Master thesis

PREDICTING HABITAT SUITABILITY FOR LITTLE OWLS IN SWITZERLAND ON DIFFERENT SPATIAL SCALES

Patrick Scherler

March 2014

Supervised by

Dr. Martin Grüebler, *Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland*

Dr. Beat Naef-Daenzer, *Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland*

Prof. Dr. Lukas Keller, *Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland*

ABSTRACT

Accurate predictions of habitat suitability depend on habitat analyses on multiple spatial scales. Broad-scale distribution and composition of land cover plays an important role for the choice of breeding locations and occurrence probabilities; home-range scale structural composition of habitats reflects resource availability influencing reproduction and survival rates. However, habitat suitability studies incorporating parameters on landscape and home-range spatial scale are scarce, which impairs comprehensive planning of conservational measures. Land-cover data are rarely sufficient to predict local habitat suitability without including fitness relevant resources. Vice versa, high definition structural habitat data are normally missing when trying to analyze landscape suitability on wide spatial scales. This study combined both spatial scales in a two-step approach for endangered little owls *Athene noctua* in Switzerland. In a first step, habitat suitability was modeled based on landscape scale parameters and breeding occurrence data for Switzerland and Baden-Württemberg (Southern Germany), resulting in habitat suitability hotspot areas. Suitable habitat hotspots were then analyzed by field survey quantifying regional differences in habitat composition, structural richness, prey accessibility, and predation risk. A comparison on both levels between Southern Germany and Swiss regions identified potential factors responsible for the virtual absence of little owls in Switzerland. Suitable habitats for little owls on landscape scale were fruit orchard rich regions, distant to forests and urban areas. Switzerland showed less and highly scattered suitable habitat (4.23% of total area, Southern Germany: 15.59%) due to patchy forests and highly urbanized lowlands. On home-range scale Swiss suitable habitats were shown to be distinguished from Southern German sites by intensive meadow management, lower structural richness, and lower availability and complexity of tree cavities. The pattern was detected in all Swiss suitability hotspot regions, though in Western and Northern Switzerland habitat characteristics were more similar to Southern Germany. Little owl presence in Switzerland is therefore likely to be restricted by the missing structural diversity in available suitable habitats, rather than by a general lack of suitable habitats. Based on these results region specific conservation measures can be planned. Local and regional differences on both spatial scales demonstrate the importance of a multi-scale evaluation to predict suitable habitats. Our two-step approach was most adequate and efficient to detect multi-scale suitable habitats for little owls in Switzerland.

Key words: Conservation, habitat suitability, multi-scale, predictive model, little owl, GIS-modeling, species-habitat relationship, resource availability

TABLE OF CONTENT

ABSTRACT **2**

TABLE OF CONTENT **3**

INTRODUCTION **4**

MATERIAL AND METHODS **7**

Study species *7*
Landscape scale *8*
Home-range scale *10*
Field survey 10
Statistical analysis 12

RESULTS **14**

Landscape scale *14*
Home-range scale *20*
Meadow management 20
Nesting and roosting site characteristics 21
Richness in structural habitat elements 22
Prey availability and predation risk 24
Discriminating factors 25

DISCUSSION **27**

Landscape scale *27*
Home-range scale *28*
Advantages of multi-scale habitat assessment *29*
Conservation implications *30*

ACKNOWLEDGEMENTS **32**

STATEMENT OF AUTHORSHIP **32**

REFERENCES **33**

APPENDIX 1 – SUPPORTING INFORMATION ON LANDSCAPE SCALE ANALYSIS **36**

APPENDIX 2 – SUPPORTING INFORMATION ON HOME-RANGE SCALE ANALYSIS **40**

INTRODUCTION

The evaluation of habitat suitability for a species requires comprehensive analysis of species-habitat relationships including different spatial and temporal scales. Factors affecting habitat quality may act differently on broad spatial scale, than on small spatial scale. Whilst, for example the use of open-spaced landscape for efficient predator identification is a consequence of predator avoidance on landscape scale, on home-range scale predator avoidance may be characterized by highly structured habitats providing sufficient hide-outs. To account for these differences the choice of adequate analysis scales is of high importance (Graf et al. 2005, du Toit 2010, Gottschalk et al. 2011a). To predict habitat suitability it is therefore mandatory to conduct studies on at least two spatial scales according to the preferred configuration of landscapes, as well as to its local resource requirements on home-range scale. Often, studies are limited to certain aspects of either spatial scale and therefore only depict the partial truth when it comes to evaluating habitat suitability. Studies focusing on landscape scale distribution patterns in occupied habitats and expansion probabilities to unoccupied habitats, including small-scale resource availability are scarce. Reliable and efficient methods to conduct studies on several spatial scales are not yet standard in habitat suitability analysis.

In applied species conservation, the knowledge of the availability of suitable habitats is indispensable for the implementation of specific measures to enhance population spread. These measures are normally based on one spatial scale. On one hand, broad-scale conservation implications evaluating range expansion of endangered and fragmented populations often rely on estimates of a species' potential distribution range obtained by expert knowledge and correlative modeling approaches based on actual occupancy (Guisan & Zimmermann 2000, Jaberg & Guisan 2001, Gottschalk et al. 2011b). On the other hand, studies covering certain aspects of the species' habitat requirements on a small spatial scale, normally conducted with field surveys, serve to plan more detailed conservation measures with a narrow geographical focus. This is mainly implemented with the aim to change demographic parameters, i.e. to increase survival or productivity by enhancing limiting factors. Although both, large-scale distribution modeling and small-scale habitat requirement surveys are needed to establish effective conservation plans, most habitat suitability studies and resulting conservation measures do not aim at enhancement of small-scale habitat quality. In contrast, conservation measures often are based on species-habitat associations. Under the assumption of habitat types reflecting resources, effective resource availability is often neglected, potentially leading to inefficient conservation efforts.

Computational advancements over the last years led to new possibilities in habitat modeling. Several authors show that correlative modeling of habitat suitability with geoinformational software (GIS) based on high-resolution landscape layers and either breeding site or movement data leads to reliable habitat suitability predictions (Gottschalk et al. 2011b, Lundy et al. 2012, Marcer et al. 2013, Bellamy et al. 2013). The resulting habitat suitability maps show possible limitation of available habitats and define conservational hotspot areas (Brambilla et al. 2009, Fernandez & Gurrutxaga 2010, Wilson et al. 2011). Due to limited availability of resource relevant data on large geographical scales, this approach neglects specific small-scale use of the preferred habitat by the target species, not taking into account any fitness relevant habitat parameters such as prey availability, predation risk or roosting and breeding site quality (Delattre et al. 1996). This niche-based knowledge is normally the basis of an analysis of local population dynamics or of the local availability of suitable habitats, but it is rarely used to show regional habitat suitability as it is time consuming to gather this kind of information on wide geographical ranges. Often, studies on both spatial scales are available but are hardly comparable with each other (studies performed on different populations under different conditions), leaving room for uncertainties when they are used as planning instruments in species conservation. Therefore, a combination of landscape scale modeling and niche-relevant habitat factors acquired on home-range scale provides a comprehensive insight into effective habitat suitability. All aspects of habitat requirement are taken into consideration. That is, not only landscape requirements defining spatial ranges and distribution limitations, but also local quality aspect based on home-range scale parameters covering trophically relevant aspects crucial for habitat choice are taken into account. Approaches addressing different spatial scales at once are rarely implemented in a single study (Brambilla et al. 2009) but help to optimize planning of conservation projects by providing reliable habitat suitability measures.

Many European avian raptor species suffered dramatic decreases in population sizes over the last few decades (Knaus et al. 2011). In order to prevent regional or even global extinction of these species, vast conservation efforts have been undertaken. Most changes in abundance can be linked to changes in landscape structure and habitat distribution (Fuller 2012) or to anthropogenic changes within habitats such as intensified management in agricultural fields (Birrer et al. 2011, Sanderson et al. 2013). A correlation between altered landscapes and variation in raptor distribution has been shown using GIS-modeling for various species (Martinez et al. 2003, Heuck et al. 2013). Other studies have revealed small-scale changes in habitats such as effects of pesticide input in food chains (Hernandez & Margalida 2008), loss of small structural elements in agricultural environment (Vickery & Arlettaz 2012, Morelli et al. 2014) or change in forest structures (Graf et al. 2007, Cahall et al. 2013) using empirical correlative or experimental on-site designs.

The aim of this paper is to introduce a practicable method which combines habitat suitability evaluations on different scales as an instrument for comprehensive planning of conservation measures for endangered species. We provide a habitat suitability analysis for a nocturnal avian raptor species, the little owl *Athene noctua*, in Switzerland. In a two-step approach, a landscape scale habitat suitability model will be calculated first, using high resolution landscape data and occupancy data from Baden-Württemberg, a state in Southern Germany adjacent to Switzerland. Suitability hotspots will be identified from the landscape scale model. In a second step, the resulting suitability hotspots will be assessed regarding home-range scale parameters in a field survey. We suggest that differences on both spatial scales are potential factors explaining differences in occupancy between regions. The combination of two spatial scales and different assessment strategies allows us to cover a broad spectrum of habitat parameters and therefore also a wide range of niche properties. In addition, this enables us to identify crucial factors for the species' presence. The use of this two-step evaluates the distribution of suitable habitat for this species in Switzerland.

Additionally the results of this study may help to resolve the riddle of little owl absence in Switzerland that conservationists have been confronted with for the last 10 years and which is assumingly based on differing habitat structures compared to occupied areas in Southern Germany.

MATERIAL AND METHODS

The study focused on two different spatial scale, landscape scale and home-range scale, and therefore used different methods to predict habitat suitability for little owls in the area of Switzerland and the Southern German state of Baden-Württemberg. Available breeding site data were used to identify potential habitats by modeling landscape scale habitat suitability. The resulting habitat suitability map was then used to identify hotspot areas with high densities of suitable habitat. Subsequently, the resulting potential habitats within the hotspot areas were analyzed on a more detailed level by a field survey measuring habitat parameters on home-range scale.

Study species

The little owl *Athene noctua* is a small nocturnal raptor which inhabits mainly fruit orchards and open-spaced low-intensity farmland areas in middle Europe (Van Nieuwenhuyse et al. 2006 pages xv-xviii). Despite its opportunistic feeding behavior with a broad spectrum of prey (Van Nieuwenhuyse et al. 2006 page 218), this species depends on highly structured habitats providing high accessibility to prey (McCracken & Tallowin 2004, Van Nieuwenhuyse et al. 2006 pages 202-204, Apolloni et al. 2013). Cavities with different entry openings are essential as breeding and roosting sites. Nevertheless, little owls also accept artificial nest boxes located on trees as well as on buildings (Van Nieuwenhuyse et al. 2006 pages 333-366). This opportunistic cavity breeder suffered an extreme decrease in Switzerland with only five isolated populations remaining with no more than a hundred breeding pairs in total (Schaub et al. 2006). Despite intensive habitat restoration efforts in Northern Switzerland and the provision of artificial breeding sites only a slight increase in population densities has been observed (Brahier et al. 2012). In contrast, populations in Southern Germany showed exponential population increase after the implementation of nesting box provision. Although little owls breed right across the Swiss border in Southern Germany, no new broods were detected in this area on Swiss soil so far. This implies differences in habitat suitability on at least one spatial scale. The populations are well studied and monitored (Burbach 1997, HGON 2005) providing us with the possibility to include knowledge concerning habitat preferences, spatial movement patterns and nesting behavior into our analyses. The combination of broad distribution in Southern Germany as opposed to the fragile status of the Swiss populations, and the extensive knowledge of the species' ecology make the little owl an eligible study organism for a habitat suitability analysis on different spatial scales.

Landscape scale

Breeding location data (n=356) from Southern Germany served as the basis for a GIS-based analysis of potential habitats on landscape scale within the study area. Breeding locations were compiled by Thomas Gottschalk and provided by little owl ringers in Baden-Württemberg from 2007 to 2010 (Gottschalk et al. 2011b). Each breeding site location served as a presence point. The equal amount of "pseudo-absence points" (absence points) was randomly generated with a minimum distance of 1000 m (avoiding overlap). A uniform high resolution (10x10m) land-cover map was generated for Baden-Württemberg and Switzerland. Land-cover data for Southern Germany were based on information from the Corine Land Cover 2006 (CLC) and ATKIS (Amtliches Topographisch-Kartographisches Informationssystem); Swiss geoinformational data was acquired from vector25 land-cover map and DHM elevation model by Swisstopo, as well as from the Arealstatistik 2004 of the Bundesamt für Statistik (bfs). All data layers were combined into a single land-use map for the whole study area covering both countries. The land-use map finally included parameters of 10 different land-use classes (arable land, forest, shrub and low vegetation areas, water, wetlands, orchards, meadows, settlements and hedges, see table 1). Additionally meteorological data, namely the average temperature and precipitation models from March to May 2010 for Baden-Württemberg and Switzerland were included in the analysis. Besides the local land-use class and meteorological data at the location of breeding sites or absence points (local variables), variables on the surrounding matrix within a 400 m radius (i.e. covering a little owl's maximum home-range size; Grzywaczewski 2009), were generated for each matrix cell (10x10 m). Besides the landscape diversity (Shannon index), the percentage of important land-use classes in a 400 m radius and distances to important land-use classes was calculated with SLICER 3.0 by moving window technique (Gottschalk et al. 2008). The values of all variables at presence and absence points served as predictor parameters for the modeling process. All GIS analyses were performed with ArcMap GIS 10.0 (ESRI Environmental Science Research Institute Inc., Redlands, CA, USA) with help of the implemented statistics package GEPARD (Gottschalk et al. 2007).

All parameters were checked for intercorrelation by Spearman rank correlations. A generalized linear model with a logit link function and a binomial error distribution was used to analyze the effect of land-use and meteorological variables on the occurrence probability of little owls. The most accurate model was determined by Corrected Akaike's Information Criterion comparison (backward AICc; Burnham & Anderson 2002). The model showing the highest AICc weights was used for all further calculations. In order to calculate a habitat suitability raster matrix, the resulting regression parameter estimates were used to predict occurrence probability of little owls for each raster matrix element. To facilitate the visualization and analysis, ten explicit habitat suitability classes were derived from the occurrence probability values (habitat suitability class 1 → occurrence probability 0.0 to 0.1, habitat suitability class 2 → occurrence probability 0.1 to 0.2, etc.). The application of this model based raster formula was restricted to areas below 600 meters above sea level (a.s.l.), which represents the historically known vertical distribution boundary in Switzerland (Knaus et al. 2011, Van Nieuwenhuyse et al. 2006 page 90). Only occurrence probabilities from 0.5-1 were taken into consideration for the illustration of habitat suitability (habitat suitability classes 6-10).

The resulting habitat suitability map based on breeding sites, representing a landscape of occurrence probabilities, was validated by a comparison of habitat suitability with habitat use data from Baden-Württemberg based on a five year radio-tracking survey of 394 little owls (n=45'118 locations) in a population in the surrounding area of Ludwigsburg. Radio-tracking data were recorded year-round from individuals of all age classes (i.e. dispersing juveniles or breeding birds) from 2007 to 2013 (own unpublished data). Breeding sites of radio-tracked little owls were not included in the habitat suitability model as presence data. Thus, validation was done with independent little owl individuals.

