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Little owls in big landscapes: Informing conservation using multi-level resource selection functions

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ABSTRACT

Habitat models are fundamental tools for designing evidence-based conservation measures, particularly for locating sites with high potential for promoting a species' recolonisation and occupancy. However, it remains challenging to respond to both the need for large-scale general rules, and for fine-scale information concurrently. Multi-level habitat models provide all-in-one surfaces that explicitly account for conditional dependencies among single-level selection probabilities. We integrated occurrence data obtained from citizen-science species observation data with radio-tracking data to develop multi-level resource selection functions for the little owl (*Athene noctua*), a species of conservation concern in Central Europe. The results of our habitat selection analyses confirmed that suitable little owl habitat is located in widely open agricultural landscapes that often exist in the vicinity of human settlements. We mapped habitats at fine resolution (40 × 40 m) over an area covering 77,313 km^2 in Switzerland and Baden-Württemberg, Germany. We validated the models with external out-of-sample data, and we demonstrated good predictive ability and transferability over the broad landscape. Overall, a fifth of the modelled landscape was estimated to be suitable for little owls. Habitat suitability scores in Switzerland were generally lower than in Baden-Württemberg due to higher elevation, fewer orchards, and more forest patches. Extant populations currently occupy c. 15% of the potential suitable habitats in Baden-Württemberg, and 2% in Switzerland, suggesting that considerable space for recolonisation is available. However, while Baden-Württemberg offers vast open landscapes, lowlands in Switzerland show narrow swaths of habitat along valleys and lakes. We showed that the simultaneous integration of different levels of habitat selection behaviour into a multi-level habitat suitability map creates a promising tool for conservation planning of endangered species over large geographical areas. Our multi-level model allowed for identification of both large-scale habitat suitability patterns to develop conservation strategies, and fine-scale clusters of high quality habitats where conservation measures can be applied at once, thereby increasing relevance of such all-in-one habitat maps for policy makers, wildlife managers and conservations practitioners alike.

1. Introduction

Understanding the relationships between a species and its environment is at the core of ecology (Krebs, 2009), and is pivotal to the design of evidence-based conservation measures (Harding et al., 2001). Spatial patterns in crucial resources are considered major determinants of the distribution and abundance of a species (Boyce et al., 2016; Weber et al., 2017). Generally, the reproductive output and survival, thus fitness, of animals are assumed to be related to the selective use of resources in their environment (Morris, 2003; Thomas and Taylor, 2006; Uboni et al., 2017). Under this assumption, habitat suitability or quality can be inferred from the study of habitat selection, defined as the disproportional use of habitat features to their availability in the landscape (Johnson, 1980; Manly et al., 2002). Habitat selection is determined by different sets of ecological factors at different spatio-temporal scales (Mayor et al., 2009; Meyer and Thuiller, 2006), and using habitat suitability models to inform species conservation by identifying the most important regions and places for conservation measures requires a multi-scale approach (Mayor et al., 2009; Rettie and Messier, 2000).

A hierarchical framework of nested orders to study habitat selection at various spatiotemporal levels has been long-recognised and widely

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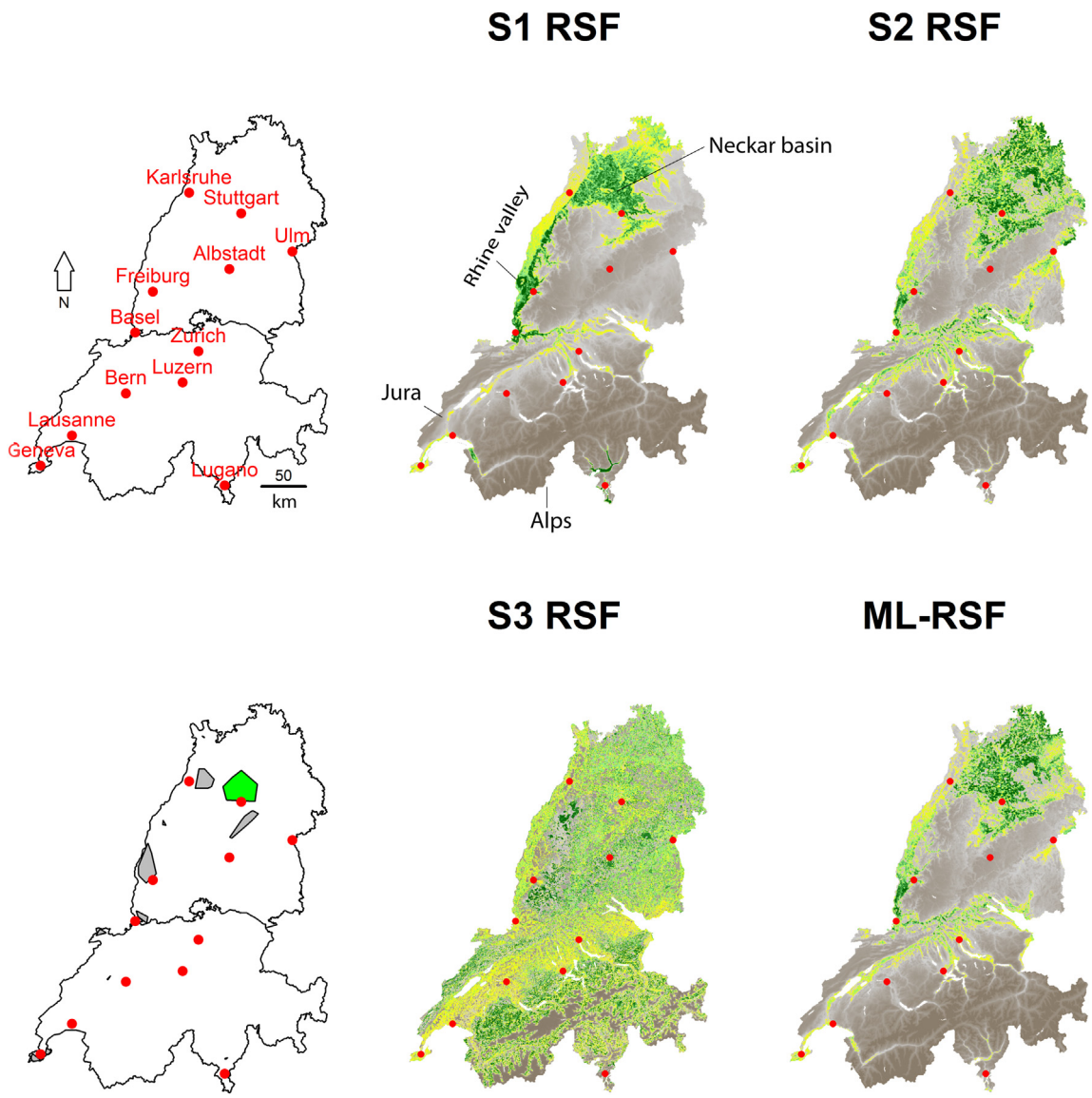

