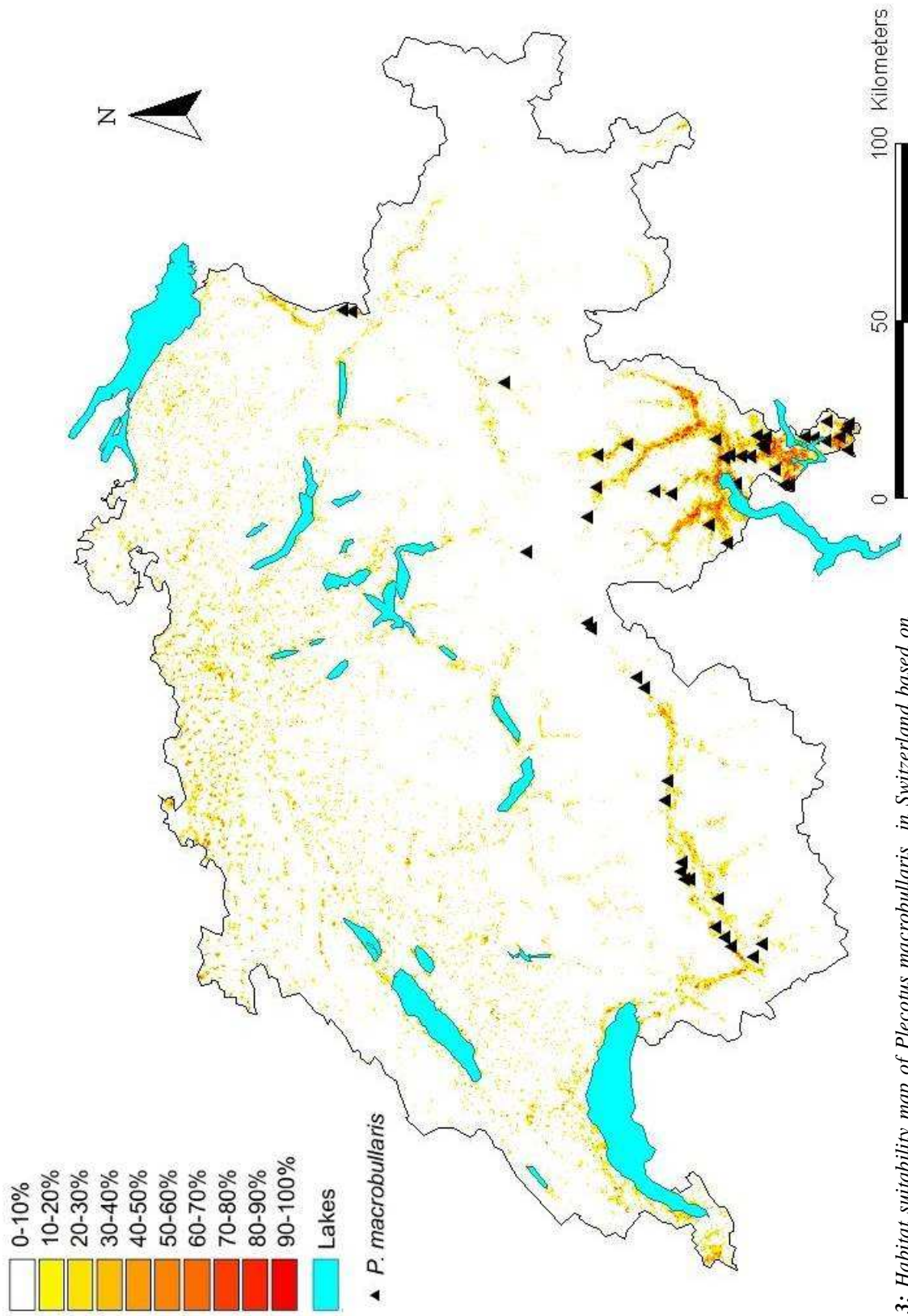