Based on the habitat suitability map, regions showing high densities of suitable habitats (high occupancy probabilities) were identified by performing a weighted Kernel density analysis. This Kernel analysis used ArcMap default parameters to define search radius (maximum area extent divided by 30) and to calculate kernel densities for each country of the study area separately to account for high differences in density of suitable habitats. This quantitative interpretation of the habitat suitability results on landscape scale was then used to determine the borders of Swiss hotspot regions. Kernel density values were subdivided into 10 classes. Only the eight highest density classes were included in the extraction of the hotspot regions. This threshold was chosen by reducing classes stepwise until unconnected hotspot regions emerged. Hotspot regions containing these Kernel densities were extended according to geographical regions, topographical boundaries of Switzerland and expert knowledge on similarities concerning regional habitat composition and cultivation patterns. Four hotspot regions were identified in Switzerland (NJ: Northern Switzerland, SL: Western Switzerland, TG; Eastern Switzerland, ZS: Central Switzerland, Fig. 1). An additional hotspot region (DE) was delimited by Minimum Convex Polygon (MCP) including all radio-tracking locations used for model validation in Baden-Württemberg. This region shows high densities of little owls. Regions located south of the Alps (Valais and Ticino) were not included due to a considerable influence of differing meteorological conditions and differing habitat requirements of southern little owl populations. All five hotspot regions served as study regions for the home-range scale habitat analysis.

Table 1: Variables used as model predictors for presence/absence modeling of little owl occurrence probability based on breeding location data in Baden-Württemberg, Southern Germany.

GEOINFORMATIONAL VARIABLES	VARIABLE TYPE
mean spring precipitation (March - May)	local variable
mean spring temperature (March - May)	local variable
local land-cover class: arable land	local variable
local land-cover class: forest	local variable
local land-cover class: vegetation free area	local variable
local land-cover class: wetlands	local variable
local land-cover class: open water	local variable
local land-cover class: fruit orchard	local variable
local land-cover class: other land-cover types	local variable
local land-cover class: meadow	local variable
local land-cover class: urban area	local variable
local land-cover class: hedges and single trees	local variable
distance to next hedge or single tree	local variable
distance to next wetland or open water	local variable
percentage of arable land area	surrounding matrix variable (radius of 400 m)
percentage of forest area	surrounding matrix variable (radius of 400 m)
percentage of fruit orchard area	surrounding matrix variable (radius of 400 m)
percentage of urban area	surrounding matrix variable (radius of 400 m)
land-cover diversity (Shannon)	surrounding matrix variable (radius of 400 m)

Home-range scale

Field survey

For the home-range scale habitat suitability analysis, we recorded parameters known to be crucial for survival and reproduction of little owls directly in the field (Tomé et al. 2004, Van Nieuwenhuyse et al. 2006 pages 160-276, Żmihorski et al. 2009, Brahier et al. 2012, Bock et al. 2013, Apolloni et al. 2013, Table 2). For each hotspot region, 100 study sites of an area of 1 ha were chosen randomly in the top 10% of suitable habitats, resulting in a total of 500 study sites. The study sites were all centered to the next available fruit tree, because they are known as the main breeding site of little owls in Central Europe. Furthermore, the study site had not to consist of more than one third of sealed soil; otherwise it was moved to the nearest fruit tree meeting this requirement. The choice of habitat parameters at home-range scale was based on mechanisms in the ecology of little owls. Loss of natural cavities as breeding and roosting sites due to shifts in orchard structures is considered to be the main reason for the decline of little owls in Central Europe (Van Nieuwenhuyse et al. 2006 pages 184-192, Bock et al. 2013). Similarly, a negative influence of high intensity farmland on relevant resources and structures is assumed (Birrer et al. 2011, Sanderson et al. 2013). Therefore, the focus of the field survey was on standard fruit tree orchard structures on one hand, and on agricultural field-use and habitat composition on the other hand. In total, the parameters cover aspects of habitat quality in terms of breeding and roosting sites, prey availability and accessibility, as well as predation risk. Each tree (breast height diameter > 30 cm) in the study site was measured individually. We recorded stem diameter (at breast height), quantity of suitable cavities (entrance diameter > 6 cm, depth > 20 cm; Bock et al. 2013), type and connectivity of cavities (woodpecker cavity, connected to other cavities) and number of available artificial nest boxes. Furthermore, land-use classes (artificial grassland, natural meadow and arable land with respective crop identification), indication for grazing, intensity of natural meadow management in three intensity classes relying on indicator grassland plant species (MVP – "Mit Vielfalt Punkten" manual of the Swiss ornithological Institute, Jenny et al. 2011). In addition to high land-use diversity, high structural diversity is suggested to be an important habitat feature for little owls (Apolloni et al. 2013, Bock et al. 2013). Thus, small structures such as wood piles, piles of branches or stones, percentages of fallow land, gardens, fruit plantations, hedges and marginal stripes serving as foraging structures were counted. In addition, anthropogenic structures such as farm houses, shelters and accessible hiding places at houses were also recorded. These structural elements were then summarized for further analysis (number of structural elements, Table 2). A high rodent prey availability is crucial for the survival and breeding success of little owl fledglings (Thorup et al. 2010, Perrig et al. submitted). Therefore, the relative abundance of rodents was measured based on the count of field signs, such as runways, piles and holes. These signs along three transects of 5 m per study site give a proxy for rodent abundance. Using this transect method allows a reliable relative density estimates of common voles *Microtus arvalis* (Brown et al. 1996, Bruegger et al. 2010, Apolloni et al. 2013). For each study site, three transect counts were conducted, one in an orchard, one on a natural meadow outside the orchard and one on a field margin. All transect positions were chosen randomly within the respective land-use types (orchard, natural meadow and field margin) and the sum of rodent tracks per transect was multiplied by the according area of the land-use type available at the study site. Resulting values from orchard transects and meadow transects were summed up to an index for grassland rodent availability, whilst the value for field margins served as an index for rodent availability in arable field areas. Additionally, a point count of potential predators was conducted at the center of each study site. For two minutes, all birds of prey visible with binoculars (Zeiss Conquest HD, 10 x 42) inside and outside the study site were counted by species. Acoustic species records were also included, when birds were out of sight. Counts were separated by common buzzards (main diurnal predator of little owls; Van Nieuwenhuyse et al. 2006 page 296) and red kites (unknown predation effects on the little owl) and summed-up to a total of potential predators seen.

Statistical analysis

Variables measured in the field were combined and reduced to an overall of 16 variables for further analysis (Table 2). In order to reduce the often highly correlated number of variables and to structure them according to the habitat requirements of little owls, thematically related variables were converted to principal components. Three thematically coherent principal component analyses (PCAs) were performed covering variables related either to orchard structure, cavity availability and characteristics or prey availability and accessibility. The PCAs were based on correlation matrices using JMP statistical software package (Version 10.0. SAS Institute Inc., Cary, NC.). The number of principal components included was defined by a threshold of 45% of the explained cumulative variance. The data acquired separately from each tree were combined to single values per study site (average or sum). The resulting parameters were compared individually between hotspot regions and countries using an analysis of variance ANOVA and generalized linear models (GLM) according to the type of dependent variable and the distribution of residual errors, respectively. This analysis was performed with R 3.0 statistical package (R Development core team 2013). In order to identify crucial factors for the discrimination between hotspot regions on home-range scale, the reduced variable set was tested for the discriminating character by a linear discriminant analysis. This analysis was performed with SPSS statistical package (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.) using a stepwise parameter reduction by Wilks-Lambda method (significance level: 0.05). The goodness-of-fit of the linear discriminant analysis was tested by cross validation.

Table 2: Overview of all home-range scale parameters. Parameters have been condensed for further analysis to 16 factors (indicated by numbers in Analysis variable column). See Table 4 for respective variable names.

VARIABLE NAME		DESCRIPTION	ANALYSIS VARIABLE
Inclination / exposition		Degrees / 8 direction categories	
% area of arable land			**15,16**
% cover of arable land by plants			
	freshly sown		**1**
	rape (*Brassica napus*)		**1**
	corn (*Zea mays*)		**1**
	bread wheat (*Triticum aestivum*)		**1**
	potato (*Solanum tuberosum*)		**1**
	fleshy taproot (*Beta* sp.)		**1**
	vegetables		**1**
	artificial meadow		**1**
% area of natural meadow			**4,5,6**
Grazing		signs of grazed meadows (fences, cattle tracks,…) present/absent	**6**
% area of high meadow-use intensity		Standardized MVP category (Meadow type A)	**1,3**
% area of intermediate meadow-use intensity		Standardized category (Meadow Type B)	**4**
% area of low meadow-use intensity		Standardized category (Meadow type C)	**1, 5**
different mowing patterns within study site		present/absent	**7**
stone piles / dry stone wall		volume (m^3) / length (m)	**2**
stack of wood		volume (m^3)	**2**
pile of branches		volume (m^3)	**2**
Hedge		length (m)	**2**
wetland/water surface		percent of study site	**2**
fruit plantation		percent of study site (wine yards/highly productive fruit plantations)	**2**
Garden		percent of study site	**2**
fallow land		percent of study site	**2,15,16**
narrow field edges		length (m) x 1m	**15,16**
wide field edges		length (m) x 2m	**15,16**
garden shed		Number	**2**
farm house		Number	**2**
not maintained building		Number	**2**
agricultural shelter building		Number	**2**
mouse transects		3 transects of 5m per study site (orchard, off-orchard meadow, field edge)	
	number of runways		**15,16**
	number of vole piles		**15,16**
	number of mole piles		**16,15**
	number of holes		**15,16**
number of common buzzards (*Buteo buteo*)		point count (2 min) for all visible predators	**8,9**
number of red kites (*Milvus milvus*)		point count (2 min) for all visible predators	**8,10**
number of common kestrel (*Falco tinnunculus*)		point count (2 min) for all visible predators	**8**
number of other potential predators		point count (2 min) for all visible predators	**8**
number of trees			**11,12**
mean tree diameter per study site		all trees measured at breast height	**11,12**
mean number of cavities per tree		cavities: openings in the tree with diameter >6 cm and depth >20cm	**13,14**
mean number of cavities per study site			**13,14**
number of connected cavity entries			**13,14**
number of woodpecker cavities			**13,14**
number of main branch cavities		first branch circle	**13,14**
number of hollow trees			**13,14**
% dead/missing tree matter			**13.14**
number of cut trees			**11,12**
number of different tree species			
	apple trees (*Malus* sp.)		**11,12**
	pear trees (*Pyrus* sp.)		**11,12**
	cherry trees (*Prunus avium*)		**11,12**
	walnut trees (*Juglans regia*)		**11,12**
	plum trees (*Prunus domestica*)		**11,12**
number of little owl nest boxes			**2**

RESULTS

Landscape scale

In the best model fit (AICc: 326.26, explained deviance: 70.64%, df: 713; see Appendix 1 for model output and comparison) all local land cover classes were included except for arable land, vegetation free spots and wetlands (Table 3). Additionally, percentage of surrounding arable land and mean local precipitation in spring were excluded from the best model. Little owl breeding sites were located significantly more often in orchards and on meadows (in single trees) compared to random pseudo-absence points (Table 3). It was shown that forest and urban areas were not used as breeding sites (significantly negative effects). Additionally, high percentage of forests or urban areas in the proximity appeared to have a strong negative effect on breeding occupancy. In contrast, high percentage of fruit orchards surrounding the location had a strong positive effect on breeding occupancy. The findings regarding surrounding areas fully corresponded with the findings regarding local variables. Furthermore, occupied breeding sites also showed higher spring temperatures and higher land cover diversity (Shannon diversity index) than random absence points. Small but significant differences in the proximity to wetlands (or waters) and to hedges between breeding sites and absent points were detected. Breeding sites were more distant to these two land cover classes than absence points.

The model validation with year-round (including dispersal periods) radio-tracking data (n=45’118 locations) revealed that 79.54% of all telemetry locations laid within suitable habitats (habitat suitability class 6-10) and 34.8% in potential top habitats (habitat suitability class 10).

Table 3: Estimates of the best generalized linear model fit (AICc 326.26) investigating breeding occupancy in relation to land use parameters, Shannon land cover diversity index and meteorological data. Land cover parameters were included as local variable (prevalent land-use class at location), distance variable (distance from location to nearest matrix pixel of the respective land-use class; only for wetland/water and hedges) and relative occurrence (percentage of area of respective land cover class surrounding the location in a radius of 400m; only for arable land, forest, fruit orchard and urban area). All variables not listed below were excluded from the best model fit such as local mean precipitation in spring and land cover variables (arable land, wetland and vegetation free areas), as well as the relative occurrence of arable land in a radius of 400 meters (Percentage of area).

PREDICTOR VARIABLE	COEFFICIENT	STANDARD ERROR	P-VALUES
Intercept	-25.020	3.485	0.000
Distance to hedges	0.005	0.000	0.000
Distance to wetlands and open water	0.001	0.000	0.009
Percentage of area of surrounding fruit orchards	0.105	0.032	0.001
Percentage of area of surrounding urban area	-0.023	0.015	0.114
Percentage of area of surrounding forest	-0.096	0.017	0.000
Shannon diversity Index	2.611	0.725	0.000
Local mean daily temperature in spring	0.152	0.024	0.000
Local land cover class: Open water	-16.180	786.800	0.984
Local land cover class: Fruit orchard	3.176	0.492	0.000
Local land cover class: Unspecified area	0.802	1.392	0.564
Local land cover class: Meadow	1.903	0.364	0.000
Local land cover class: Urban area	-2.848	0.964	0.003
Local land cover class: Forest	-2.395	1.333	0.072
Local land cover class: Hedge	0.529	1.142	0.643