Fig. 1. Level-specific and multi-level habitat suitability for little owls in Switzerland and Baden-Württemberg, south-western Germany. Good habitat (yellow to green) is defined as the amount of habitat that captured 90% of the out-of-sample validation occurrence data. Below this threshold, the shades of grey represent suitability values for unsuitable habitat (dark brown to light grey). Large cities are shown for reference. The twelve extant little owl populations in this landscape are shown (light grey polygons), including the telemetry study area (green polygon).

acknowledged in the literature (Johnson, 1980; Meyer and Thuiller, 2006; Rettie and Messier, 2000). Species distribution is driven by environmental conditions that operate at large spatiotemporal scales, described by Johnson (1980) as first order selection (hereafter 'S1'). Within the species range, at the individual level, home range placement (second order; 'S2'), and within-home range habitat use (third order; 'S3') are related to medium to fine scale conditions. In the classic hierarchical nested design (Johnson, 1980), inferences are specific to each level (Boyce, 2006; Mayor et al., 2009). However, factors operating at the broader scales may constrain habitat availability at the finer scales, and conversely, large-scale patterns can also result from individual behavioural processes at finer scales (Mayor et al., 2009; Meyer and Thuiller, 2006).

These conditional relationships among the hierarchical levels of selection have recently been explicitly modelled into so-called 'scale-integrated' (DeCesare et al., 2012; Holbrook et al., 2017; Pitman et al., 2017), and 'multi-level' models (McGarigal et al., 2016; Zeller et al., 2017) that transcend single-level models by integrating the different levels of selection. As pointed by Zeller et al. (2017), such integrations are relatively easy to achieve, as the hierarchical conditional probabilities collapse to a simple equation that is the product of the relative probabilities (DeCesare et al., 2012). Also, while changes in spatiotemporal scales are implicit to Johnson's (1980) hierarchical design and multi-level models, the approach does not explicitly determine the size of the ecological neighborhood at which organisms respond to each environmental covariate at a given selection level ('characteristic scale'; McGarigal et al., 2016). Optimizing the characteristic scale of selection of each covariate within each of the model level is a central focus of recent habitat selection modelling (McGarigal et al., 2016, Zeller et al., 2017). Such scale-optimized, multi-level models provide a more integral insight into animal-habitat associations than single-level models, but they rarely have been applied in a conservation context (DeCesare et al., 2012; Pitman et al., 2017; Zeller et al., 2017). An all-in-one habitat suitability model provides a better basis to inform conservation strategies over large spatial extents as well as local conservation measures, thereby responding simultaneously to both the needs of policy makers who call for large-scale general rules and to the needs of the practitioners in the field who call for fine-scale information (DeCesare

Table 1
Explanatory environmental covariates used for developing resource selection functions at three levels of selection for little owls in Switzerland and Baden-Württemberg, south-western Germany. Characteristic scales are indicated for each level of selection. Analytical grain was 40 m × 40 m for all covariates.

Explanatory variable	Characteristic scale (m)		
	First order (S1)	Second order (S2)	Third order (S3)
Elevation	1000	40	40
Slope	1000	1000	440
NDVI[a]	1000	680	40
% croplands	1000	1000	40
% forests	1000	680	120
% orchards	1000	1000	120
% meadows	1000	1000	120
% hedge	1000	920	680
% built-up	1000	1000	280
Distance to forest edge	40	40	40

[a] NDVI = Normalized Difference Vegetation Index.

et al., 2012).

Our aim was to develop multi-level habitat suitability models for the little owl (*Athene noctua*) over a large area comprising Switzerland and the neighbouring Baden-Württemberg state, south-western Germany. In both countries, and in many other central European countries, the little owl is listed as an endangered species on the red list (Haupt et al., 2009; Keller et al., 2010). The species is associated with various open landscapes, often in areas of high structural diversity with patches of low agricultural intensity (van Nieuwenhuyse et al., 2008). However, it remains poorly-known where the most promising conservation areas are located. The identification of currently good habitat areas is pivotal to inform where conservation efforts and recovery programs should be directed.