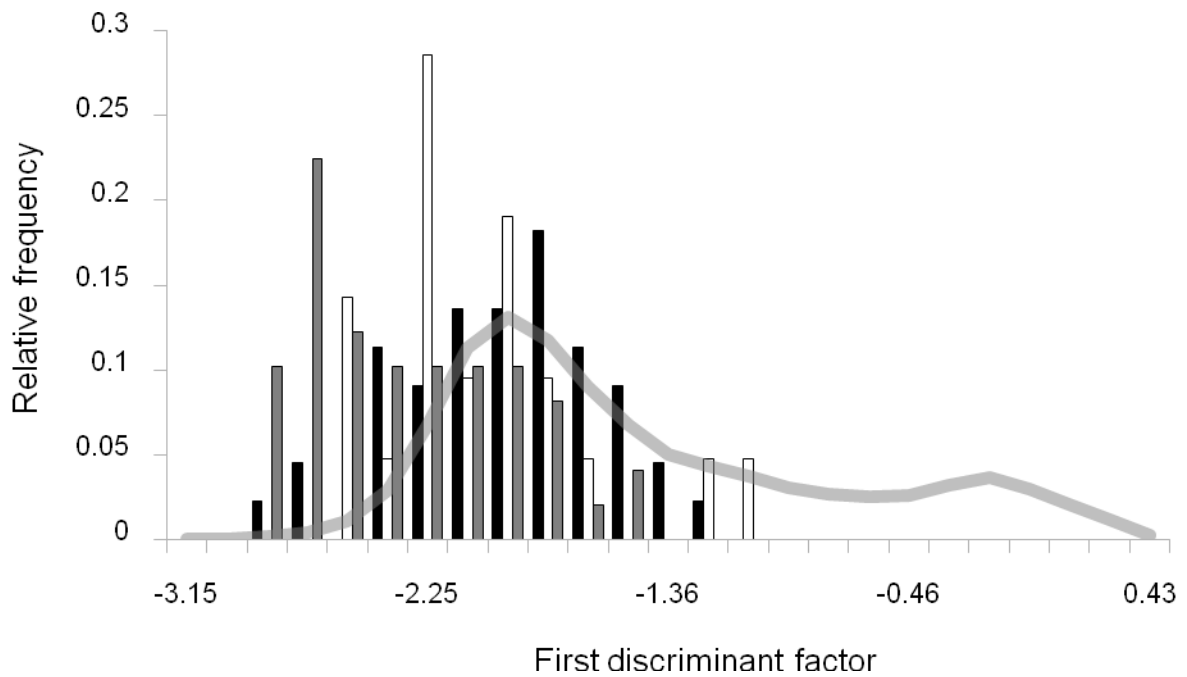