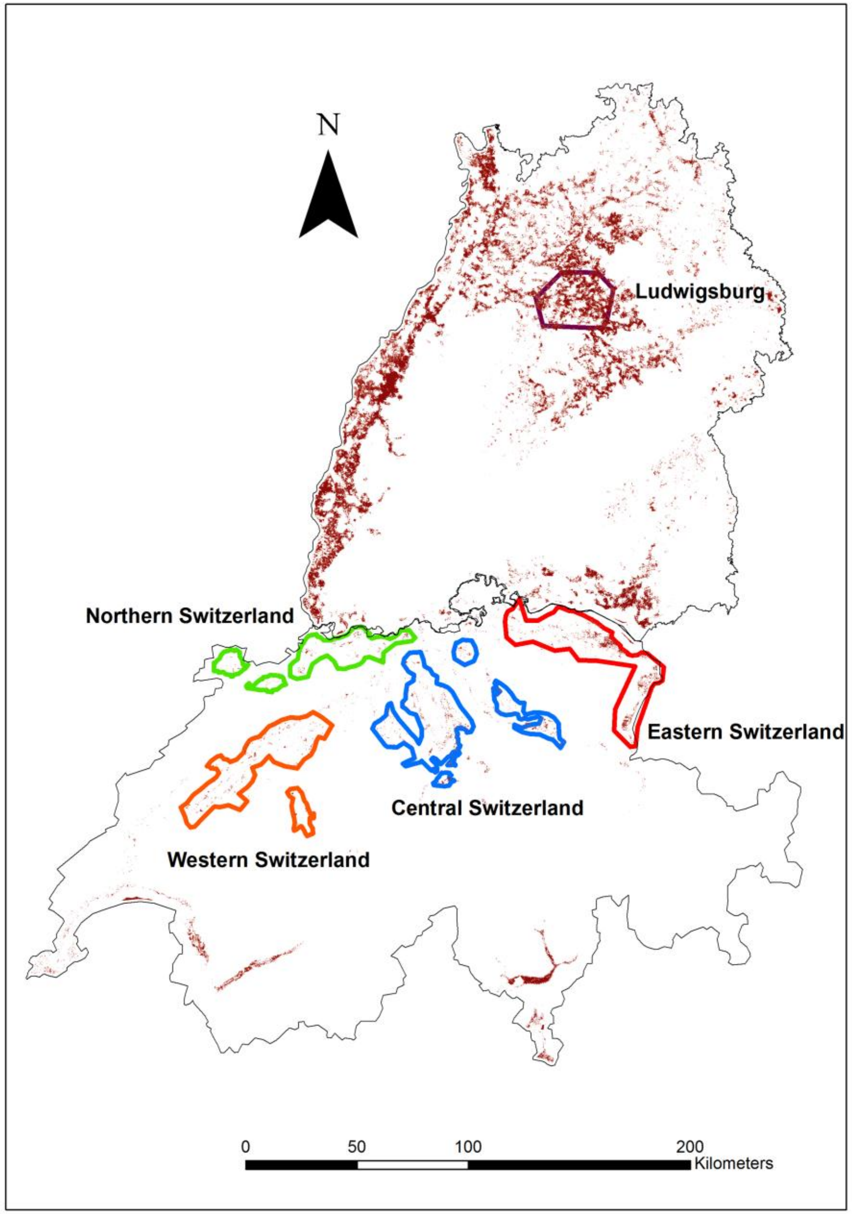
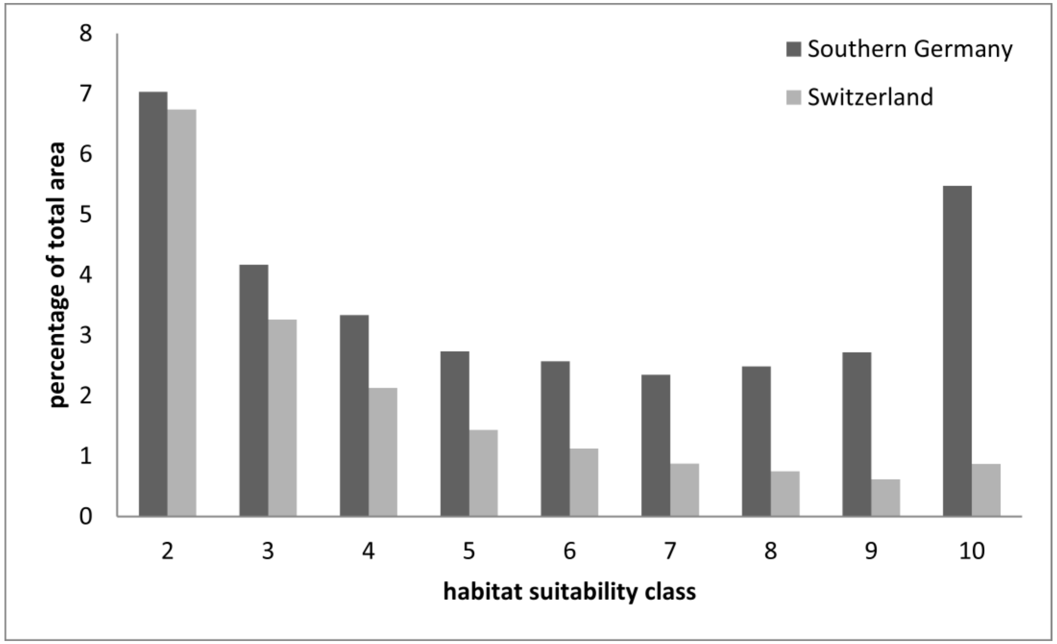


Fig. 1: suitable habitats (dark red, occurrence probability >50%) in Switzerland and Southern Germany (left) show differences in distribution and abundance between the two countries. The five focal regions (outlined by colored lines) were extrapolated from hotspot analysis by kernel density analysis for Switzerland and Minimum Convex Polygon (MCP) on nesting sites of a single population in the region of Ludwigsburg. Suitable habitats above 600 m a.s.l. were excluded due to known elevation limitation in little owl breeding. Highly suitable habitats are less abundant than less suitable habitats in both countries (below). Southern Germany (DE) provides 1607.1 km^2 of suitable habitat (15.6% of the total area below 600 m a.s.l., habitat suitability class 6-10), meanwhile Swiss (CH) suitable habitats are restricted 428.55 km^2 (4.2% of total area). Top suitable habitats (occurrence probability 90-100%) represent a large portion of all available suitable habitats in Southern Germany, whilst this class is not equally abundant in Switzerland. Habitat suitability class 1 (not suitable, occurrence probability 0-10%) was excluded from the figure below (CH 82.2%, DE 67.1%).



Applying the model to the landscapes of Southern Germany and Switzerland and illustrating the habitat suitability revealed large differences in the distribution of suitable habitats between the two countries. Suitable habitats were scarce in Switzerland compared to Southern Germany. Moreover, they were highly fragmented and surrounded by large areas of unsuitable habitats. Often, single top potential habitat patches (10x10m, occurrence probability 90-100%) were surrounded by non-hospitable habitats (Fig. 1). Overall, suitable habitats (suitability classes 6-10) only formed a proportion of 4.23% (428.55 km^2) of the total area (below 600 m a.s.l.) in Switzerland, whereas in Southern Germany suitable habitats accounted for 15.59% (1607.05 km^2) of the area. Most of the suitable habitats in Southern Germany were well-connected and formed a continuous suitability corridor from the northern parts of Baden-Württemberg along the Rhine valley to the Swiss border (Fig. 1). In Switzerland, suitable habitats occurred mainly in low mountain valleys and the highly urbanized area between the Alps and the Jura hills known as “Mittelland” (Swiss lowlands). The distribution of suitable habitats is limited by the highly populated and forest-dominated landscape of Switzerland. Nevertheless, Kernel density analysis of habitat suitability revealed several suitability hotspots in Switzerland (Fig. 2).). In North-Eastern Switzerland one hotspot along Lake Constance occurred mainly due to the high density of fruit orchards in this region. As a result of the weighted Kernel density analysis four hotspot regions covering all hotspots in Switzerland north of the Alps were defined for further analysis on home-range scale (Fig. 1 and Fig. 2). Although Northern Switzerland has been the target of the main conservation efforts for the little owl, it does not show an especially high density of suitable little owl habitats. Nevertheless, it has been investigated as a hotspot region due to its possible importance as immigration path of little owls from Southern Germany, Alsace and Jura (France) and recent local sightings of little owls. As explained earlier, suitable habitats in the Valais and the Ticino were not taken into consideration even though they also represent suitability hotspots. Populations in these southern parts of Switzerland, mainly the Ticino, are known to have very different habitat preferences in terms of nesting sites (stone cavities and old buildings), which is why the informative value of the model output is limited in this region.

Fig. 2: Weighted Kernel density analysis (red) of the landscape habitat suitability matrix revealed potential hotspot areas in Switzerland and Southern Germany. Only top 80% of kernel densities are shown to identify suitability hotspot areas. Habitat suitability class was used as weighting factor for Kernel densities. Borders of Swiss Cantons are indicated by greyish lines and lakes are projected in light blue. High densities of suitable habitats are represented by color darkness (high densities: dark red).

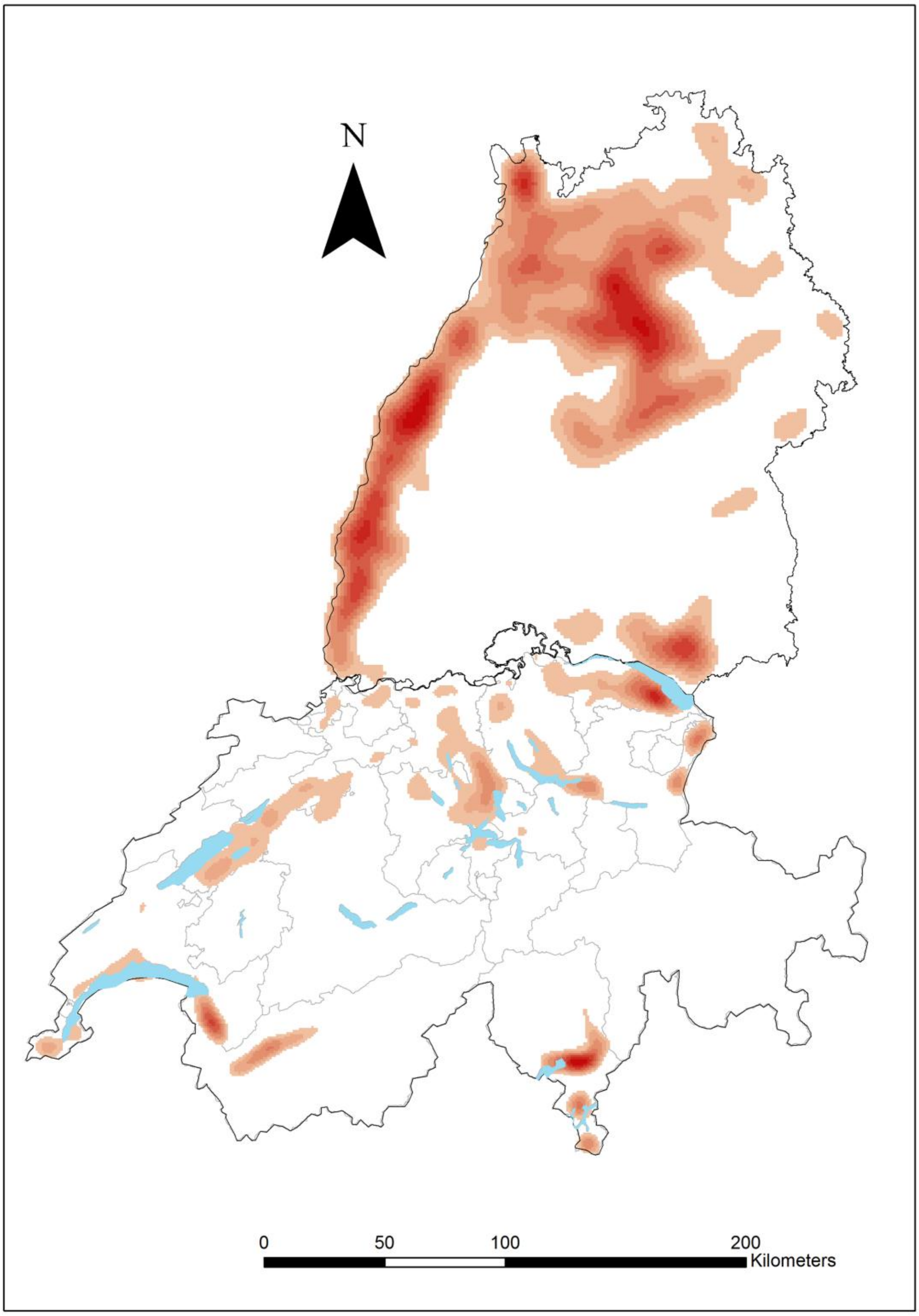


Table 4: Overview of means and variances of summarized final variables derived from field survey variables (Table 2). Means of Swiss regions varying significantly from Southern Germany are highlighted. Differences were calculated using linear regression models and generalized linear models with binomial or Poisson error distribution according to data format.

VARIABLE	**TOTAL** (n=500)		**COUNTRY**				**SWISS REGIONS**							
			CH (n=400)		**DE** (n=100)		**NJ** (n=100)		**SL** (n=100)		**TG** (n=100)		**ZS** (n=100)	
	mean	SD	mean	SD	Mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
1 Number of land-use classes	2.85	1.00	2.82	1.01	2.99	0.95	3.11	1.18	2.91	0.91	2.50	0.83	2.75	1.00
2 Structural elements	2.85	2.44	2.32	2.12	5.01	2.44	1.93	1.93	3.52	2.24	1.69	1.98	2.12	1.83
3 High meadow-use intensity	0.33	0.38	0.40	0.38	0.04	0.11	0.23	0.30	0.21	0.31	0.60	0.38	0.55	0.38
4 Intermed. meadow-use intensity	0.19	0.52	0.21	0.57	0.12	0.23	0.24	0.32	0.25	0.30	0.15	0.30	0.21	1.01
5 Low meadow-use intensity	0.20	0.30	0.12	0.23	0.54	0.34	0.18	0.28	0.15	0.23	0.05	0.15	0.09	0.21
6 Grazing	0.45	0.50	0.54	0.50	0.11	0.31	0.47	0.50	0.69	0.46	0.52	0.50	0.47	0.50
7 Mowing pattern	0.51	0.50	0.43	0.49	0.86	0.35	0.42	0.50	0.48	0.50	0.46	0.50	0.34	0.48
8 Total predation	1.12	1.62	1.22	1.74	0.74	0.88	1.15	1.02	0.94	1.03	1.32	2.43	1.45	2.03
9 Common buzzard	0.32	0.67	0.31	0.69	0.38	0.56	0.33	0.59	0.12	0.36	0.38	0.68	0.41	0.96
10 Red kite	0.42	1.08	0.51	1.19	0.07	0.29	0.34	0.64	0.40	0.64	0.58	1.90	0.71	1.09
11 PC1 orchard structure	0.00	1.57	- 0.36	1.38	1.45	1.45	- 0.97	1.21	- 0.21	1.02	0.37	1.56	- 0.63	1.32
12 PC2 orchard structure	0.00	1.19	- 0.09	1.19	0.34	1.13	1.00	0.98	0.09	1.06	- 0.84	0.76	- 0.59	1.02
13 PC1 cavities	0.00	1.71	- 0.25	1.59	1.00	1.79	- 0.33	1.33	0.26	2.12	- 0.54	1.22	- 0.40	1.45
14 PC2 cavities	0.00	1.20	0.27	0.86	- 1.08	1.68	0.29	0.75	0.46	1.21	0.09	0.58	0.23	0.75
15 PC1 mouse availability	0.00	1.33	0.03	1.31	- 0.11	1.42	0.39	1.48	0.41	1.18	- 0.43	1.10	- 0.25	1.25
16 PC2 mouse availability	0.00	1.15	0.03	1.16	- 0.11	1.11	0.15	1.16	- 0.14	1.11	- 0.02	1.23	0.11	1.12

Home-range scale

In general, Southern Germany and Switzerland showed large differences in home-range scale habitat characteristics. Thus, even Swiss hotspot regions differed significantly from Southern Germany in terms of land-use and structural habitat parameters. Among the final habitat variables (as shown in Table 4) no significant correlations were present, and therefore all parameters were included in the analyses.

Meadow management

While the percentage of grassland area in the study sites showed no large differences between hotspot regions (DE: 70.3%, SD = 26.6%; NJ: 46.8%, SD = 30.2%; SL: 61.6%, SD = 27.1%; TG: 79.8%, SD = 24.9%; ZS: 75.5%, SD = 25.9%), all Swiss hotspot regions showed a higher proportion of intensively used meadows than the Southern German study sites. Western and Northern Switzerland seemed to be more equilibrated concerning meadow-use intensities, showing higher values in intermediate and extensive meadow-use intensity than Central and Eastern Switzerland (Fig. 3).

The amount of grassland areas showing signs of grazing was significantly higher in Swiss than in German study sites. In Switzerland 54% of all study sites showed signs of grazing (up to 69% in Western Switzerland), whilst in Southern Germany just 11% of the study sites were grazed (Table 4). No significant differences were detected among Swiss hotspot regions. We found similar results in the mowing patterns of meadows. Switzerland was lacking areas with different grass vegetation height due to different mowing dates (43% of study sites showed mowing pattern), whereas 86% of German study sites showed a mosaic of grassland areas of different vegetation heights within the study areas. Missing mowing mosaics and high meadow-use intensity reflected Switzerland's high intensity dairy farming (Table 4). Only marginally significant differences were found in the number of different land-use classes per study site, restricted to Eastern Switzerland showing less land-use diversity than Southern Germany and also than the rest of Switzerland.