Here, we applied resource selection functions (RSF; Manly et al., 2002) to model (i) the potential species distribution at the landscape scale (S1) based on little owl occurrence data recorded in citizen-science databases; (ii) the selectivity of home range placement within little owl landscapes (S2); and (iii) the within-home range selection of habitat patches (S3) based on radio-telemetry data. We then (iv) integrated the three orders of selection to account for scale dependencies in a multi-level model, and we identified habitats by projecting these models to the entire study area. The resulting maps represent the distribution of habitat patches for little owls covering large areas.

2. Methods

2.1. Study area and occurrence data

We modelled little owl habitat in Switzerland (45.8°–47.8° N, 5.9°–10.5° E; 41,245 km^2), and Baden-Württemberg, south-western Germany (47.5°–49.8° N, 7.5°–10.5° E; 36,068 km^2; Fig. 1). The study area was a typical Central European human-dominated landscape, with a mosaic of forests, croplands, and human settlements in the lowlands, typically ranging between 400 and 600 m in elevation. The south of the study area in Switzerland is bordered by the Alps, with mountain tops up to 4500 m. The Jura Mountains on the north-western border of Switzerland with France range up c. 1700 m. To model habitat suitability for little owl at the population level (S1), we used occurrence data from 5 populations in Switzerland, and 7 populations in Baden-Württemberg, south-western Germany (Fig. 1) reported in citizen-science databases between 2005 and 2017 (ornitho.de, Ornithologischen Gesellschaft Baden-Württemberg, and ornitho.ch databases; n = 6950). In Baden-Württemberg, we combined these data with locations of occupied nest boxes (H. Keil pers. obs.; n = 176). As all extant populations in the study area are supplemented with nest boxes, we acknowledge that some occurrence data in the Swiss populations might also consist of observations at nest boxes, but this information was unavailable to us.

To model habitat suitability at the individual level for home range placement (S2) and within-home range selection (S3), we used radio-tracking data of breeding adult little owls collected between 2009 and 2012 from one population in the Ludwigsburg District, Baden-Württemberg (48° 53′ N, 9° 11′ E, 950 km^2). The telemetry study area was a mosaic of intensive agriculture fields, meadows, orchards and vineyards (Apolloni et al., 2017; Grüebler et al., 2014). More than 700 nest boxes were available to the c. 220 breeding pairs of the study population (Michel et al., 2016). We ringed and tagged little owls with a VHF radio-transmitter of our own construction. We mounted the transmitter with a backpack figure-8-harness (total c. 7 g; 4.5% average adult body mass; Naef-Daenzer, 2005). We used homing-in to record individuals' position and fate at least three days weekly (Michel et al., 2016). In total, we recorded 23,416 locations from 106 adult little owls (57 females, 49, males) throughout the year. Little owls are monogamous territorial, resident birds, with mean annual home ranges of 0.3 km2 (Michel et al., 2017).

2.2. Landscape covariates

We selected candidate explanatory covariates based on previous studies of little owl habitat selection (Table 1). In Central Europe, little owls are strongly associated with high-stem fruit orchards (Apolloni et al., 2017; Šálek et al., 2016) and open, low-intensity agricultural landscapes where they hunt ground-dwelling prey on bare ground or in vegetation < 10 cm high, mostly on flat terrain (Framis et al., 2011; Šálek and Lövy, 2012). Little owls negatively associate with forest, and tend to avoid forest edges up to 150 m (Michel et al., 2016). Their association to human infrastructure is less clear, as their breeding success positively correlates with distance away from human settlements (Tomé et al., 2004), but isolated farm buildings provide suitable nest sites in the absence of natural tree cavities (Šálek et al., 2016). Little owls are sensitive to extended snow cover periods, and avoid areas above 600 m in the region (Meisser and Juillard, 1998).

To characterize the landscape, we computed the proportion of land cover at a 40 m × 40 m resolution using fine-grained land cover maps produced for Baden-Württemberg and Switzerland. Land cover categories in Baden-Württemberg were compiled at a 10 × 10 m resolution based on geometry and land-use information of the Amtliches Topographisch-Kartographisches Informationssystem, and on information of the European Union Integrated Administrative and Control System (Heuck et al., 2013). Land cover in Switzerland was resampled to the German layer resolution using information from Arealstatistik (100 × 100 m; Arealstatistik 2004/09 © Bundesamt für Statistik) and vector25 data (Swisstopo 2010, 25 × 25 m, PK25 ©swisstopo DV002232.1; Scherler, 2014). To account for forest edge avoidance by little owls (Michel et al., 2016), we calculated the distance to the edges of the forest land cover category. We transformed this covariate with an exponential decay (Whittington et al., 2011) of the form

$$y = 1 - e^{-\alpha d}$$

where d is the distance in meters, and α was set to 0.02 to define the 150-meter threshold for declining effect of distance to forest (Michel et al., 2016). We used a 10-year average of the Normalized Difference Vegetation Index (NDVI-MODIS 20) to measure the relative amount of greenness as a proxy for vegetation types, and we extracted elevation and derived slope from a digital elevation model (Copernicus EU-DEM European Environment Agency). We resampled all covariates at 40 × 40 m grain for computation.