Figure 3: Habitat suitability map of *Plecotus macrobullaris* in Switzerland based on $N=49$ locations (black circles). HS-values range between 0 and 100%.

(a)



(b)

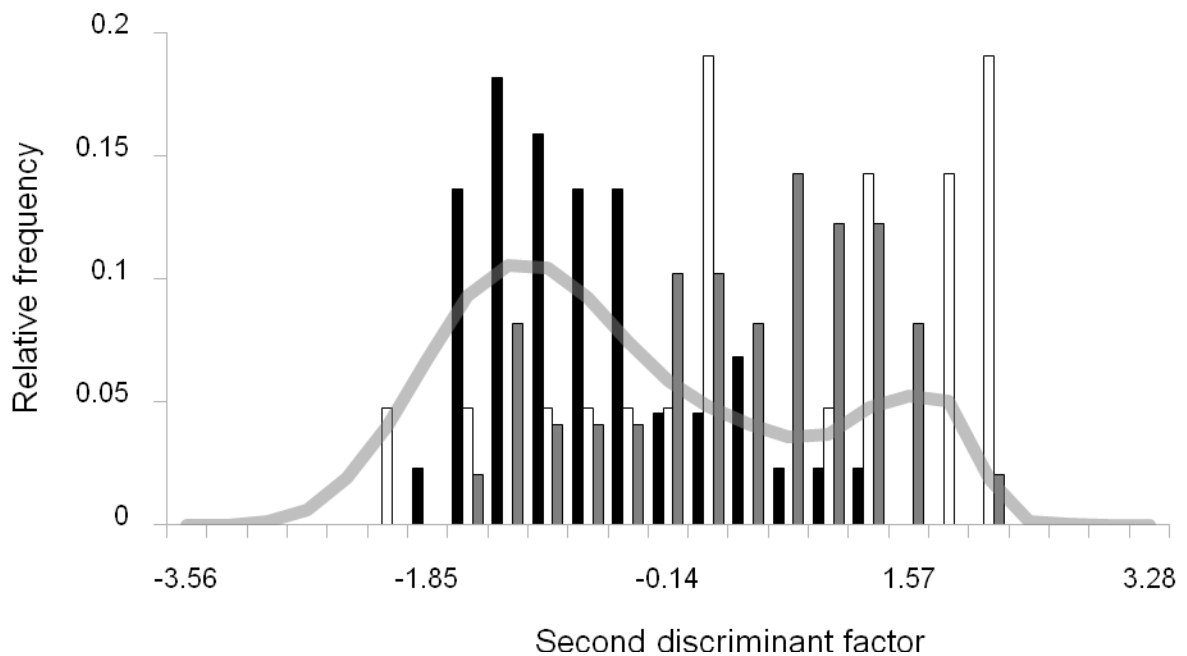
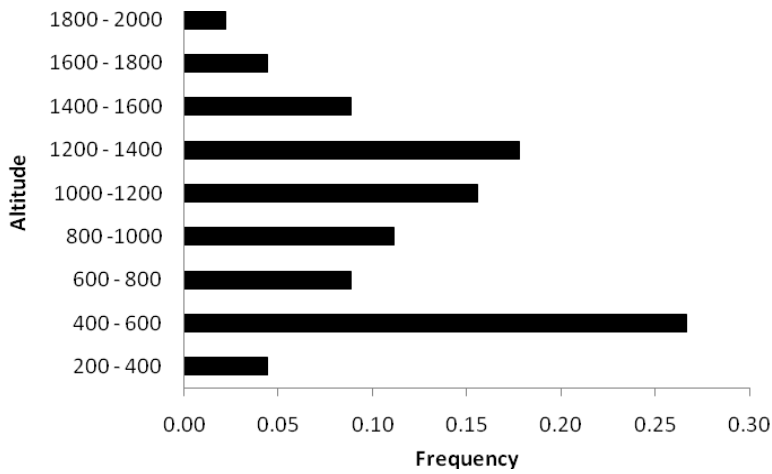
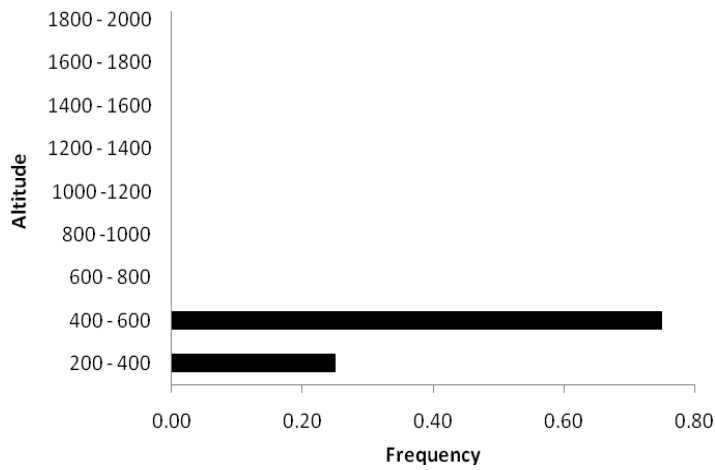


Figure 5: Discriminant analysis of *P. auritus* (black), *P. austriacus* (white) and *P. macrobullaris* (grey) in Switzerland. Relative frequency of species presence along the discriminant factors is compared to the frequency distribution of global cells (grey line). The first (a) and second (b) discriminant factor are calculated as to maximise the differences between three species in the environmental space.