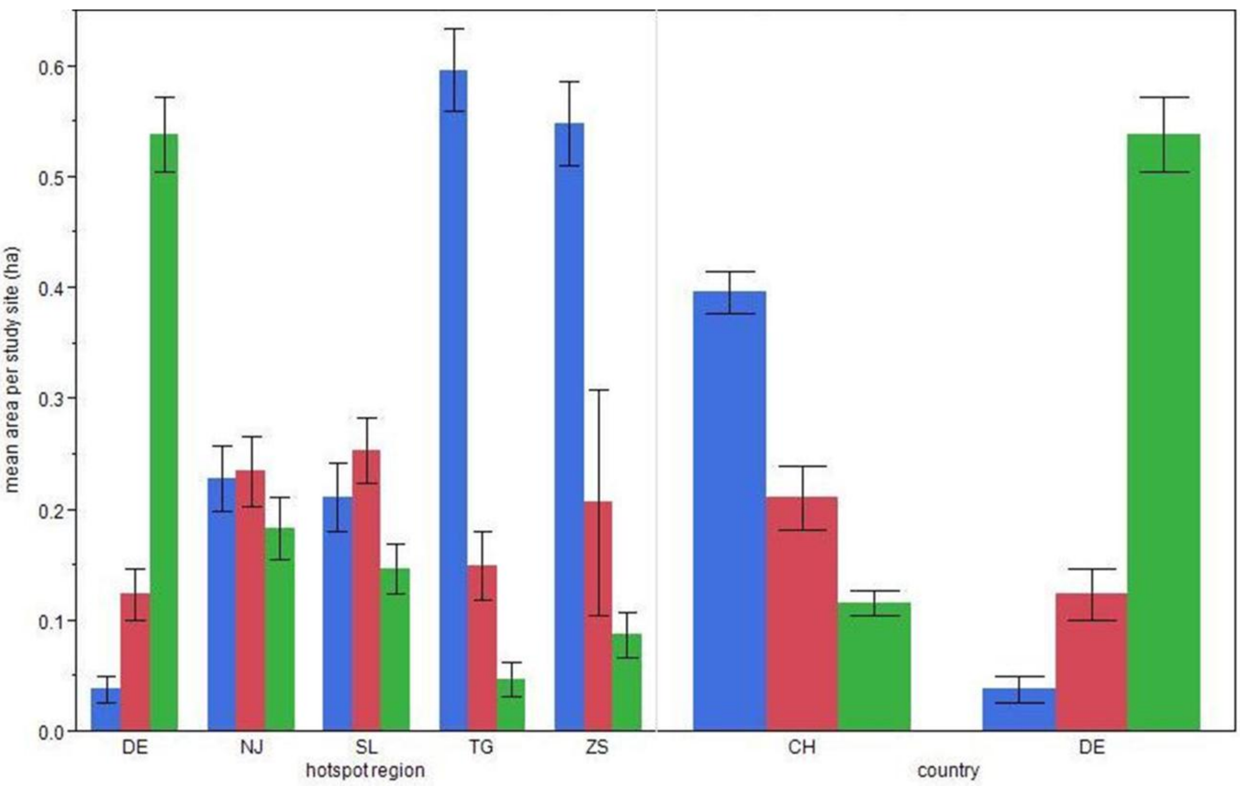


Fig. 3: Meadow-use intensity (blue: high meadow-use intensity, red: intermediate meadow-use intensity, green: low meadow-use intensity) in the different hotspot regions (DE: Baden-Württemberg, Southern Germany; NJ: Northern Switzerland, SL: Western Switzerland, TG: Eastern Switzerland, ZS: Central Switzerland) and countries (CH: Switzerland; DE: Southern Germany). Error bars indicate ± SE.

Nesting and roosting site characteristics

By conducting a principal component analysis (PCA, see Table 5), a broad variety of cavity specific variables, measured at a total of n=15'201 trees, was merged into two main variables explaining 62.25% of the variance of all cavity variables. Principal component 1 (PC 1) was mainly characterized by the effective cavity availability (total number of cavities per study site), cavity accessibility (cavities per tree), proportion of woodpecker cavities and by the proportion of hollow trees per area. The second principal component (PC 2) was mainly influenced by the number of cavities per site, the number of hollow trees and the proportion of cavities resulting from woodpecker activity. The second principal component therefore characterized study sites regarding the abundance of woodpecker cavities hollow trees relative to the total number of cavities, i.e. differences in the number of woodpecker cavities and hollow trees between sites of equal total number of cavities. Southern Germany showed high values for PC 1 compared to Switzerland, demonstrating higher numbers of tree cavities in Southern Germany than in Switzerland (Fig. 4). Within Switzerland, Western Switzerland showed higher values than the rest of Switzerland, indicating a trend towards similar conditions to the ones found in Southern Germany. For PC 2 no significant differences among Swiss regions were found.

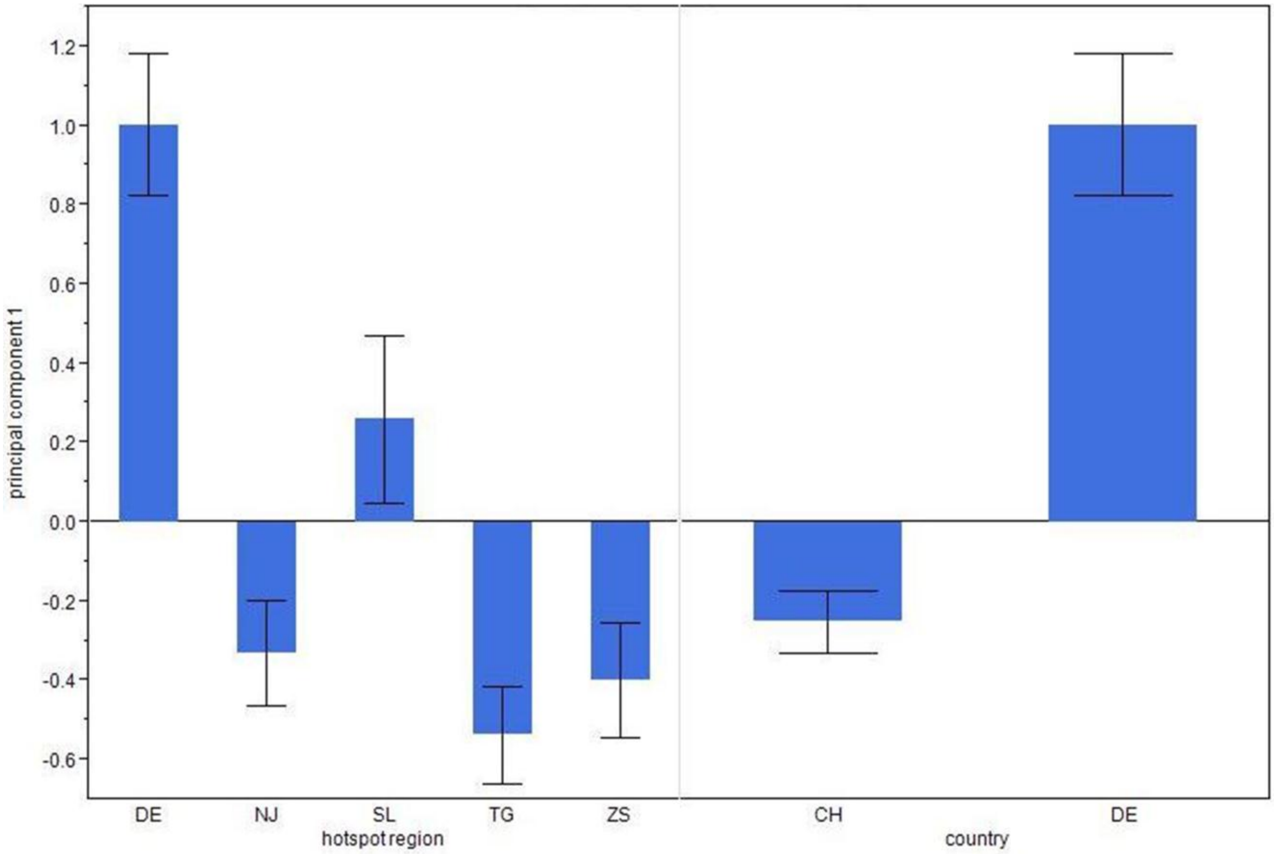


Fig. 4: Cavity availability and complexity based on principle component 1 of the cavity structure PCA for the different hotspot regions (DE: Baden-Württemberg, Southern Germany; NJ: Northern Switzerland, SL: Western Switzerland, TG: Eastern Switzerland, ZS: Central Switzerland) and countries (CH: Switzerland; DE: Southern Germany). Error bars indicate ± SE.

Richness in structural habitat elements

A higher structural richness in Southern Germany than in Switzerland was not only found on a meadow-use level (Fig. 3) and in cavity availability (Fig. 4), but also in small structural elements, such as wood and stone piles, percentages of fallow land, gardens, fruit plantations, hedges, marginal stripes and also anthropogenic structures like housing and farming facilities. The number of structural elements per study site was high in German habitats with top suitability showing 5.01 (SD=2.44) structural elements in average, compared to only 1.69 (SD=1.98) in Eastern Switzerland (Fig. 5). Again, Western Switzerland (3.52 structural elements per study site, SD=2.24) showed the smallest difference of all Swiss hotspot regions compared to Southern Germany.

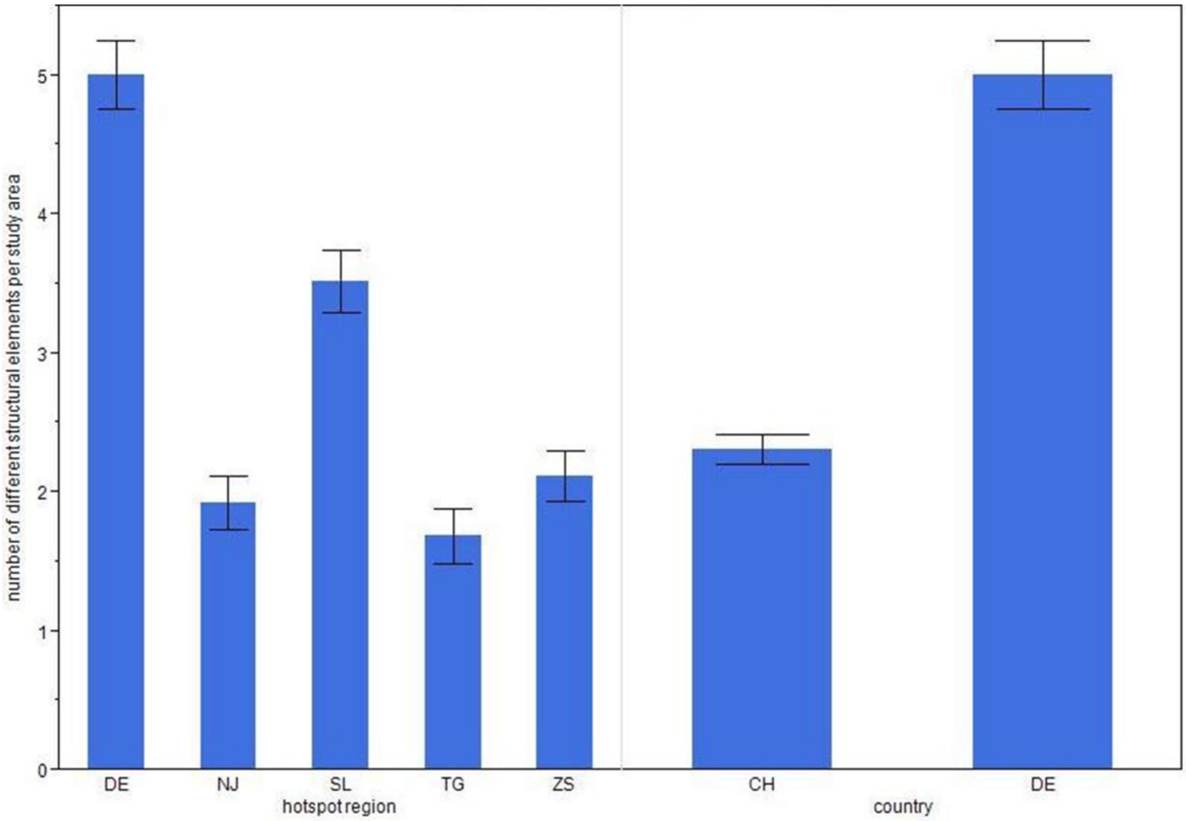


Fig. 5: The mean number of different structural habitat elements as index for structural richness among hotspot regions (DE: Baden-Württemberg, Southern Germany; NJ: Northern Switzerland, SL: Western Switzerland, TG: Eastern Switzerland, ZS: Central Switzerland) and countries (CH: Switzerland; DE: Southern Germany). A maximum of 11 different structural elements per study site was possible. Error bars indicate ± SE.

The principal component analysis of orchard structure showed that principal component 1 is mainly characterized by the number of trees per area, proportion of apple trees and mean diameter of the trees (Table 5). Principal component 2 was dependent on proportion of pear, cherry and plum trees, representing structural and species diversity. It was shown that Southern Germany has a higher tree density and a higher proportion of apple trees compared to Switzerland. In this case Eastern Switzerland was closest to Southern Germany due to the high proportion of apple trees. The principle component 2 showed high densities of plum and cherry trees in Northern Switzerland and low values for Eastern and Central Switzerland. Only Western Switzerland was not distinguishable from Southern Germany in tree composition.

Table 5: Results of the principal component analyses (PCA) for three thematically grouped variable sets (cavity related parameters, orchard structure, prey availability and accessibility). For all three PCAs the loadings of the first two principal components (PC1, PC2) are presented. They were included in further analysis. Loading matrices of the PCAs represent the impact of variables on separate principal components. Correlations > |0.5| are highlighted.

VARIABLE	PCA cavities		PCA orchard structure		PCA mouse availability	
	PC1	PC2	PC1	PC2	PC1	PC2
Cavities per tree	0.762	0.426				
Cavities per area	0.735	-0.607				
Cavity connectivity	0.724	0.014				
Main branch cavities	0.390	0.253				
Woodpecker cavities	0.599	-0.744				
Hollow trees	0.786	0.480				
% dead tree matter	0.373	0.216				
Number of trees			0.651	0.267		
Mean tree diameter			-0.731	-0.332		
% cut trees			0.497	0.069		
% apple trees			0.784	-0.472		
% pear trees			-0.301	-0.500		
% cherry trees			-0.490	0.626		
% walnut trees			-0.257	0.029		
% plum trees			0.142	0.578		
Fallow land					-0.181	0.212
Narrow field edges					0.633	-0.227
Wide field edges					0.398	0.695
Meadow mouse density					-0.501	0.505
Field edge mouse density					0.582	0.637
Area of cultivated fields					0.771	-0.275

Prey availability and predation risk

Comparisons of prey availability of rodents were based on the principal component analysis of rodent density index in field margins, fruit orchard and natural meadows according to transect counts, field edge areas, fallow land and area of arable land. Principal component 1 was characterizing narrow field edges, field edge mouse densities and area of arable land (Table 5). Meanwhile, meadow mouse density, wide field margins and field margin mouse density influenced PC 2, not showing any significant differences among hotspot regions and countries (Table 4). PC 1 was lower in Southern Germany, Central and Eastern Switzerland than in Northern and Western Switzerland, indicating differences in field margin distribution of rodents.

The density of common buzzards *Buteo buteo* observations showed no differences between Southern Germany and Swiss hotspot regions, except for lower values observed in Western Switzerland (Table 4). Red kites *Milvus milvus* appeared more often in all Swiss hotspot regions than in Southern Germany, except for Northern Switzerland (Table 4). Overall only Central and Eastern Switzerland showed significantly higher total predation pressure than Southern Germany.