2.3. Habitat suitability modelling

2.3.1. Habitat use data and used-available sampling design

We sampled landscape covariates in a used-available design (Manly

et al., 2002) with a 1:5 presence: pseudo-absence ratio at each hierarchical level using the package 'raster' (Hijmans, 2016) in the R environment (R Core Team, 2017). To sample habitat use at S1, we first screened the citizen-science data for occurrences with exact coordinates, and with a breeding Atlas code indicating 'probable' and 'confirmed' breeding ($n = 4065$) to identify breeding populations ($n = 12$). We built population ranges around clusters of occurrences using a 100% Minimum Convex Polygon (MCP). We defined discrete populations based on a threshold dispersal distance of 10 km (van Nieuwenhuyse et al., 2008). Population ranges were ranging from 1 km^2 to 950 km^2. We generated within each population MCP a number of random points proportional to the MCP area and corresponding in total to the number of telemetry relocations ($n = 10{,}275$, see below). To sample availability at S1, we generated 51,375 random pseudo-absences within the whole study area (training extent). We reserved 3061 occurrences with exact locations but without Atlas code or with an Atlas code for 'possible breeding' for external model validation with out-of-sample data.

To standardise sampling frequency of the telemetry data across individuals at the S2 and S3 levels, we randomly selected one location per individual per 12-hour period. To define resource use at the second order and to sample availability at the third order, we built annual 100% MCP home ranges for individuals with ≥10 relocations per season in two consecutive breeding (1 April–31 August) and non-breeding seasons (1 September–31 March). In total, we used 10,275 relocations of 87 individuals (43 females, 44 males) over 4 years (121 individual-years, 55 females, 66 males). We reserved the 8155 relocations of the individual-years that did not meet this criterion for external model validation with out-of-sample data. We chose MCP as our aim was not to estimate home range size, but to capture an approximate home range to define resource use at the second order and to sample availability at the third order (Holbrook et al., 2017).

We defined individual annual home range as used (DeCesare et al., 2012). To sample habitat use at S2, we generated in each annual home range 85 random points, equal to the mean number of annual relocations per individual-year ($n = 121$). To sample habitat availability, we generated random pseudo-absences at a 1:5 ratio within the population range of each focal individual, defined as the 100% MCP including all telemetry relocations of all individuals in that population (training extent), corresponding to the S1 population ranges above.

At S3, we defined annual telemetry relocations (total: $n = 10{,}275$; individual-year mean ± sd: 84 ± 24; range: 32–141) as used points within each individual's annual home range (individual-year mean ± SD: 0.49 ± 0.63 km^2), and we sampled availability within each home range at 1:5 ratio random pseudo-absences.

2.3.2. Resource selection functions (RSF)

We fitted generalised linear models with binomial error distribution to the binary used-available data to assess habitat selection at the species distribution (S1), home range placement (S2) and within-home range (S3) selection orders (Johnson, 1980; Meyer and Thuiller, 2006). At each level, we followed a two-step approach to first optimize the characteristic scale for each covariate, and then build a multi-variable RSF (Zeller et al., 2017). To optimize the characteristic scale, we used the R package 'smoothie' (Gilleland, 2013) to compute a disk kernel smoothing at 13 ecological neighborhoods (40 to 1000 m grain size, corresponding to 3 average home range radii, with 80 m increments, corresponding to one 40 × 40 m cell in each direction from the focal cell). We fitted each covariate at each neighborhood in single variable regressions, including quadratic response to elevation and NDVI, and we identified the characteristic scale for a given covariate based on the model with the lowest value of the Akaike's Information Criterion corrected for small sample size (AICc; Zeller et al., 2017).

We screened for collinearity among all environmental covariates at their selected characteristic scales using a threshold Spearman's rho ($|r| > 0.6$). Among correlated covariates, we selected the one best fitting the data based on AICc, and we combined all uncorrelated covariates in a multivariate fixed-effects model and we conducted a manual backward-stepwise model selection procedure, removing all non-significant covariates from the multivariate model until the effects of all remaining covariates were significant $P < 0.05$ (Hosmer et al., 2013). To account for repeated sampling of the populations (S1) or the individuals (S2 and S3), we fit the final best fixed-effects models with population identity (S1) or little owl individual identities (S2 and S3) as a random intercept in generalised linear mixed-models (GLMM) using the R package 'lme4' (Bates et al., 2015). We scaled all covariates with a mean of 0 and a standard deviation of 1 prior to fitting GLMM.

2.3.3. Multi-level integration

To account for conditional nested dependencies among selection orders, we integrated the single-level models into a multi-level RSF (hereafter: 'ML-RSF'; DeCesare et al., 2012; Zeller et al., 2017). Using the fixed-effect coefficients of the mixed-models, we first estimated S1, S2, and S3 RSF predicted values representing relative probability of use w for a given pixel x over the entire study area (projected extent) to generate level-specific RSF maps (Manly et al., 2002), as

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k)$$

We rescaled the resulting RSF's between 0 and 1 (DeCesare et al., 2012), as.

$$w_{RSF} - hat = (w_{SRSF}(x) - w_{SRSF\,min})/(w_{SRSF\,max} - w_{SRSF\,min})$$

To develop ML-RSF across the study area ($w_{ML\text{-}RSF}$), we followed the approach of DeCesare et al. (2012) in exploiting the conditional relationships of selection among levels for any pixel in the landscape of being within the population-level home ranges occupied by owls (P[S1]), being within an individual's home range given that it is within a population home range (P[S2] | P[S1]), and being used by an owl given that it is within an individual's home range (P[S3] | P[S2]). Therefore

$$w_{ML-RSF} = P(S1) \times P(S2 \mid S1) \times P(S3 \mid S2)$$

that collapses into the multiplication of the probabilities across levels to estimate an integrated relative probability of use for a given pixel (DeCesare et al., 2012), as

$$w_{ML-RSF} = P(S1) \times P(S2) \times P(S3)$$

where *P(S1), P(S2)*, and *P(S3)* are the relative probability of use for a given pixel at the first, second and third level, respectively.