(a) *P. auritus*



(b) *P. austriacus*



(c) *P. macrobullaris*

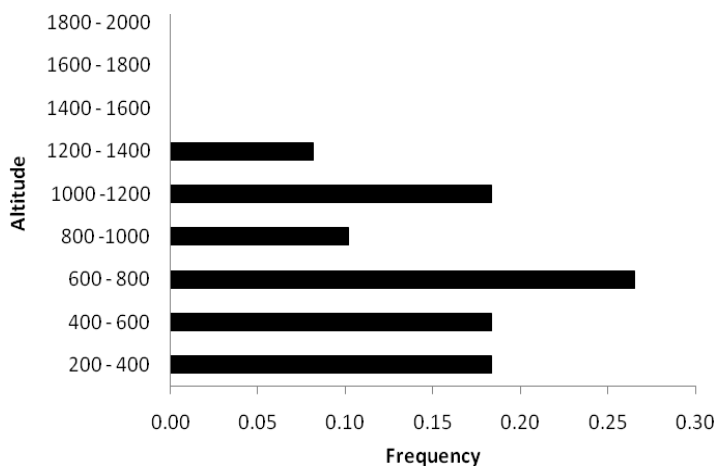


Figure 6: Frequency of locations of (a) *P. auritus* ($N=45$), (b) *P. austriacus* ($N=21$) and (c) *P. macrobullaris* ($N=49$) in different altitudinal ranges in Switzerland.

LOCAL MODEL

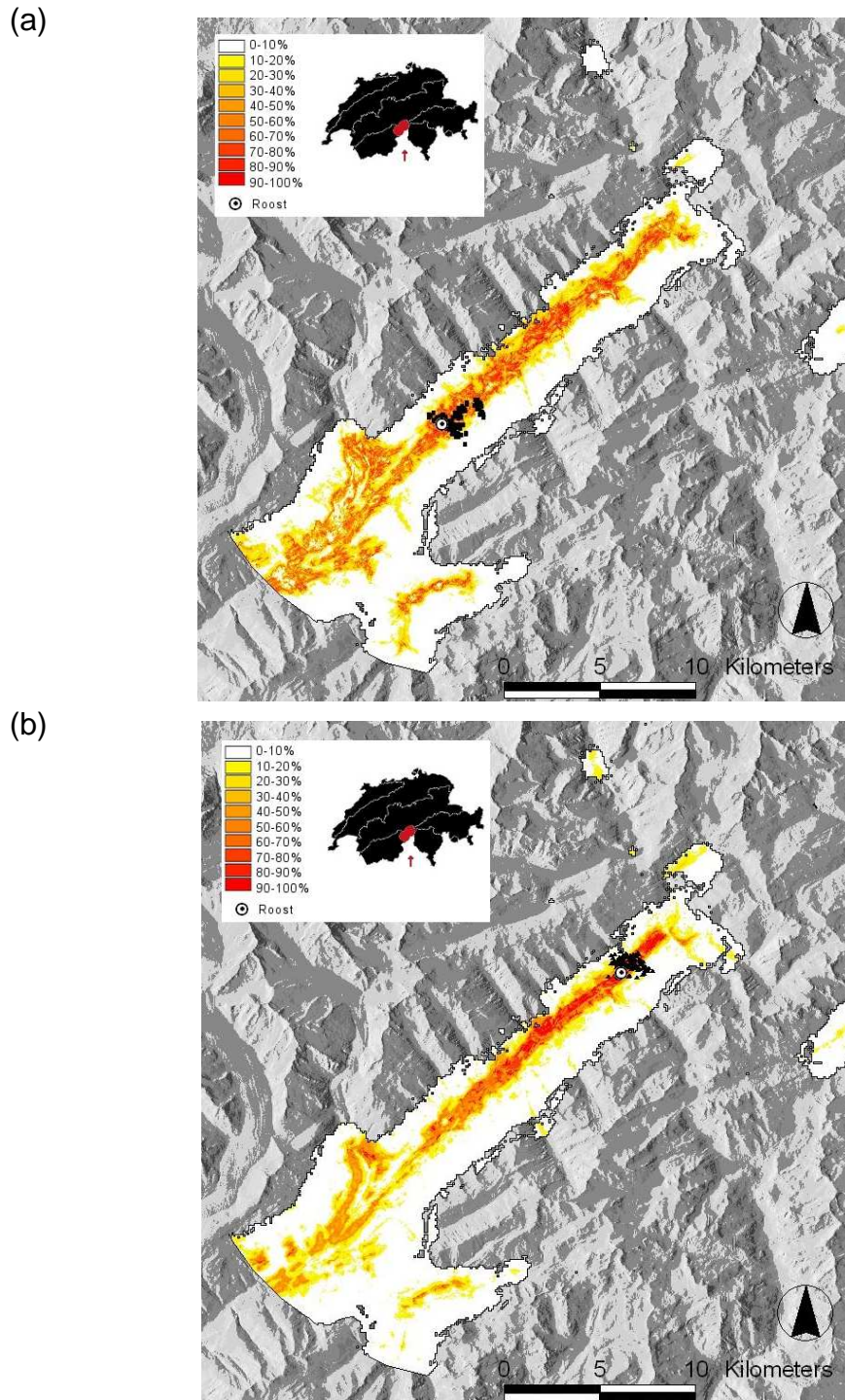


Figure 7: Habitat suitability maps as generated in the local-scale models using presence-data of (a) four radio tracked female *P. auritus* (black squares) and of (b) four female *P. macrobullaris* (black triangles). The area for the local was delimited by the predicted suitable area of the landscape model.