Discriminating factors

The important factors for the distinction between hotspot regions were identified by performing a linear discriminant analysis. In total, the first two linear discriminant functions explained 91% (linear discriminant function 1: 57.24%; linear discriminant function 2: 33.46%) of the variance (Table 6). On average 59.6% of 500 study sites (DE: 79%, NJ: 59%, SL: 51%, TG: 56%, ZS: 40%) were classified correctly (56.8% in cross validation with single cases were left out). The first discriminant function was highly associated with intensity of meadow management and cavity characteristics of habitats and explained the main part of the differences between the two countries (Fig. 6, Table 6). Thus, the important differences between the countries were a higher intensity of meadow management and lower cavity availability and complexity in Swiss regions than in Southern Germany. The main factor separating Northern and Western Switzerland from Central and Eastern Switzerland was tree species composition (PC 2 orchard structure, see table 6) and meadow-use intensity.

Table 6: Standardized linear discriminant coefficients resulting from stepwise linear discriminant analysis based on all 16 final home-range scale variables (Table 4). Variable reduction was based on correlation matrix (i.e. on Wilks-Lambda evaluation, significance level: 95%). In total, 6 variables were excluded from the analysis (compare Table 4). The most significant correlations of variables with linear discriminant function are highlighted.

VARIABLE	LINEAR DISCRIMINANT FUNCTION			
	1	2	3	4
Number of land-use classes	0.270	0.172	0.065	-0.131
Structural elements	0.348	-0.176	0.470	-0.596
high intensity land-use	-0.327	-0.436	-0.388	-0.242
Low intensity land-use	0.383	-0.107	-0.372	-0.114
Grazing	-0.257	0.366	0.492	0.168
Total predators	-0.226	-0.129	-0.048	-0.115
PC1 orchard structure	0.302	-0.327	0.311	0.860
PC2 orchard structure	0.158	0.815	-0.281	0.310
PC1 cavities	0.266	0.054	0.083	-0.259
PC2 cavities	-0.193	0.373	0.400	0.233

Western and Northern Switzerland, as well as Central Switzerland and Eastern Switzerland showed a similar habitat composition referring to linear discriminant analysis. Western and Northern Switzerland were more similar to Southern German areas than it is the case with Eastern and Central Switzerland (Fig. 6). Even though, linear discriminant function 3 was of limited explanatory power (6.66% of explained variance) it separated Western Switzerland from all other regions by slightly higher values in structural elements, less predators and more grazed areas.

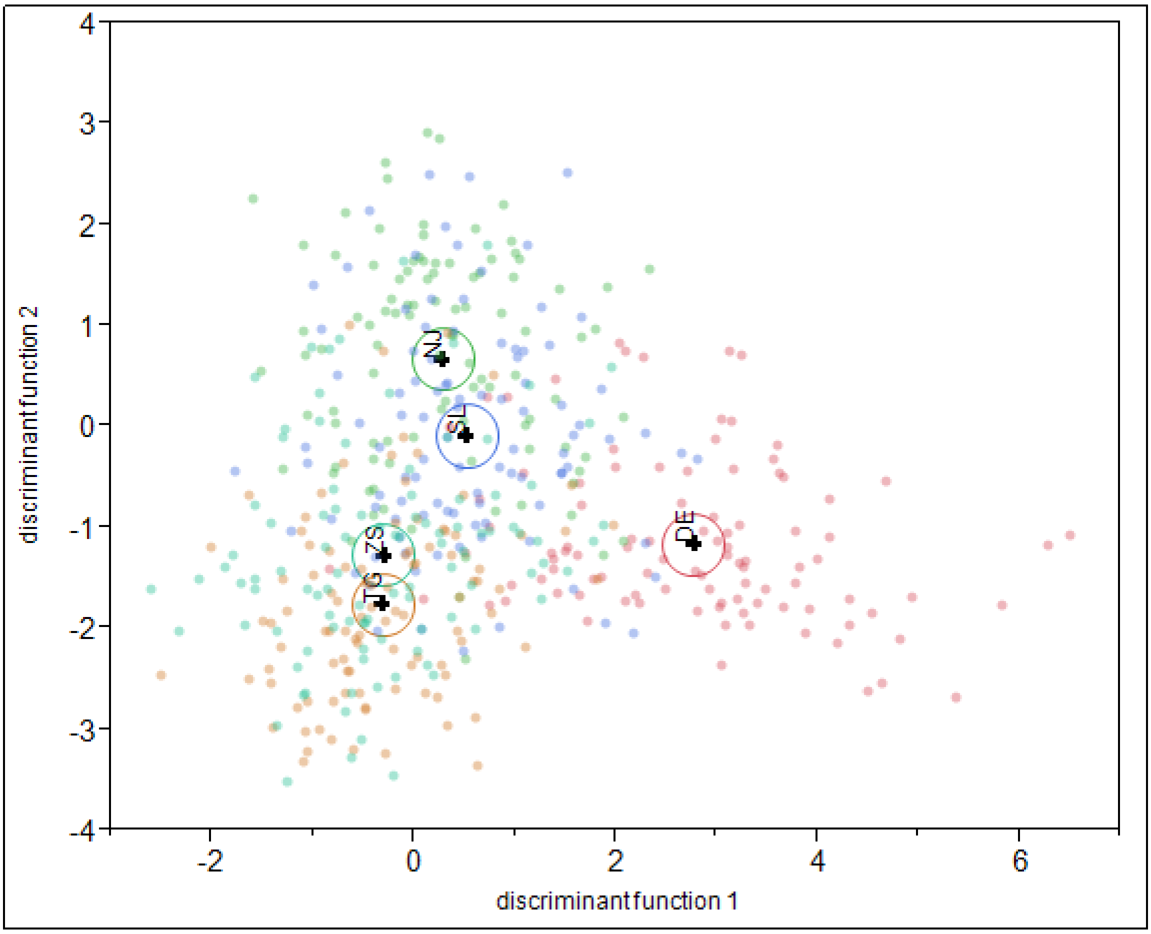


Fig. 6: Linear discriminant analysis shows the relation between the different focus regions (DE=Ludwigsburg, ZS=Central Switzerland, NJ= Northern Switzerland, SL= Western Switzerland, TG= Eastern Switzerland), by positions of group centroids with 95% confidence ellipsoids. Function 1 (Eigenvalue 1.39, canonical correla-tion 0.76) and function 2 (Eigenvalue 0.81, canonical correlation 0.67) are plotted.

DISCUSSION

The analysis of habitat suitability on landscape scale showed that occupancy in Southern Germany was related to fruit orchards as main habitat and to avoidance of forests and urban areas. Furthermore, high land-use diversity was identified to have a positive effect on occurrence probability. Suitable habitats for little owls were considerably smaller and more fragmented in Switzerland than in Southern Germany. In Switzerland, highest densities of suitable habitats were detected in orchard-dominated landscapes in the Eastern part of the country, large open lowland plains with high land-use diversity or large grassland areas, as well as in broad and deep climate-favored Alpine valleys. On the home-range scale, occupied Southern German habitats showed meadow management of lower intensity, lower amount of intensively grazed areas, higher small-scale diversity in mowing patterns and higher structural richness, such as cavity availability, compared to Swiss hotspot regions. The four Swiss regions of high landscape suitability significantly differed in structural richness, small-scale land-use diversity and cavity availability favoring Western and Northern Switzerland, instead of orchard-dominated Eastern and Central Switzerland. These results reflect the combination of the aspects of little owl habitat requirements on landscape scale and on home-range scale.

Landscape scale

Results of the habitat suitability model corroborate known habitat-species associations of little owls in Central Europe. Differences in the quantity and quality of suitable habitats reflect limitations of current distribution of little owls in Switzerland and demonstrate the excellent basis for recent population expansion in Southern Germany. Whilst the large areas of German suitable habitats show high connectivity, Swiss suitable habitats are highly fragmented and surrounded by larger areas of unsuitable habitat, due to distribution of forests and urban sprawl. Highly fragmented landscape patterns with small forest patches restrict suitable habitats in Switzerland to flat areas in the Swiss lowlands, which are dominated by highly intensive agricultural use. Forests patches pose high predation risks by tawny owls *Strix aluco* and therefore areas closer than 200m to forests are avoided by little owls (Van Nieuwenhuyse et al. 2006 page 207/296, Sunde et al. 2009, Michel et al. 2014 unpublished data).

Although suitable habitats are scarce in Switzerland, regions of higher habitat suitability were detected covering many parts of the Swiss lowlands. Highest suitable habitat density was found to be located in Eastern Switzerland known for the traditional cultivation of apples in standard tree orchards. Nowadays persisting orchards are often cultivated in a highly intensified manner. In comparison to Eastern Switzerland, suitable habitats in the remaining areas of Swiss lowlands, limited by the

Alps and the Jura hills, were found to be distributed in open landscapes where traditionally fruit trees were more abundant and in present days highly intensive agriculture dominates. In these areas potential habitats are located where the landscape is free of forest and urban structure but due to high parceling, land-use diversity is increased. Furthermore, Northern Switzerland shows a combination of open-spaced landscapes with relatively high amounts of remaining orchards (mainly cherry trees). Due to topographical conditions forests are posing limits to suitable habitats in this undulating landscape. It is to be expected that remaining Swiss suitable habitat patches, even if not as prevalent as in Southern Germany, represent a sufficient basis on landscape scale for little owls to spread current populations in the border regions.

Home-range scale

Suitability hotspot regions in Switzerland differ mainly from Southern German habitats in the intensified meadow-use, the smaller quality and quantity of cavities and the lack of structural habitat elements. These parameters represent general habitat requirements which are crucial for breeding success, survival and dispersal of little owls. Less intensive meadow management accompanied by different mowing patterns favor prey availability and accessibility for little owls (Apolloni et al. 2013). In hotspot regions of Switzerland the majority of these parameters is widely missing when compared to German suitable habitats. For example, Swiss suitable habitats show a lower density of natural roosting and nesting sites. They also show a complete absence of artificial nesting sites and are therefore not able to compensate for this deficiency. These differences certainly affect the possibility of finding roosting sites in winter and nesting sites during breeding season. Higher amounts of natural cavities are not only essential as potential breeding sites, but also provide more roosting sites during daytime as predator avoidance and during dispersal and winter as well isolated hide-outs (Bock et al. 2013). In general Swiss hotspot regions also show a trend to higher predator densities, probably resulting in higher direct predation pressure and indirect predation effects (omnipresent red kites) inhibiting movement between suitable habitat patches. Only marginal differences were found when looking at rodent availability between the two countries. Lower meadow rodent densities in Switzerland caused by intensive meadow-use, can assumingly be compensated with higher field margin rodent densities. Field margin rodent density is of higher priority in Switzerland due to the small parceling of arable land resulting in higher field margin density. Nevertheless, higher rodent abundance by changed meadow-use would result in more sustainable prey availability than relying on field margin rodent populations. Mainly the missing structural richness and high meadow-use intensity seem to be critical factors impeding prey availability and accessibility. These differences on home-range scale identify the main challenges which little owls are facing in Switzerland. However, we should be aware that additional unknown habitat characteristics might be responsible for differences in population densities and trends.

Within Switzerland, hotspot regions differ in the extent of habitat deficiency. Regions of high landscape suitability (in particular Eastern Switzerland) do not coincide with suitability on home-range scale. In fact, Eastern and Central Switzerland show similarities concerning their high intensity of meadow-use and absence of structures serving as hide-out for little owls and their prey at the same time. These structures were shown to be crucial for prey accessibility and predator avoidance (Van Nieuwenhuyse et al. 2006 pages 202-208, Bock et al. 2013). Meanwhile, Western and Northern Switzerland show higher abundance of natural tree cavities and small structures as well as less intensified use of meadows below fruit trees. In general, they show more aspects to be found in German habitats, than Eastern and Central Switzerland. Certainly these regions (SL and NJ) seem to be more suitable on home-range scale than the tree-rich but intensely managed Eastern Swiss fruit orchards. This finding emphasized that tree density is not a crucial factor for little owl habitat quality. Rather, single trees or small orchards are likely to be adequate for little owls to persist. It can be inferred that optimum habitat quality is often met by Southern German fruit orchards occupied by little owls. However, the habitat quality there is less characterized by the high density of trees, but primarily due to structural richness and low intensity meadow-use. This also explains the high suitability on home-range scale of study sites with low tree densities, but high structural richness, which can be found in many parts of Switzerland, but in higher densities in Northern and Western Switzerland. Focusing on prey abundance detected by rodent tracks, field margin rodent availability seems to be an important factor, varying highly between Swiss hotspot regions. This effect assumingly gets stronger in regions with higher percentages of arable land and small parceling, as is often the case around orchards in Northern and Western Switzerland. It has to be mentioned that the year of data collection (2013) was an exceptionally bad year for common voles (own data), compared to the preceding years probably resulting in lower densities and therefore smaller differences between regions. Additionally, other factors, such as contamination with pesticides may affect prey quality even if it is abundant (Beersma & Beersma 2001).

Advantages of multi-scale habitat assessment

The combination of two spatial scales in the analysis of habitat suitability resulted in a more comprehensive understanding of available habitats. It was possible to consider parameters responsible for habitat selection on landscape scale, which resulted in the definition of suitability hotspot areas. By identifying important hotspot region, the analysis of resource availability on home-range scale could be focused on suitable areas without relying on expert knowledge, but on occurrence data of remaining populations. Results confirm that identifying suitable habitats on landscape scale is important, but not enough. It is necessary to include any kind of resource linked parameter on home-range level. Once focusing on suitability hotspot regions, there is no need of spatially inclusive and resource intensive data collection covering areas of low landscape scale suitability. Due to the fact that the analysis of potential habitats for little owls in Switzerland was performed on two spatial scales in comparison with occupied habitats of an intact population, it is possible to formulate region specific conservation measures pointing at deficiency in habitat characteristics on the home-range scale, as well as nation-wide conservation measures focusing on abundance, quality and connectivity of potential habitats on the landscape scale. Furthermore, it is possible to evaluate different scenarios of recolonization and expenses to be made to facilitate the return of this species. Under these circumstances limited conservation resources can be placed directly where needed. This approach based on breeding data of nearby populations has shown to be an effective way of revealing habitat potential on all relevant levels. Our results demonstrate that considering different spatial scales is necessary to achieve insights into a species' habitat requirements in unoccupied areas. Thus, by applying this method, we are able to synthesize comprehensive conservation measurements on the small home-range scale based on the wide-scale distribution potential and dispersal barriers.

Conservation implications

The distribution of suitable habitats might represent one major barrier for little owls to recolonize Swiss lowlands. Although dispersal was shown to be more flexible and of greater extent than suspected (Perrig et al. submitted, Michel et al. unpublished data), landscape barriers between suitable habitats, such as extensive forest areas might prevent expansion of little owl populations in certain regions of Switzerland. In conclusion, suitable habitat outside hotspot regions can be of crucial value serving as stepping stones during dispersal (Saura et al. 2014). Furthermore, it can be inferred that recolonization of suitable areas mainly depends on the quality of these suitable habitats on home-range scale and on successful dispersal by the use of stepping stones which meet little owls requirement concerning roosting sites and prey availability. Assuming prey availability, structural habitat configuration and nesting site availability to be sufficient, it seems likely that either individuals showing long distance dispersing behavior or individuals using available potential habitat patches as stepping stones would represent the driving force behind the recolonization of suitability hotspot regions. One example is a successful brood of little owls occurring in Western Switzerland's hotspot region over the last years with changing mating partners (P. Mosimann, personal communication), of which at least one individual originates from the Geneva population (connected to France). This finding supports that by region-specific compensation of lacking habitat elements and punctual melioration of habitats the recolonization by little owls, which rely on small home-ranges (average 19.9 ha, Grzywaczewski 2009), might be possible in all hotspot regions. Nevertheless, recolonization is more likely to be accomplished in Northern and Western Switzerland, also due to the current distribution of surrounding populations.