2.3.4. Model validation

We validated the final models using internal and external methods. Internal validation of the S1, S2 and S3 models consisted of tests of sensitivity and specificity using the area under the receiver operating curve (AUC; Hosmer et al., 2013). We validated the models externally by assessing the predictive ability of the single-level S1, S2, S3, and multi-level ML-RSF models using the out-of-sample validation data, following Boyce et al. (2002). We reclassified the models into 10 equal-area bins using percentile breaks at 10% intervals. We extracted the reclassified landscape bin values to the out-of-sample validation data. A greater number of validation data in habitat bins of higher quality (positive Spearman's correlation r_s) indicates a good predictive ability of the model (Boyce et al., 2002). To determine the amount of habitat in the landscape, we reclassified the landscape into 100 equal-are bins based on percentile breaks at 1% intervals, and we computed the cumulated proportion of validation data across equal-area bins. We used a threshold of 90% predicted use to determine the cut-point between habitat versus non-habitat in the landscape (Holbrook et al., 2017).

Table 2
Standardised fixed-effect beta coefficients and standard errors of the generalised linear mixed-models with binomial error distribution resource selection functions at three levels of selection for little owls in Switzerland and Baden-Württemberg, south-western Germany.

Explanatory variable	First order (S1)		Second order (S2)		Third order (S3)	
	β	SE	β	SE	β	SE
(Intercept)	−80.124	1.396	−127.100	5.666	−2.366	0.424
Elevation	29.794	0.646	62.860	2.592		
Elevation^2	−173.238	3.193	−285.600	12.980		
Slope			−2.132	0.125	1.412	0.135
NDVI	0.744	0.441	18.040	1.553	6.784	2.256
NDVI^2	0.293	0.296	−14.110	1.144	−4.592	1.664
% cropland			0.954	0.024	−0.411	0.012
% forest	−0.479	0.022	−1.287	0.109	−1.280	0.251
% orchard			0.273	0.010		
% meadow	−0.501	0.027	1.710	0.041		
% built-up	0.040	0.012			−0.536	0.027
Distance to forest (150 m exponential decay)					−0.380	0.056

3. Results

3.1. Habitat modelling

The optimal characteristic scale of the land-use covariates was congruent to the levels of habitat selection (Table 1). At the landscape level (S1), little owl occurrence responded to environmental covariates over a wider scale than at the home range level (S2) or the within-home range level (S3). At the landscape level (S1) little owl occurrence was related to low elevation, low proportion of woodland, and high proportion of built-up area. Furthermore we found a non-linear relationship of occurrence with greenness (NDVI), and the probability of occurrence was highest at intermediate NDVI values. Additionally occurrence was negatively related to the proportion of meadowland (Table 2). Both intermediate NDVI and meadowland characterized cropland-dominated agricultural areas. Areas with high habitat suitability at the landscape level therefore occurred in the German part of the Rhine valley, the Neckar basin and the fluvial plains of the Swiss plateau (Fig. 1).

Within these open landscapes, little owls selected for relatively flat areas and low proportion of woodland to place their home ranges (S2). We found a strongly positive response to the proportion of meadowland, orchards and cropland (Table 2). This indicates that home ranges included a high diversity of agricultural field types, and were closely related to the availability of scattered trees.

At the within-home range level (S3), we found a positive relationship of the relocations with slope, indicating that little owls preferred the undulating areas over totally flat parts. Little owls strongly avoided forest edges, and we found a negative effect of cropland and built-up areas on the relocation density. This suggests that owls preferred using meadows and orchards at some distance from forest edges and settlements. These were frequently located in the slightly hilly parts of the agricultural areas which are by tradition cultivated with fruit trees and meadows.

3.2. Model validation

Single-level S1 and S2 models showed high predictive accuracy internally ($AUC_{S1} = 0.931$; $AUC_{S2} = 0.820$; Table 3) while S3 showed moderate predictive accuracy ($AUC_{S3} = 0.633$). External validation showed that all single-level S1, S2, and S3 models had a high predictive ability of out-of-sample validation data at their training extent (r_s range 0.886–1.000, $p < 0.05$, Table 3, Fig. 2).

Table 3
Internal and external validation statistics for single-level and multi-level resource selection functions (RSF) for little owls in Switzerland and Baden-Württemberg, south-western Germany.

Model	Training extent				Projected extent		
	AUC	N	r_s	p	N	r_s	p
First-order RSF (S1)	0.931	3061[a]	0.886	0.003	3061[a]	0.886	0.003
Second-order RSF (S2)	0.820	8155[b]	1.000	< 0.001	3061[a]	0.970	< 0.001
Third-order RSF (S3)	0.633	8155[b]	1.000	< 0.001	3061[a]	0.418	0.232
Multi-level RSF	–	–	–	–	3061[a]	0.952	0.001

AUC = Receiver-Operator Curve Area Under the Curve; N = number of out-of-sample validation data points; r_s = rho Spearman's rank correlation. Validation datasets used were: (a) reserved occurrences from citizen-science databases with exact locations without Atlas code or with 'possible breeding' Atlas code; (b) reserved radio-tracking data of adult little owls with < 10 relocations per season in two consecutive breeding and non-breeding seasons.

