

## 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<sup>2</sup> 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

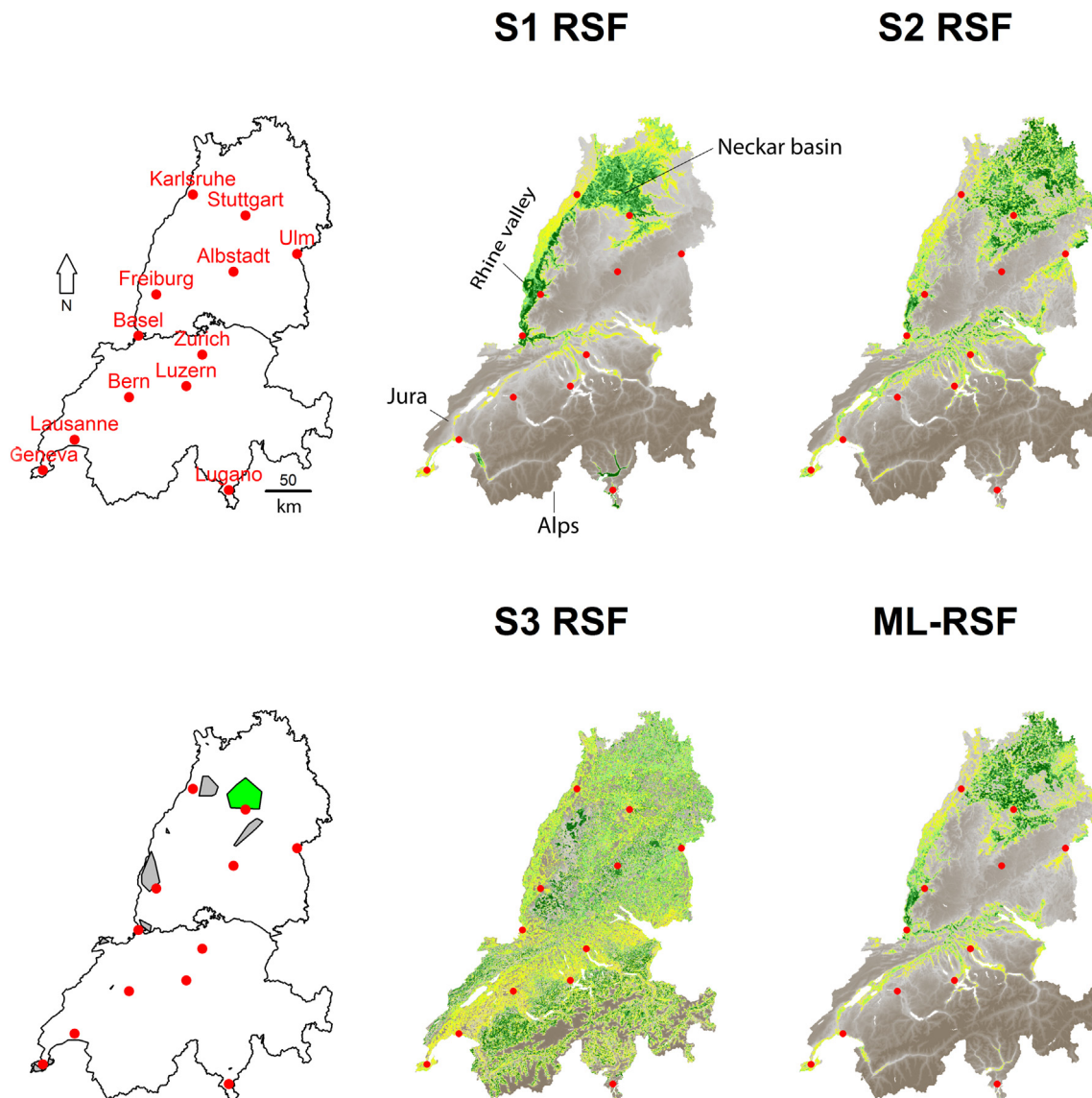
Understanding the relationships between a species and its environment is at the core of ecology (Krebs, 2009), and is pivotal to the design of evidence-based conservation measures (Harding et al., 2001). Spatial patterns in crucial resources are considered major determinants of the distribution and abundance 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; Ubani 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

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