In conclusion, Swiss little owl population expansion seems to be limited mainly by insufficient small-scale habitat quality, namely by the lack of breeding sites and structural richness, as well as extensively managed meadows. Concerning the lack of breeding opportunities, populations in Southern Germany show that by installing artificial nest boxes in high densities, populations are able to recover and disperse rapidly even if not all habitat requirements are met. Therefore, this approach could also be recommended for Switzerland. By local improvement of structural richness, the provision of less intensified agricultural patches and installation of artificial roost and nest sites, home-range scale habitat quality can be enhanced specifically. These measures can be focused on relatively small areas within hotspot regions due to the small home-range and the high site fidelity to successful breeding sites of adult little owls (Sunde et al. 2009, Grzywaczewski 2009). Furthermore, the connectivity of regions with high habitat suitability should be increased in order to facilitate dispersal into suitable regions and to provide stepping stones to existing populations. With focus on these actions on regional and national level it is likely that little owls can persist and recover in Switzerland.

ACKNOWLEDGEMENTS

I would especially like to thank Dr. Martin Grüebler and Dr. Beat Naef-Daenzer for their support in planning and conducting this study. Without their extensive input on structural framework, choice of field survey parameters, analysis techniques and the writing process, this project would not have been realized to this extent. Furthermore, Sophia Franke and Prof. Dr. Thomas Gottschalk from the Hochschule für Forstwirtschaft in Rottenburg (Germany) provided little owl occupancy data and land-cover data for Southern Germany, as well as their knowledge and support in GIS-based modeling. I am highly grateful for the supervision of my master thesis by Prof. Dr. Lukas Keller at the Institute of Evolutionary Biology and Environmental Studies of the University of Zurich. Funding of the project and the supervision was provided by the Swiss Ornithological Station in Sempach. For critical inputs leading to the improvement of this manuscript and their support conducting field work I would like to thank Jael Hoffmann, Julia Stadler, Christoph Hottiger and my family.

STATEMENT OF AUTHORSHIP

I hereby declare that I have used no sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Zürich, 31.03.2014

Patrick Scherler

REFERENCES

APOLLONI N., NAEF-DAENZER B. & ARLETTAZ R. (2013): Master thesis on: Landscape use, foraging habitat selection and relationships to food resources in breeding little owls: recognizing the importance of scale for species conservation management. Abteilung Conservation Biology, Institut für Ökologie und Evolution der Universität Bern, Switzerland.

BEERSMA P. & BEERSMA W. (2001): Little owls *Athene noctua* and biocides: reasons for concern? Oriolus, 67/2-3, 94-99.

BELLAMY C., SCOTT C. & ALTRINGHAM J. (2013): Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. Journal of Applied Ecology, 50/4, 892-901.

BIRRER S., JENNY M. & ZBINDEN N. (2011): Bestandsentwicklung der einheimischen Brutvögel im Landwirtschaftsgebiet 1990–2009. Agrarforschung Schweiz, 1/2, 66-71.

BOCK A. et al. (2013): Roost site selection by Little Owls *Athene noctua* in relation to environmental conditions and life-history stages. IBIS, 155/4, 847-856.

BRAMBILLA M., CASALE F. & BERGERO V. et al. (2009): GIS-models work well, but are not enough: Habitat preferences of *Lanius collurio* at multiple levels and conservation implications. Biological Conservation, 142/10, 2033–2042.

BRAHIER A., MEISSER C., CRELIER D. & EGGER V. (2012): Überblick der Schutzbemühungen für den Steinkauz *Athene noctua* in der Ajoie (Kanton Jura) zwischen 2002 und 2012. Nos Oiseaux, 59/4, 187-200.

BROWN K.P., MOLLER H., INNES J. & ALTERIO N. (1996): Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. New Zealand Journal of Ecology, 20, 271-275.

BRUEGGER A., NENTWIG W. & AIROLDI J.-P. (2010): The burrow system of the common vole (*M. arvalis*, Rodentia) in Switzerland. Mammalia, 74, 311-315.

BURBACH K. (1997): Steinkauz – *Athene noctua*. Avifauna von Hessen. Hessische Gesellschaft für Ornithologie und Naturschutz (eds.). Echzell, Germany.

BURNHAM K.P. & ANDERSON D.R. (2002): Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York.

CAHALL R.E, HAYES J.P. & BETTS M.G. (2013): Will they come? Long-term response by forest birds to experimental thinning supports the "Field of Dreams" hypothesis. Forest Ecology and Management, 304, 137-149.

DELATTRE P., GIRAUDOUX P., BAUDRY J., QUERE J.-P. & FICHET E. (1996): Effect of landscape structure on Common Vole (*Microtus arvalis*) distribution and abundance at several space scales. Landscape Ecology, 11, 279-288.

DU TOIT J.T. (2010): Considerations of scale in biodiversity conservation. Animal Conservation, 13/3, 229-236.

ESRI ENVIRONMENTAL SYSTEMS RESOURCE INSTITUTE (2010): ArcMap version 10.0. ESRI, Redlands, California.

FERNANDEZ J.M. & GURRUTXAGA M. (2010): Habitat suitability models for assessing bird conservation goals in 'special protection areas'. Ardeola, 57/Special Issue, 79-91.

FULLER R.J. (2012): The bird and its habitat: an overview of concepts. Birds and Habitat: Relationships in Changing Landscapes (ed. R.J. Fuller), pp. 3-36. Cambridge University Press, Cambridge.

GOTTSCHALK T. K., AUE B., HOTES S. & EKSCHMITT K. (2011a): Influence of grain-size on species-habitat models. Ecological Modelling, 222/18, 3403-3412.

GOTTSCHALK T.K., BERTLING M., WOLTERS V. & BIERMANN J. (2008): A new MW algorithm to speed up landscape index calculation of high resolution maps. In: Geoinformatics paves the Highway to Digital Earth (eds. Schiewe J., Michel U.). 29-32. Osnabrück, Institut für Geoinformatik und Fernerkundung, University of Osnabrück.

GOTTSCHALK T.K., ECKSCHMITT K. & WOLTERS V. (2007): GEPARD – ein GIS-basiertes Modell für die faunistische Beurteilung von Umweltszenarien. Natur und Landschaft, 82/7, 306-311.

GOTTSCHALK T. K., EKSCHMITT K. & WOLTERS V. (2011b): Efficient Placement of Nest Boxes for the Little Owl *Athene noctua*. Journal of Raptor Research, 45/1, 1–14.

GRAF R.F., BOLLMANN K., BUGMANN H. & SUTER W. (2007): Forest and landscape structure as predictors of capercaillie occurrence. Journal of Wildlife Management, 71/2, 356-365.

GRAF R.F., BOLLMANN K., SUTER W. & BUGMANN H. (2005): The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. Landscape Ecology, 20/6, 703-717.

GRZYWACZEWSKI G. (2009): Home range size and habitat use of the Little Owl *Athene noctua* in East Poland. Ardea, 97, 541-545.

GUISAN A. & ZIMMERMANN N.E. (2000): Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186.

HERNANDEZ M. & MARGALIDA A. (2008): Pesticide abuse in Europe: effects on the Cinereous vulture (*Aegypius monachus*) population in Spain. Ecotoxicology, 17/4, 264-272.

HEUCK C., BRANDL R., ALBRECHT J. & GOTTSCHALK T.K. (2013): The potential distribution of the Red Kite in Germany. Journal of Ornithology, 154/4, 911-921.

HGON AG EULEN (2005): Ergebnis der Brutzeiterfassung von sechs Eulenarten in Hessen 2005.

IBM CORP. (2013): IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.

JABERG C. & GUISAN A. (2001): Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. Journal of Applied Ecology, 38, 1169–1181.

JENNY M., ZELLWEGER-FISCHER J., PFIFFNER L., BIRRER S. & GRAF R. (2011): Leitfaden für die Anwendung des Punktesystems. Biodiversität auf Landwirtschaftsbetrieben im Projekt «Mit Vielfalt punkten», Schweizerische Vogelwarte und Forschungsinstitut für biologischen Landbau, Sempach und Frick.

JMP STATISTICAL SOFTWARE PACKAGE (2013): Version *10.0*. SAS Institute Inc., Cary, NC.

KNAUS P. et al. (2011): Historischer Brutvogelatlas. Die Verbreitung der Schweizer Brutvögel seit 1950/Atlas historique des oiseaux nicheurs. La répartition des oiseaux nicheurs de Suisse depuis 1950. Schweizerische Vogelwarte/Station ornithologique suisse, Sempach.

LUNDY M.G. et al. (2012): Behavioural context of multi-scale species distribution models assessed by radio-tracking. Journal for Nature Conservation, 13/2, 188-195.

MARCER A., SAEZ L., MOLOWNY-HORAS R., PONS X. & PINO, J (2013): Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. Biological Conservation, 166, 221-230.

MARTINEZ J.A., SERRANO D. & ZUBEROGOITIA I. (2003): Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. Ecography, 26/1, 21-28.

MCCRACKEN D.I. & TALLOWIN J.R. (2004): Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands. Ibis, 146, 108-114.

MORELLI F., JERZAK L. & TRYJANOWSKI P. (2014): Birds as useful indicators of high nature value (HNV) farmland in Central Italy. Ecological Indicators, 38, 236-242.

R DEVELOPMENT CORE TEAM (2013): R version 3.0. A Language and Environment for Statistical Computing. http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria.

SANDERSON F.J., KUCHARZ M., JOBDA M. & DONALD P.F. (2013): Impacts of agricultural intensification and abandonment on farmland birds in Poland following EU accession. Agricultural Ecosystems & Environment, 168, 16-24.

SAURA S., BODIN O. & FORTIN M.J. (2014): Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology, 51/1, 171-182.

SCHAUB M., ULLRICH B., KNÖTZSCH G., ALBRECHT P. & MEISSER C. (2006): Local population dynamics and the impact of scale and isolation: a study on different little owl populations. OIKOS, 115, 389-400.

SUNDE P. et al. (2009): Spatial behaviour of little owls (*Athene noctua*) in a declining low-density population in Denmark. Journal of Ornithology, 150/3, 537-548.

THORUP K., SUNDE P., JACOBSEN L.B. & RAHBEK C. (2010): Breeding season food limitation drives population decline of the Little Owl *Athene noctua* in Denmark. Ibis, 152, 803-814.

TOMÉ R., BLOISE C. & KORPIMÄKI E. (2004): Nest-site selection and nesting success of Little Owls (*Athene noctua*) in Mediterranean woodland and open habitats. The Journal of Raptor Research, 38, 35-46.

VAN NIEUWENHUYSE D., GÉNOT J.-C. & JOHNSON D. H. (2008): The little owl. Conservation, Ecology and Behavior of *Athene noctua* (eds.). Cambridge University Press, Cambridge.

VICKERY, J. & ARLETTAZ, R. (2012): The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes. Birds and Habitat: Relationships in Changing Landscapes (ed. R.J. Fuller), pp. 177-204. Cambridge University Press, Cambridge.

WILSON C.D., ROBERTS D. & REID N. (2011): Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.). Biological Conservation, 144/2, 821-829.

ŻMIHORSKI M., ROMANOWSKI J. & OSOJCA G. (2009): Habitat preferences of a declining population of the little owl, *Athene noctua* in Central Poland. Folia Zoologica, 58, 207-215.

APPENDIX 1 – SUPPORTING INFORMATION ON LANDSCAPE SCALE ANALYSIS

Model output for best model fit

```
Dependent Variable:
ALL

Independent continiuos Variables:
di_wage_ge, di_wet_ge, nied_sp_ge, p1_stk_ges, p21_ge, p41_ge, p6_stk_ges, shdi_ge, tmit_sp_ge,

Independent categorical Variables:
la_stk_ges,

******************************************

Call:
glm(formula = ALL ~ di_wage_ge + di_wet_ge + p21_ge + p41_ge +
    p6_stk_ges + shdi_ge + tmit_sp_ge + la_stk_ges, family = binomial(link = "logit"),
    data = gis_data)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.2964  -0.0966   0.0108   0.2925   3.4175

Coefficients:
               Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.502e+01  3.485e+00  -7.179 7.03e-13 ***
di_wage_ge    5.031e-03  9.794e-04   5.137 2.79e-07 ***
di_wet_ge     1.568e-04  6.018e-05   2.605 0.009186 **
p21_ge        1.045e-01  3.153e-02   3.313 0.000923 ***
p41_ge       -2.328e-02  1.472e-02  -1.582 0.113761
p6_stk_ges   -9.664e-02  1.651e-02  -5.853 4.82e-09 ***
shdi_ge       2.611e+00  7.252e-01   3.601 0.000317 ***
tmit_sp_ge    1.515e-01  2.389e-02   6.344 2.23e-10 ***
la_stk_ges11 -1.618e+01  7.868e+02  -0.021 0.983589
la_stk_ges21  3.176e+00  4.923e-01   6.450 1.11e-10 ***
la_stk_ges25  8.023e-01  1.392e+00   0.576 0.564370
la_stk_ges30  1.903e+00  3.642e-01   5.227 1.73e-07 ***
la_stk_ges41 -2.848e+00  9.635e-01  -2.956 0.003113 **
la_stk_ges6  -2.395e+00  1.333e+00  -1.796 0.072477 .
la_stk_ges80  5.298e-01  1.142e+00   0.464 0.642610
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1009.22  on 727  degrees of freedom
Residual deviance:  296.26  on 713  degrees of freedom
AIC: 326.26

Number of Fisher Scoring iterations: 15

AIC/BIC table
          Step Df Deviance Resid. Df Resid. Dev      AIC
1               NA       NA       713   296.2555 326.9728
2 - p1_stk_ges  0        0       713   296.2555 326.9728
3 - nied_sp_ge  0        0       713   296.2555 326.9728
```

Fig. A1.1: Output given by GEPARD tool (Gottschalk et al. 2007) implemented in ArcGIS 10.0 for best model fit. Dependent binomial variable (ALL) consists of presence and absence points of little owl broods. Independent (di_wage_ge: distance to hedges, di_wet_ge: distance to wetland or open water, nied_sp_ge: mean precipitation in spring, p1_stk_ges: percentage of surrounding arable land, p21_stk_ges: percentage of surrounding fruit orchard, p41_stk_ges: percentage of surrounding urban area, p6_stk_ges: percentage of surrounding forest) and dependent variables (la_stk_ges: local land-use class indicated as model parameter with la_stk_gesXX. XX representing respective numbers for land-use classes (11= open water, 21=fruit orchard, 25=other areas, 30=meadow, 41=urban area, 6=forest and 80=hedges), which were included in the generalized linear model. Backwards AICc was used for model selection.