Following projection over Switzerland and Baden-Württemberg, the S1 model had a high ($r_s = 0.886$, $p < 0.05$), and the S2 model had a very high ($r_s = 0.970$, $p < 0.05$) predictive ability of out-of-sample validation occurrence data (Table 3). As expected, the projected S3 model did not accurately predict out-of-sample occurrence data at the large extent (r_s 0.418–0.612, $p > 0.05$). The multi-level model had a high predictive ability of out-of-sample little owl occurrence data (r_s –0.952, $p < 0.05$, Fig. 2).

3.3. Resource selection functions

When defining habitat based on a threshold of the model ability to capture 90% of out-of-sample occurrence data (Fig. S1), multi-level integration identified 15,449 km^2 (22%) of suitable habitat in the study area (Table 4). Most of the suitable habitat patches were located on the Swiss Plateau between the Jura Mountains and the Alps, the south of Rhine Valley and the region north-east of the Black Forest in Baden Württemberg (Fig. 1). Relative to the multi-level habitat model, single-level models either underestimated suitability (S1, 14,309 km^2, 20%) or overestimated suitability (S2, 18,344 km^2, 27%). The projected S3 model identified suitable habitats in the Jura and the Pre-Alps (Fig. 1), and strongly overestimated the amount of habitat in the landscape (34,599 km^2, 69%).

Suitable patches covered 3231 km^2 in Switzerland (8% of the country), and 12,217 km^2 in Baden-Württemberg (34%; Table 4). Overall, 1918 km^2 were occupied by little owl populations (12% of the suitable habitat, Table 4). In Switzerland, only 76 km^2 were occupied (2%), while 1841 km^2 were occupied in Baden-Württemberg (15%).

Characteristics of the good habitats differed among occupied and unoccupied areas, and between Switzerland and Baden-Württemberg (Table S1, Fig. S2). Generally, mean suitability scores of good habitat areas were lower in Switzerland than in Baden-Württemberg (Fig. 1, Fig. S2). The underlying differences in the characteristics of habitat patches between countries were mainly the higher elevation and the lower proportion of orchards in Switzerland than in Baden-Württemberg. Habitat patches in occupied areas in Switzerland showed higher proportion of croplands and lower proportion of meadows than unoccupied patches, or habitats in Baden-Württemberg (Fig. S2). Areas of good habitat in Switzerland were also smaller (Fig. 1).

3.4. Hierarchical level relationships

The S1 and S2 models correlated strongly ($R^2 = 0.910$; Fig. S3), meaning that they identified similar levels of habitat suitability over the

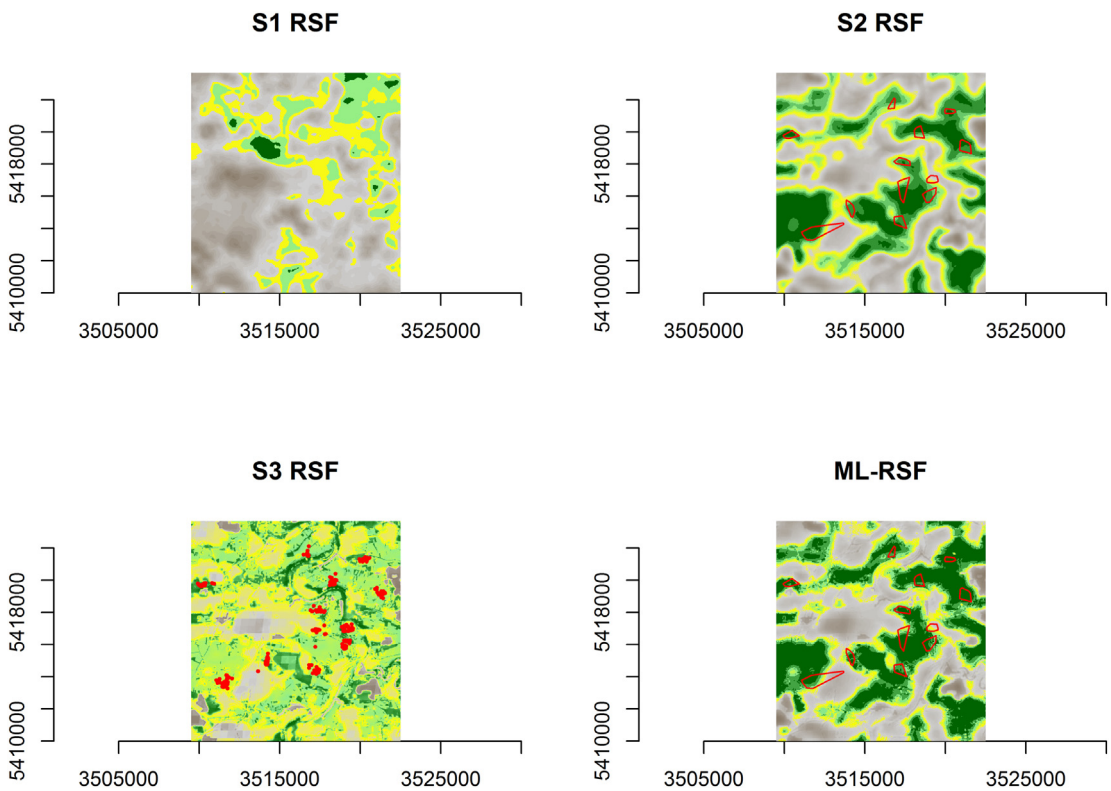

Fig. 2. Level-specific and multi-level habitat suitability for little owls in the Neckar basin, south-western Germany. Home ranges (red-outline polygons) and telemetry relocations (red dots) of twelve adult little owls are shown. The figure illustrates the advantage of multi-level maps integrating broader scale suitability with fine scale processes, and can therefore inform conservation strategies over large spatial extents as well as planning of local conservation measures with a single all-in-one surface. Suitable habitat (yellow to green) is defined as the amount of habitat that captured 90% of the out-of-sample validation occurrence data. Below this threshold, the shades of grey represent suitability values for unsuitable habitat (dark brown to light grey).

whole landscape. Considering the highest habitat suitability values however, the relationship did not appear as strong, suggesting that both levels alone adequately identified poor habitats but were not as consistent in the evaluation of the quality of good habitat. The S3 projection did not correlate with either the S1 ($R^2 < 0.001$) or the S2 ($R^2 = 0.003$) models.