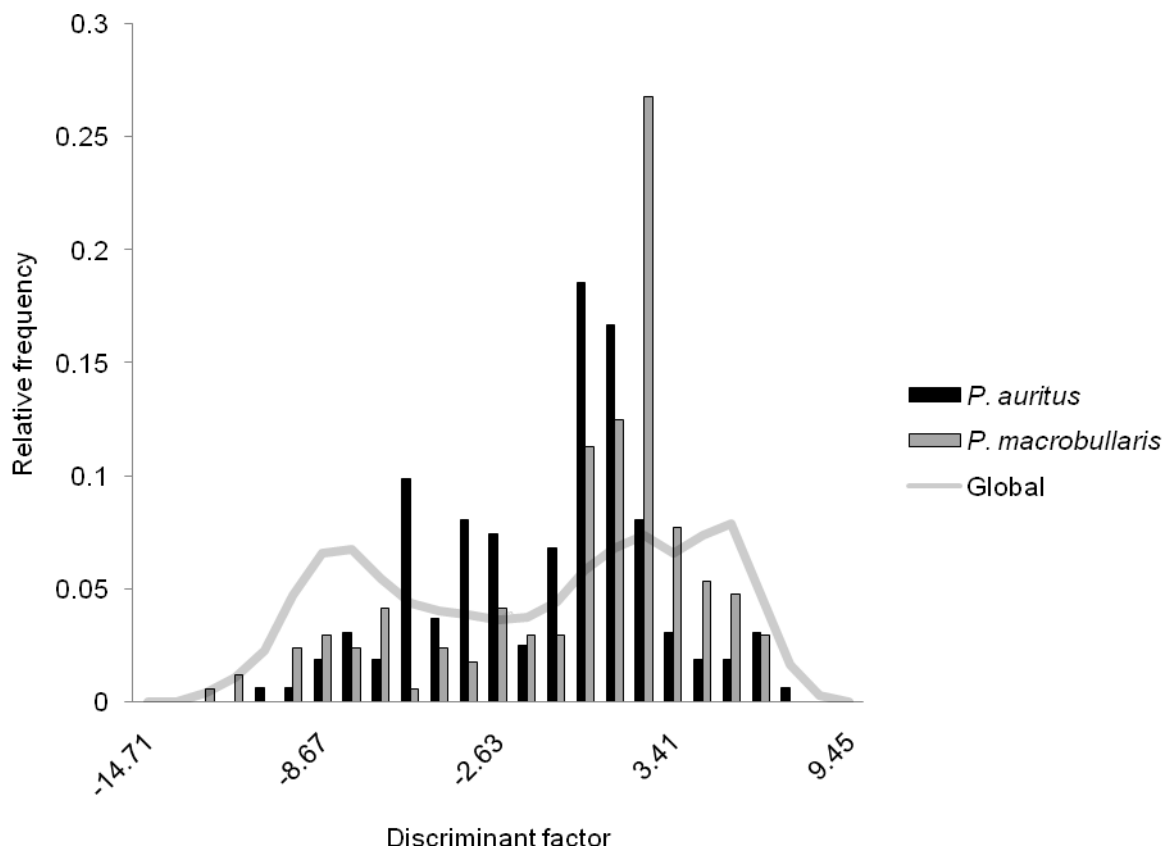


Figure 8: Discriminant analysis of *P. auritus* (black), and *P. macrobullaris* (grey) based on local-scale radio tracking data. The relative frequency of species observations along the discriminant factors is compared to the frequency distribution of all grid-cells of the study area (light grey line).

Erklärung

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass Diplomarbeit andernfalls als ungenügend taxiert werden kann.