Land-use matrix

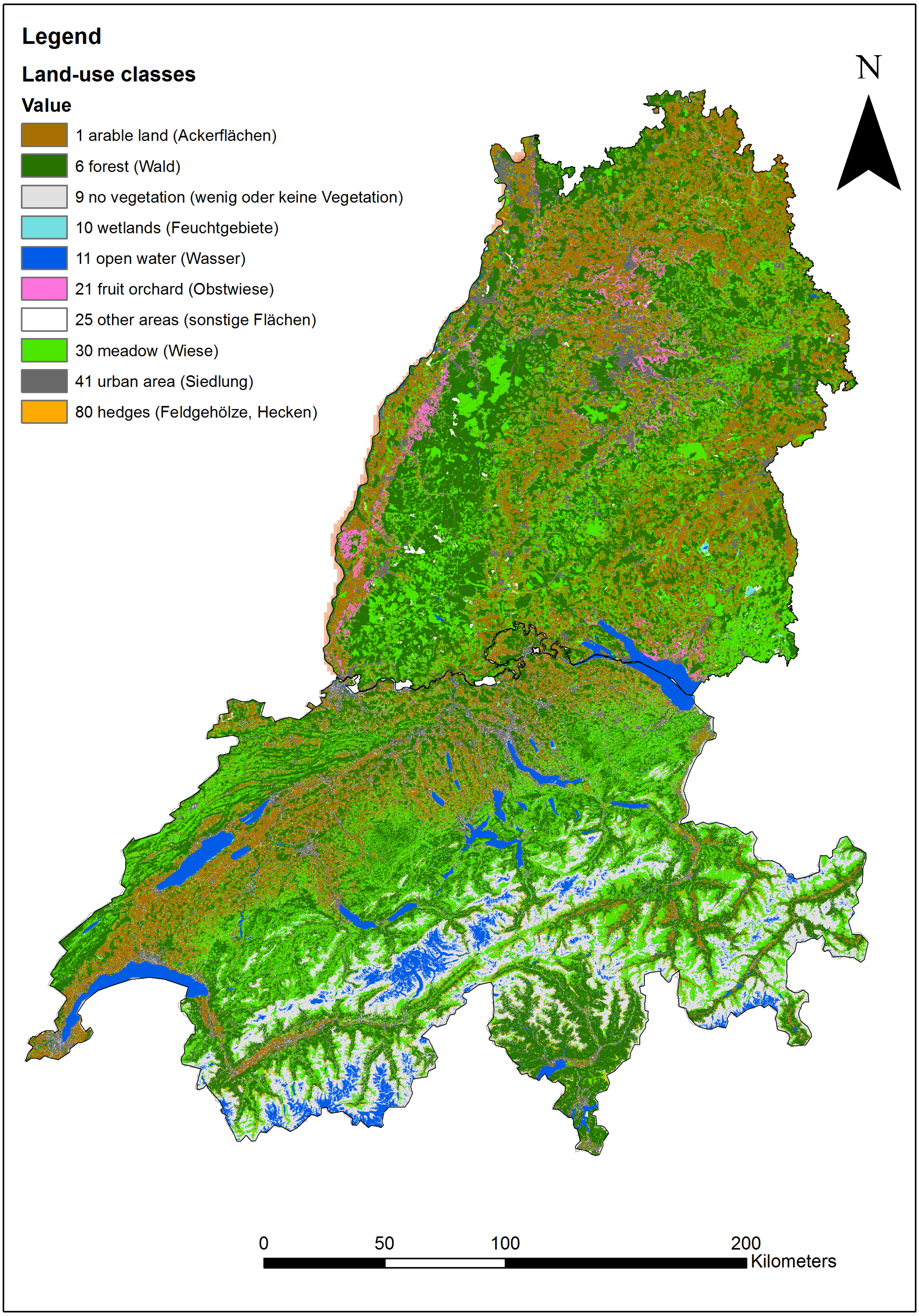


Fig. A1.2: Land-use matrix for Switzerland and Southern Germany used as basis for generalized linear model with occurrence data of little owl broods.

Model validation

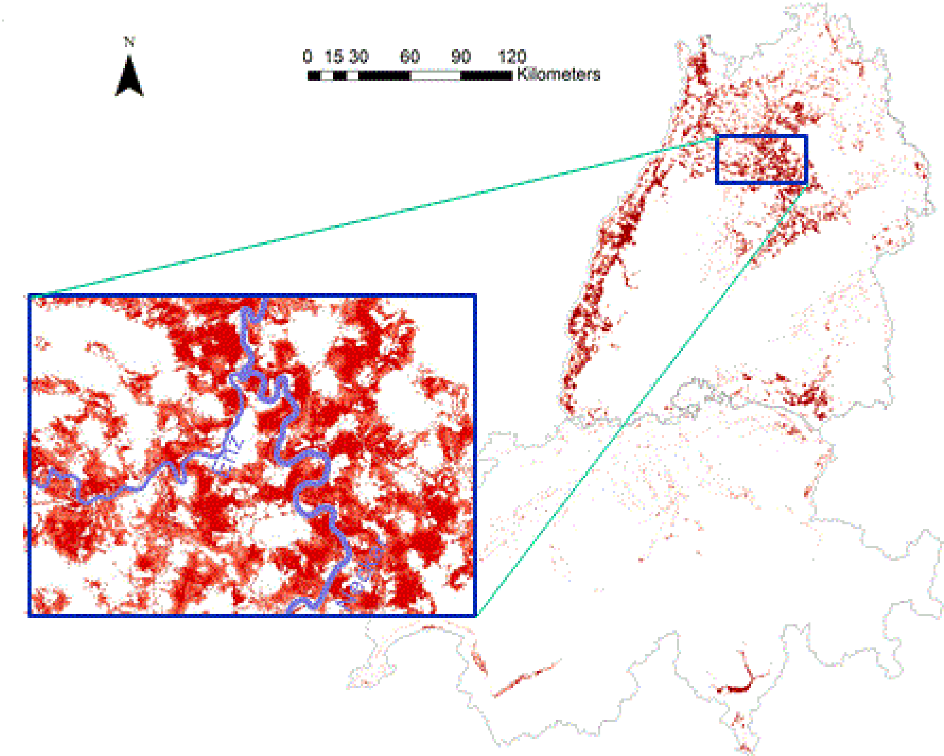


Fig. A1.2: Close-up capture of the Ludwigsburg district in Southern Germany. Results of the landscape habitat suitability model are represented in red (dark red = higher suitability).

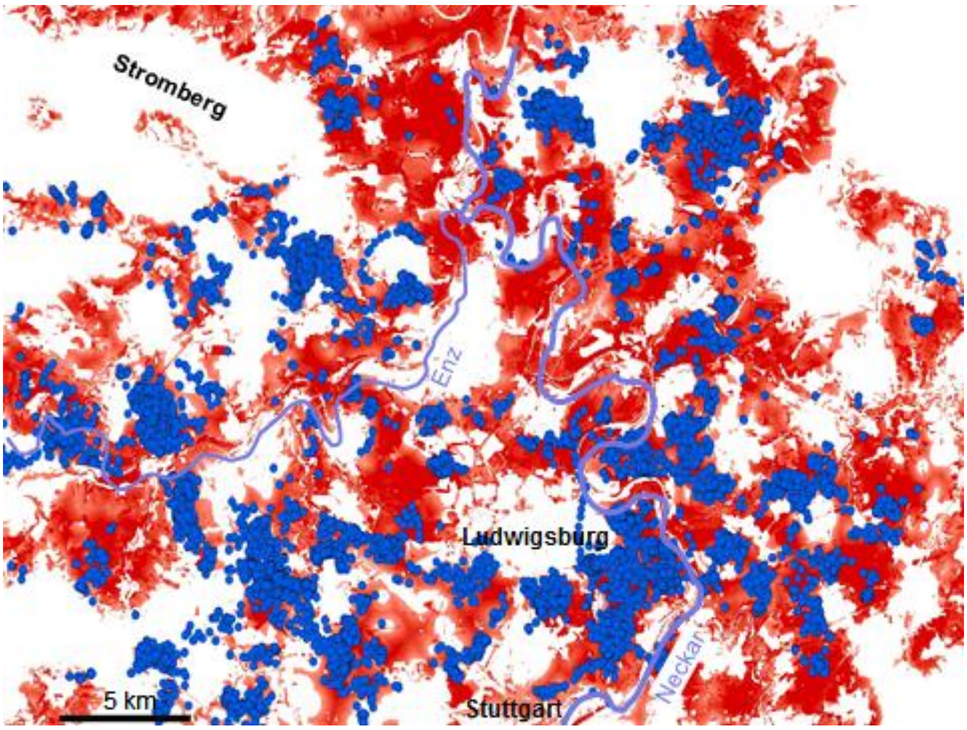


Fig. A1.3: Radio-tracking locations of little owls in the area of Ludwigsburg in Southern Germany are indicated as blue dots, overlaying results of habitat suitability map, based on the landscape scale model (red).

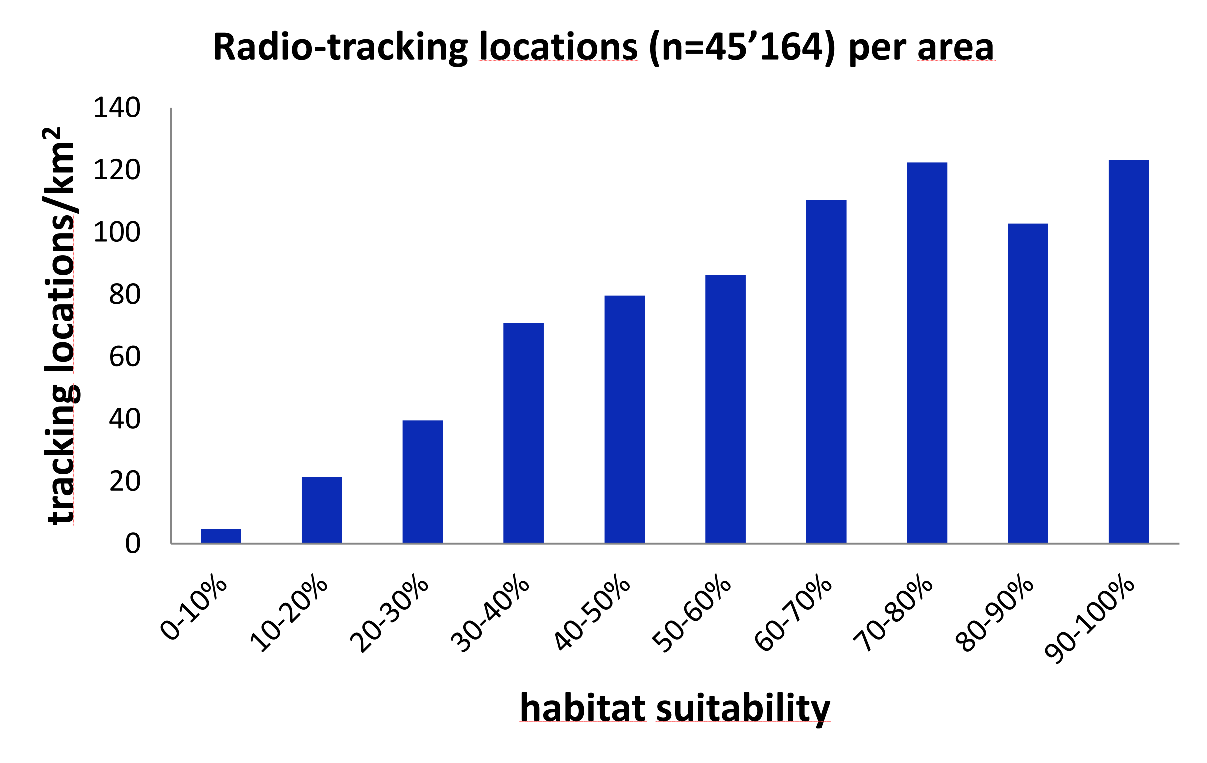


Fig. A1.4: The density of radio tracking positions for each habitat suitability class (tracking locations/habitat suitability class area in km^2). Habitat suitability higher than 50% can be assumed as suitable habitat for little owls.

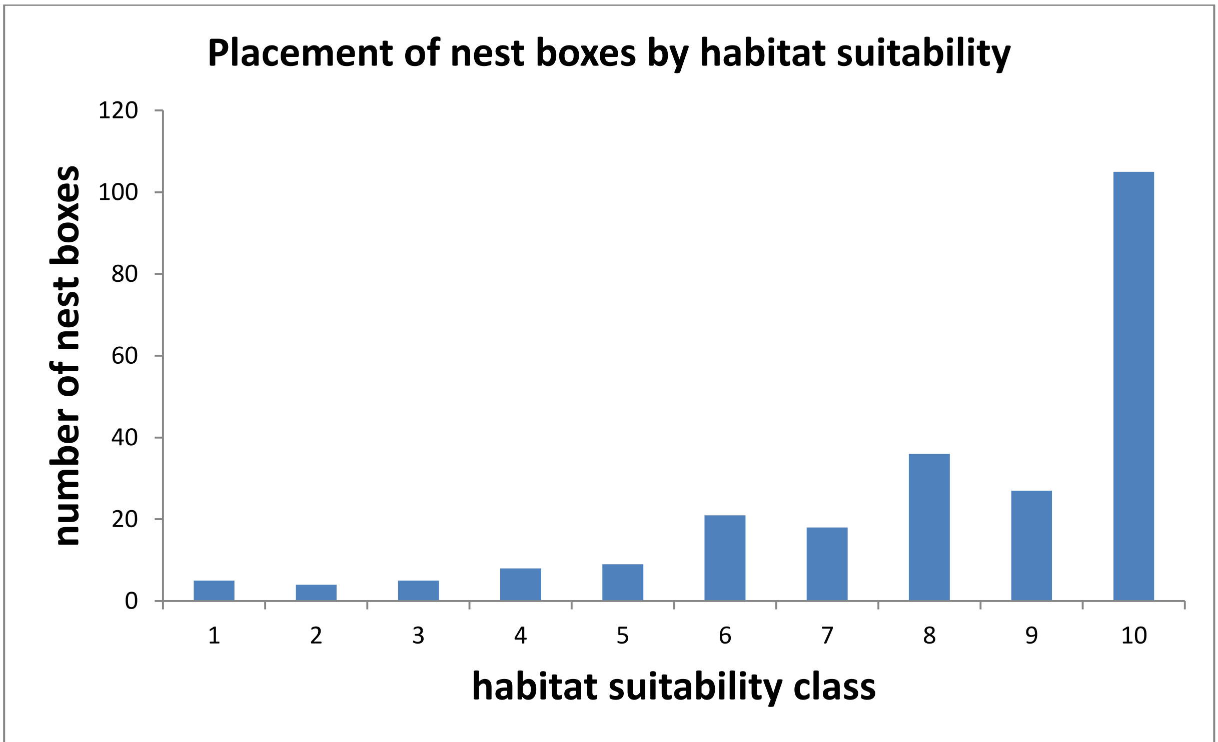


Fig. A1.5: The number of nest boxes per habitat suitability class represents the strategic placement in suitable habitats.

APPENDIX 2 – SUPPORTING INFORMATION ON HOME-RANGE SCALE ANALYSIS

Background on selected hotspot regions (background maps all © swisstopo & LGL BW)

Fig. A2.1: Close-up of study sites of the suitability hotspot region of Southern Germany. Where study sites (n=100) are in close proximity, only one area is labeled. Hotspot region boundary is indicated by colored line.

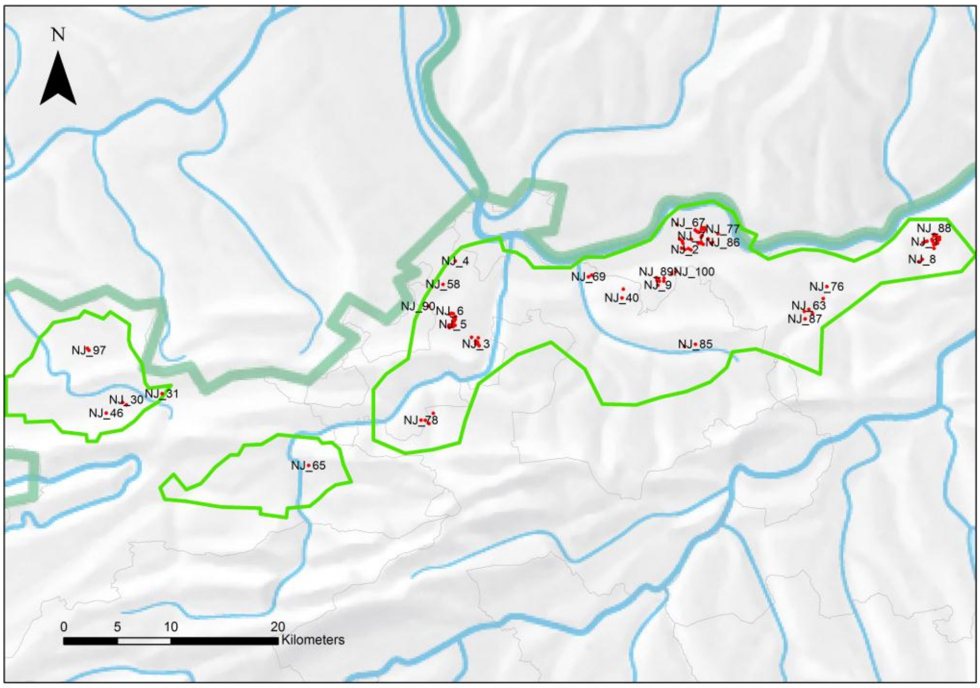


Fig. A2.2: Close-up of study sites of the suitability hotspot region of Northern Switzerland. Where study sites (n=100) are in close proximity, only one area is labeled. Hotspot region boundary is indicated by colored line.