The multi-level model correlated well with the S1 ($R^2 = 0.952$), and very well with the S2 ($R^2 = 0.987$) models (Fig. S3). These two correlations also weakened with higher suitability index values, showing that the S3 projection added important fine-scale habitat information to the multi-level model not depicted at the S1 and S2 levels alone. Alone, S3 within-home range selection did not correlate with the multi-level model ($R^2 = 0.004$).

4. Discussion

We integrated broad-scale citizen-science species monitoring data with site-specific radio-tracking habitat use data to develop a multi-level habitat suitability model for little owls. It allowed evaluating habitat suitability for the species over a large extent by using publicly available, high-resolution governmental land-use data. Our study encompasses large geographical areas of two European countries differing in their agricultural policies. This all-in-one model resolves two main issues in the conservation of an endangered species: (1) identification of large-scale suitability patterns to develop conservation strategies, and (2) identification of fine-scale clusters of high quality habitat patches where conservation measures can be applied. Level integration enhanced the estimates of suitability by considering home range selection rules at both the landscape and the home range selection levels, and habitat preferences within home ranges. The large-scale evaluation of little owl habitat suitability showed that (1) suitability values were generally lower in Switzerland than in Baden-Württemberg, and (2) the distribution of good habitat areas differed between the two countries. Single-level habitat selection models showed that occurrence of little owl populations was based on topographic factors and the large-scale avoidance of forests, while within little owl landscapes preferences for home range placement and range use were based on the availability of important vegetation and land use types.

4.1. Habitat modelling

The results of the three habitat selection analyses confirm that good little owl habitat is located in widely open agricultural landscapes that often exist in the vicinity of settlements or even suburban areas (Apolloni et al., 2017; Framis et al., 2011; Šálek et al., 2016; Šálek and Lövy, 2012; van Nieuwenhuyse et al., 2008). Such open landscapes can offer a high diversity to lose stands of trees (orchards, tree rows, tree groups) with associated meadowland. Within these areas, little owl home ranges occurred at some of forests, and are preferentially located in meadowland with scattered trees. While slope within the home range might not be of direct importance for little owls, it might correlates with fine scale characteristics of the preferred open areas, such as food availability or tree cavities. On the other hand, at the landscape level (S1), steeper slopes had a negative effect on owl occurrence, as they might not offer these preferred fine scale resources.

Characteristic scales of selection were consistent with the implicit spatial scaling of the nested selection levels. Little owl responses to environmental covariates operated over large scales at S1, over intermediate scales at S2, and over smaller scales at S3. This clearly supports claims that multi-scale, multi-level habitat models should always optimize characteristic scale of environmental covariates within each level in order to adequately capture the specificity of the selection processes

Table 4
Amount of suitable habitat for little owls in Switzerland and Baden-Württemberg, south-western Germany based on resource selection function (RSF) thresholds needed to capture 90% of out-of-sample occurrence data, and amount and proportion of suitable habitat currently occupied by extant little owl populations.

	Switzerland and Baden-Württemberg (77,313 km^2)				Switzerland (41,245 km2)				Baden-Württemberg (36,068 km^2)			
Model	Area of suitable habitat (km^2)	Suitable proportion of the landscape	Area of occupied suitable habitat (km^2)	Proportion of suitable habitat occupied	Area of suitable habitat (km^2)	Suitable proportion of the landscape	Area of occupied suitable habitat (km^2)	Proportion of suitable habitat occupied	Area of suitable habitat (km^2)	Suitable proportion of the landscape	Area of occupied suitable habitat (km^2)	Proportion of suitable habitat occupied
First order RSF (S1)	14,309	20%	2208	15%	2451	6%	68	3%	11,859	33%	2139	18%
Second order RSF (S2)	18,344	27%	1961	11%	4095	10%	81	2%	14,250	40%	1880	13%
Third order RSF (S3)	34,599	69%	1899	5%	16,851	42%	91	1%	17,748	50%	1807	10%
Multi-level RSF	15,449	22%	1918	12%	3231	8%	76	2%	12,217	34%	1841	15%

at play (McGarigal et al., 2016; Zeller et al., 2017).

As radio-tracking was restricted to a single study area, a potential limitation of our multi-level model is the use of regional information from one population only to predict home range placement and within home range habitat use over large areas. While the S2 model validated well over the training and the projected extent, as did the S1 model, the S3 model validated well over the training extent but performed poorly over a broad landscape. The poor transferability of S3 models is well-documented in the literature (DeCesare et al., 2012), and we did not intend to use S3 alone over the whole landscape. Indeed, we developed the S3 models to be integrated with S1 and S2. The final multi-level models validated well over the broad landscape, demonstrating good predictive ability and transferability. We therefore conclude that our multi-level model is accurate in identifying areas and patches of good habitat, including fine scale information. While in a cost-sensitive conservation context the use of publicly available occurrence data to build S1 species distribution models might suffice if one is only interested in estimates of broad-scale habitat patterns, multi-level modelling should be preferred if the interest lies in the detailed distribution of habitat patches at high resolution and over large areas.