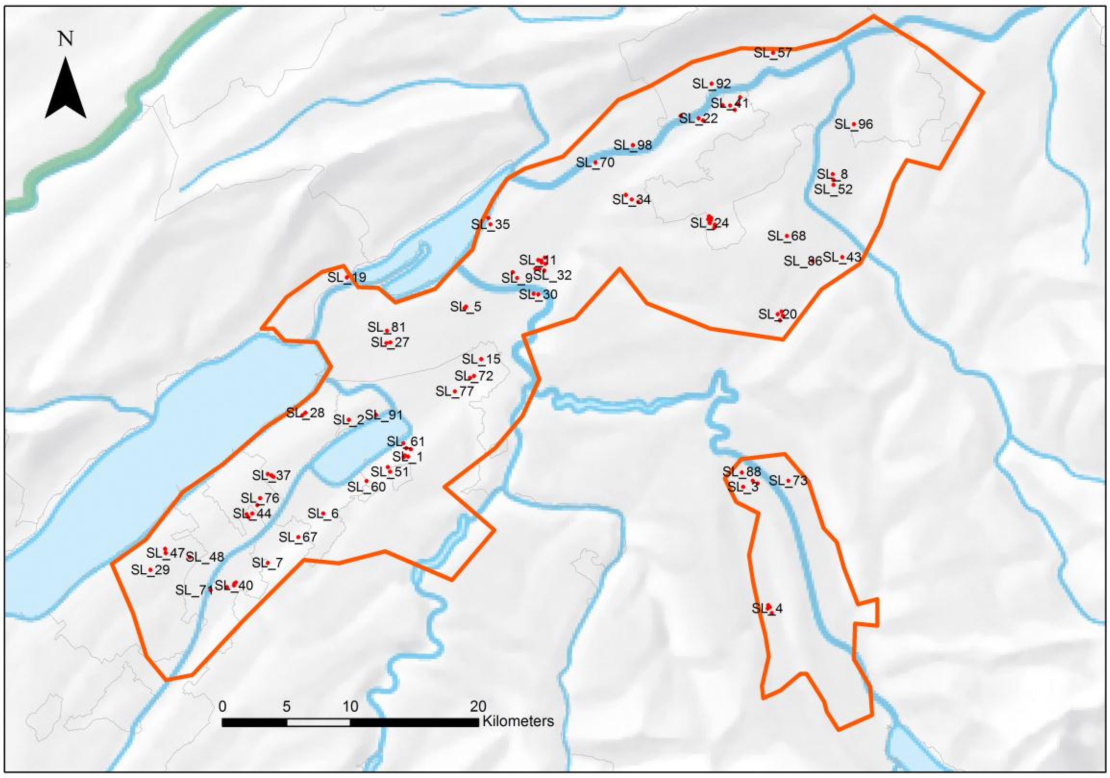


Fig. A2.3: Close-up of study sites of the suitability hotspot region of Western Switzerland. Where study sites (n=100) are in close proximity, only one area is labeled. Hotspot region boundary is indicated by colored line.

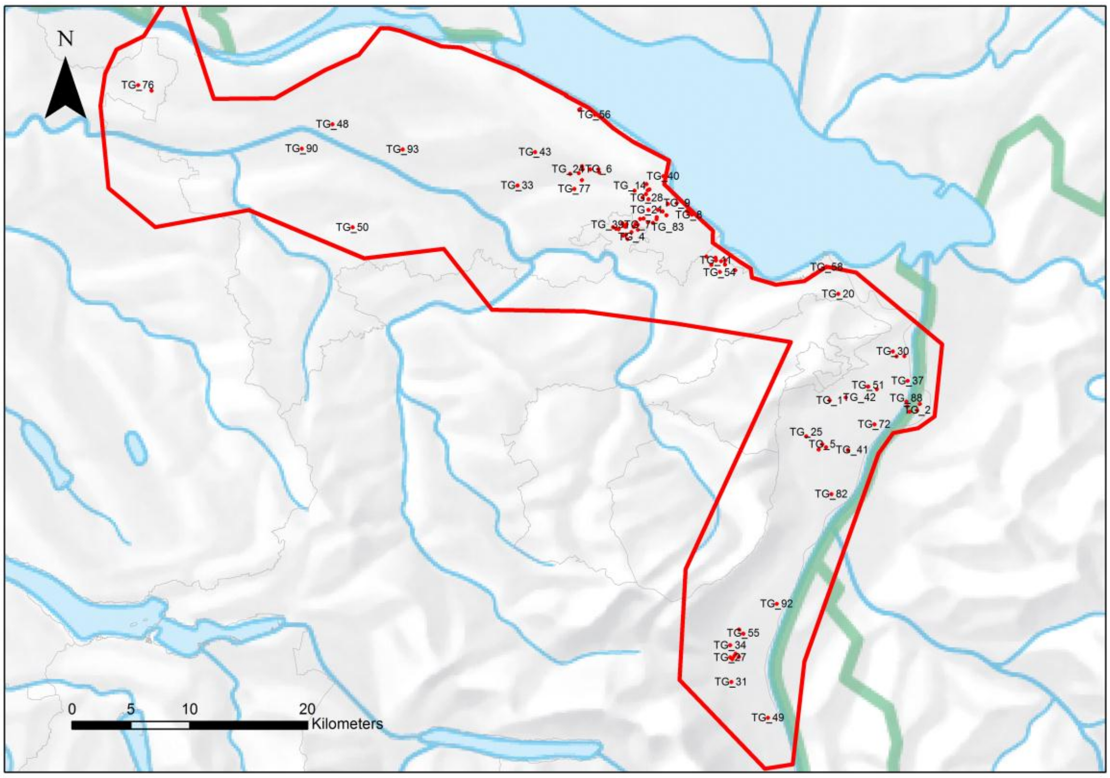


Fig. A2.4: Close-up of study sites of the suitability hotspot region of Eastern Switzerland. Where study sites (n=100) are in close proximity, only one area is labeled. Hotspot region boundary is indicated by colored line.

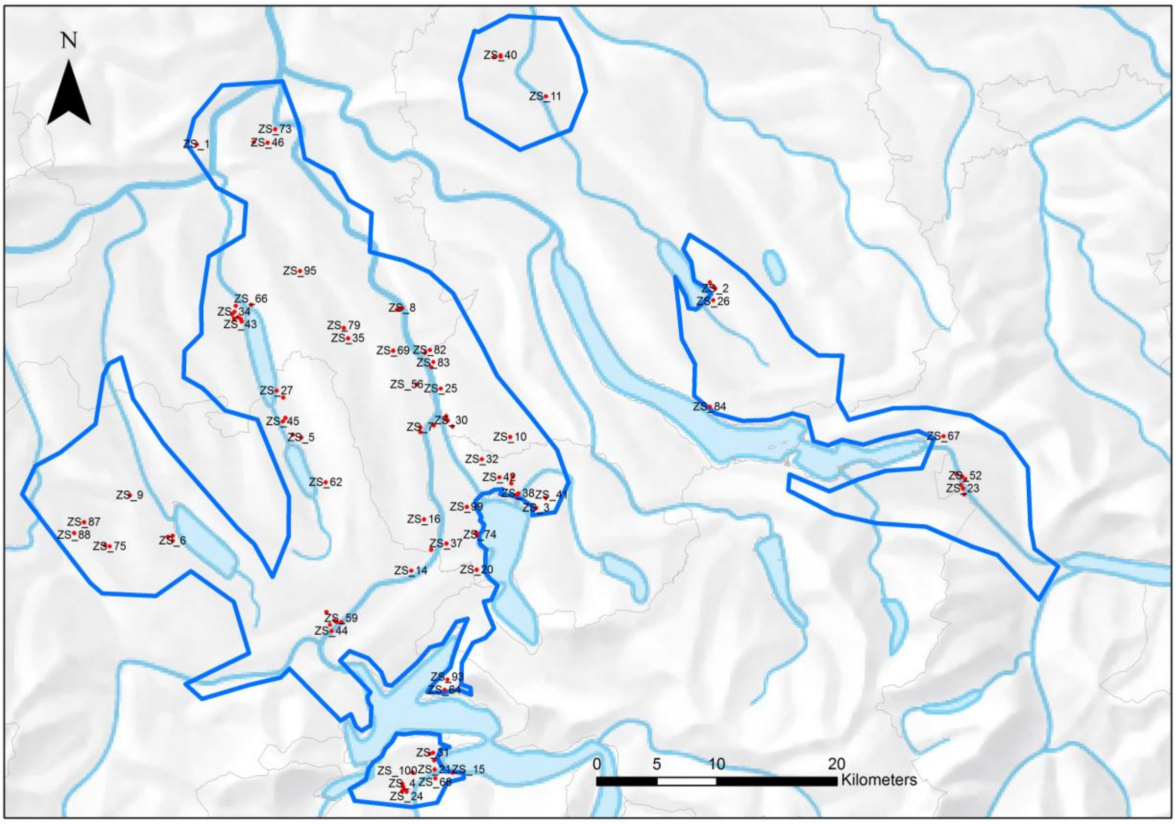


Fig. A2.5: Close-up of study sites of the suitability hotspot region Central Switzerland. Where study sites (n=100) are in close proximity, only one area is labeled. Hotspot region boundary is indicated by colored line.

Background on Principal Component analysis and linear discriminant analysis

Table A2.1: Eigenvalues and explained variance of first two principal components per PCA. Cumulative percentage of explained variance of 45% was taken as threshold for principal component inclusion in analysis.

PCA	PC NR.	EIGENVALUE	% VARIANCE EXPLAINED	CHI^2	DF	P
Cavity structure	PC1	2.9139	41.627	1675.254	19.22	<.0001
Cavity structure	PC2	1.444	20.631	1059.984	17.146	<.0001
Orchard structure	PC1	2.236	27.954	1030.151	28.650	<.0001
Orchard structure	PC2	1.385	17.315	753.326	24.195	<.0001
Mouse availability	PC1	1.777	29.616	373.826	14.719	<.0001
Mouse availability	PC2	1.317	21.942	239.508	11.512	<.0001

Table A2.2: Eigenvalues and explained variance of discriminant functions resulting from linear discriminant analysis (Table 6).

DISCRIMINANT FUNCTION	EIGENVALUE	% VARIANCE	CANONICAL CORRELATION
1	1.39	57.54	0.76
2	0.81	33.46	0.67
3	0.16	6.66	0.37
4	0.06	2.34	0.23

Table A2.3: Percentage of assignment prediction for all regions In total 59.6% of the areas were assigned properly. In cross-validation 56.8% were assigned correctly.

REAL REGION	PREDICTED REGION (%)				
	DE	NJ	SL	TG	ZS
DE	79.0	5.0	8.0	7.0	1.0
NJ	3.0	69.0	19.0	2.0	7.0
SL	9.0	23.0	51.0	6.0	11.0
TG	4.0	2.0	13.0	56.0	25.0
ZS	3.0	12.0	16.0	29.0	40.0

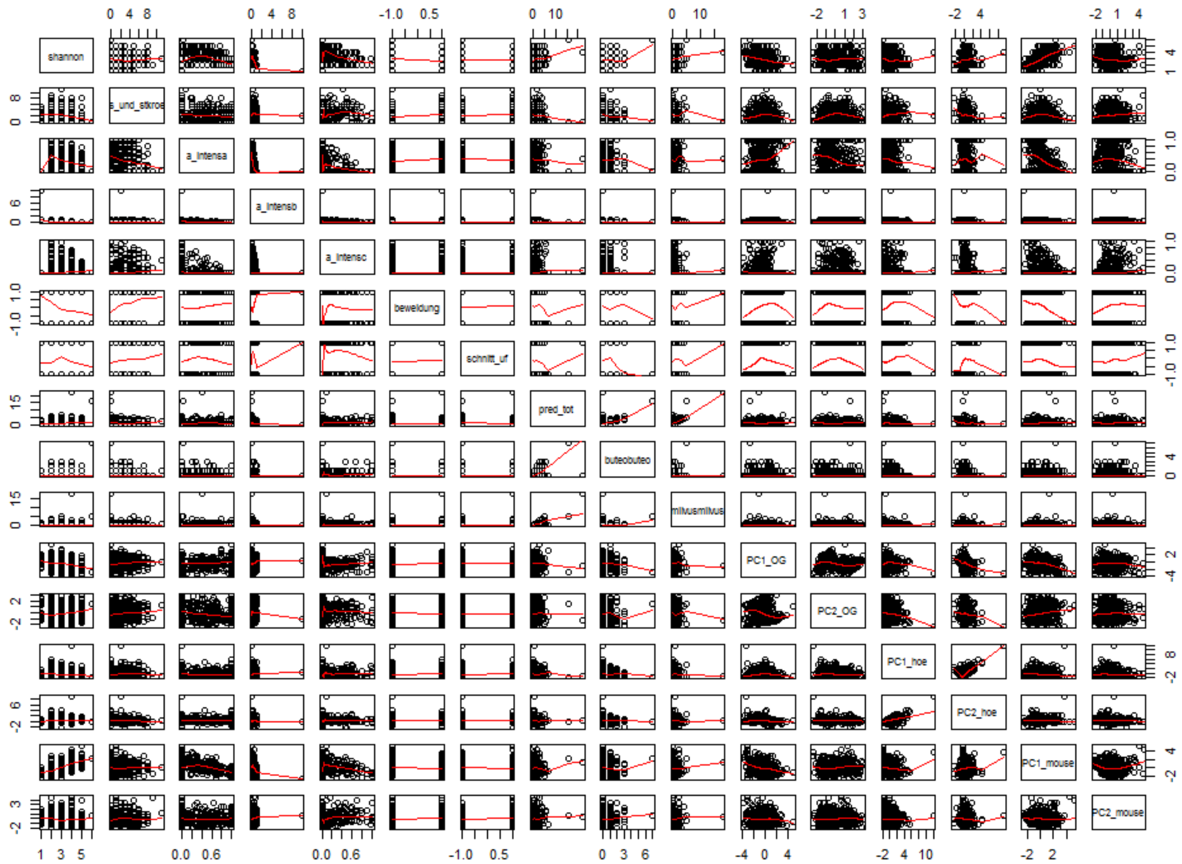


Fig. A2.6: Correlation matrix of all 16 analysis variables. No significant correlations were found and therefore all variables were included in the analysis. Parameters were renamed (from top to bottom) for representation in table 4: Shannon = number of land-use classes, ks_und_stkroe = number of different habitat structures, a_intensa = intensive meadow-use, a_intensb = intermediate meadow-use, a_intensc = low meadow-use, beweidung = grazing, schnitt_uf = mowing patterns, pred_tot = total predation,, buteobuteo = number of common buzzards, milvusmilvus = number of red kites, PC1/2_OG = PC1/2 orchard structure, PC1/2_hoe = PC1/2 cavities, PC1/2_mouse = PC1/2 mouse availability.