4.2. Little owl ecology

In Central European studies, the little owl is often characterized as an orchard specialist. However, across the entire distributional range, little owls occur in a wider diversity of landscapes, even in almost treeless areas (van Nieuwenhuyse et al., 2008). Accordingly, our model did not favour orchard regions over farmland plains at the landscape level (S1). However, within these landscapes, little owl home ranges were located selectively in areas of high agricultural and structural diversity. In our study area these were predominantly islands providing tree or building structures and grassland within the intensively used agricultural land. Thus, the results at the home-range level (S2) accorded well with previous studies of little owl habitat selection in Central Europe (Framis et al., 2011; Šálek and Lövy, 2012; van Nieuwenhuyse et al., 2008). The underlying mechanism for the preferences is likely the availability of major resources such as cavities for breeding and roosting (Bock et al., 2013; Grüebler et al., 2014), and food (Apolloni et al., 2017; Michel et al., 2017) related to vegetation types and land use.

4.3. Applications: strategies and specific measures

Overall, approximately a fifth of the included landscape was estimated suitable for little owls (score ≥ 0.78). However, populations currently occupy only a fraction of the potential habitat in this landscape, c. 15% of the potential habitat in Baden-Württemberg and c. 2% in Switzerland. The occupied areas are those where nest box provisioning programs had been conducted since 1990. Thus, our model suggests that considerable space for recolonisation is available in both countries and that the resulting map provides an important tool to direct future conservation efforts to areas with the highest potential. At the landscape-scale the maps allow selecting sites with the aim to optimally connect existing populations. They indicate regions and sites where inexpensive restoration measures such as distributing nest-boxes promise maximal efficiency. In Germany and France, several local species recovery programs have shown that installing nest boxes in good habitat areas is a first and most important measure which revealed some dramatic successes in terms of population recovery (Habel et al., 2015; van Nieuwenhuyse et al., 2008). Our tool offers the opportunity to combine new and existing, but so far isolated conservation actions into a wider concept that supports the existing populations, and potentially facilitates immigration into unoccupied suitable areas. It can also be used to simulate land-use change scenarios in order to explore the effect of conservation interventions on little owl habitat, or identify areas of possible future habitat degradation, loss or fragmentation.

There were considerable differences between the two countries: suitability scores in Switzerland were generally lower than in Baden-Württemberg. This difference likely arose due to three main reasons. First, even the lowest fluvial plains in Switzerland are situated at higher elevation than most good habitat areas in Baden-Württemberg. The negative effect of high elevation at both the landscape level and the home range placement level therefore suggests that in Switzerland the climatic conditions are harsher compared to the lower and milder areas in Baden-Württemberg. Avoidance of higher elevation is consistent with the avoidance of prolonged snow cover periods in Winter (Meisser and Juillard, 1998; van Nieuwenhuyse et al., 2008). This may potential markedly slow the rate of recolonisation into suitable habitat at lower elevation.

Second, suitable as well as occupied areas in Switzerland showed considerably fewer orchards than good habitats in Baden-Württemberg. The landscape preference for lowlands excluded many of the traditional but more elevated orchard regions in Switzerland from the most suitable areas. In contrast, hilly orchard areas at the edge of the Rhine valley and the Neckar basin are within the high suitability values at S1. Accordingly, most of the current Swiss little owl populations occur in crop-dominated areas rather than in areas with frequent orchards, while in Baden-Württemberg good habitats are found in both crop-dominated flatlands and orchard-dominated hilly areas. This suggests that while in Baden-Württemberg current conservation of remaining orchards, and supplementation of these habitats with nest boxes might result in successful recovery programs (Gottschalk et al., 2007), an additional challenge in Switzerland is to substitute important structures such as perches and roosting sites (Bock et al., 2013; Habel et al., 2015; Sunde et al., 2014), as well as the food-rich meadows in non-orchard areas (Michel et al., 2017). Nest boxes and artificial perches could substitute the perches and cavities originally found in trees. Moreover, detailed analyses of small scale resource availability have showed that high quality patches in Switzerland offer fewer roosting sites and grasslands of higher management intensity than high quality patches in Baden-Württemberg (Scherler, 2014).

Third, in addition to topography and elevation, lowlands in Switzerland have more forest patches than lowlands in Baden-Württemberg. Thus, while Baden-Württemberg offers vast open landscapes, Swiss lowlands show narrow swaths of good habitat along valleys and lakes. Further research is needed to understand how these structural differences in suitable habitats could influence on functional connectivity of the landscape and affect the rate of recolonisation of available habitats from extant population in this landscape.

5. Conclusion

In conclusion, we showed that the simultaneous integration of different spatial scales of habitat selection behaviour into a multi-level habitat suitability map creates a promising tool for conservation planning of endangered species over large geographical areas. Level integration corrected the area of good habitat in the landscape by considering home range selection processes, and corrected suitability values, and thus distribution of high quality patches, by considering habitat use within home ranges. The considerable potential habitat found for the little owl calls for restoration plans in the wider area surrounding existing populations. The single habitat suitability layer allows for adequate identification of both large-scale suitability patterns to develop conservation strategies, and fine-scale clusters of high quality where conservation measures can be applied. A same, common tool augments its relevance to policy makers, wildlife managers and conservations practitioners alike.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.09.032.

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