

Habitat selection and range use of little owls in relation to habitat patterns at three spatial scales

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Keywords

Athene noctua; food abundance; habitat selection; landscape configuration; little owl; radio-telemetry; range use; resource distribution.

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Abstract

Understanding the rules of habitat selection and the individual behavioural routines in the home-range is crucial for developing evidence-based conservation action. We investigated habitat selection and range use of adult little owls *Athene noctua* in relation to landscape configuration, habitat structure and resource distribution. We determined the preference of habitat structures by VHF-telemetry. Large- and fine-scale distribution patterns of voles – the main prey during the breeding season – were assessed by transect counts of signs of vole presence. An experiment using artificial perches was carried out to determine the fine-scale adjustment of the owls' range use in relation to prey abundance and vegetation height. Habitat selection and resource exploitation by little owls were structured at all spatial levels: (1) at the landscape scale, orchards were highly preferred over other areas. This accords with the patchy large-scale occurrence of voles, which were absent in cropland, but abundant in orchards and grassland; (2) within home-ranges, the spatial distribution of voles was highly inhomogeneous and structures with high prey abundance were used over-proportionally; (3) at the scale of foraging sites, little owls preferred patches with low vegetation over those with high prey abundance, establishing that prey availability is the crux. The results suggest that all levels of habitat selection and range use were related to farming practices and affected by current cultivation. Conservation measures should focus on the conservation and restoration of orchards on the landscape level and habitat management measures should focus on grasslands – the main food providers – by creating a mosaic of patches with short grass and tall grass. Together with other habitat structures providing food resources such as field edges, wildflower areas and structures facilitating access to prey, the quality of habitat patches in terms of food availability may be highly improved.

Introduction

Habitat selection determines the spatial structure of animal populations in response to the abundance, distribution and accessibility of resources (Dolman, 2012). Behavioural responses of individuals to environmental characteristics operate at different spatial scales, from the landscape (e.g. via settlement decisions) down to fine-scale patterns (e.g. for home-range size and foraging). Understanding these interactions is crucial for establishing species-specific ecological requirements and for developing evidence-based conservation measures (Johnson, 1980; Kristan, 2006; Fuller, 2012; Vickery & Arlettaz, 2012).

The fundamental changes in farming practices during the last decades have dramatically affected the habitats of numerous species at all spatial levels (Fuller, 2012; Vickery

& Arlettaz, 2012). At the landscape scale, suitable habitat for farmland species is often restricted to small islands within an increasingly uniform (and presumably inhospitable) matrix (Benton, Vickery & Wilson, 2003). This resulted in considerable fragmentation of populations of many farmland species. These residual areas are further influenced by farming practices via impacts on food availability (Zmihorski, Romanowski & Chylarecki, 2012), availability of breeding or roosting sites (Martínez & Zuberogitia, 2004; Tomé, Bloise & Korpimäki, 2004) and presence of predators (Tomé *et al.*, 2004). At the scale of patches of suitable habitat, variation in the availability of resources and their spatial distribution creates heterogeneity to which individuals respond by adjusting the location and size of their home-ranges. Furthermore, fine-grained habitat structures such as vegetation height and density may affect the access to resources and

the individuals' habitat use within the home-ranges (Schaub *et al.*, 2010; Arlettaz *et al.*, 2012; Tagmann-Ioset *et al.*, 2012).

For many species occurring in human-shaped habitats, the responses at relevant scales and the consequences for the spatial distribution and size of individual home-ranges are poorly understood, particularly with respect to essential resources such as food. This is a severe handicap in developing evidence-based conservation action. In this context, the little owl *Athene noctua* is a good example species. It has a trans-Palearctic distribution and occurs mainly in human-shaped semi-open lowland landscapes. In Western and Central Europe, little owls occur mainly in orchards and other extensively cultivated areas with scattered trees. The species experienced a rapid decline in Western and Central Europe because of massive loss of these specific habitat structures in the agricultural landscape (van Nieuwenhuysse, Génot & Johnson, 2008; Sálek & Schröpfer, 2008). Despite multiple recovery programmes, the little owl is still of conservation concern in many countries of Western and Central Europe (van Nieuwenhuysse *et al.*, 2008). Understanding its habitat selection and range use at different spatial scales is thus important for implementing effective conservation measures. To better understand the ecological importance of main habitat elements for the species, we first investigated the selection of habitat at the landscape scale, specifically in relation to the distribution of orchards and large-scale variation in the abundance of voles. Second, we analysed habitat use across habitat patches in relation to the abundance of voles. Third, we conducted an experiment addressing the fine-grained adjustments of resource use in relation to characteristics of foraging sites such as vegetation height.

Materials and methods

Study area

The study was conducted in Baden-Württemberg, Southern Germany in a population of about 220 breeding pairs on an area of c. 250 km² where little owls breed mainly in artificial nest cavities. The agricultural landscape of the study area is characterized by arable farmland 33.4%, orchards 9.8%, grassland 9.7% and vineyards 7.1%. Baden-Württemberg holds about 30% of the whole German stock of orchards (Küpfer & Balko, 2010). Further information on the study population is given in Bock *et al.*, 2013 and Perrig *et al.*, 2014.

Spatio-temporal variation in vole abundance

Small rodents, particularly voles, are a staple food for little owls in the study area and make up to 70% of the biomass delivered to nestlings (Müller, 2012). To estimate the abundance of voles in different habitat types, we quantified the relative abundance of common voles *Microtus arvalis* and water voles *Arvicola terrestris* by conducting quick and low-cost counts of superficial traces (Delattre *et al.*, 1990;

Giraudoux *et al.*, 1995; Lambin, Aars & Piertney, 2001). To assess large-scale variation in the abundance of voles, four regions separated by landscape barriers, namely the streams Neckar, Enz and Murr (Regions NE, NW, SE, SW) were sampled. The standard approach by live-trapping (Baker & Brooks, 1981; Salamolard *et al.*, 2000; Arlettaz *et al.*, 2010; Butet *et al.*, 2010) would have been too demanding to cover these large areas. We counted field signs of voles (runways, holes and molehills) on transects within three habitat types [cropland (mostly wheat, maize, rape and sugar beet), grassland and orchards] comprised in the area used by the tracked owls. In each of these areas, nine randomly selected sampling points were performed per habitat type, totalling 27 sampling points per area. At each sampling point, a randomly located transect of 5 m length was completed. Along each transect, a zone of 50 cm width (i.e. 2.5 m² per transect) was meticulously scanned for traces of current vole presence. Fresh grass clippings and droppings, food remains and newly dug earth were indicators for the freshness of traces. The data were collected within individual home-ranges as determined from telemetry data and in 1-2-month intervals. The abundances along field edges were post-hoc extracted using ArcGIS by assigning counts within a buffer zone of 2 m along the edge of every sampling area. All other sampling points were located at least 10 m away from a field edge. From February to October 2011, we surveyed a total of 3815 transects.

To check whether transect counts were correlated with live-trapping data, we trapped voles at two sites, where transect counts had also been collected. Additionally, the repeatability of transect counts was tested by repeat counts per sampling point. These tests revealed that counts of field signs were highly correlated with live-trapping data and that the repeatability of transect counts was high (for further details, see supplementary material).

Habitat selection and habitat use

The placement of adult little owl home-ranges on the landscape scale and the habitat patch use was recorded by radio-telemetry. Adult birds were caught by mist netting either in the pre-breeding period or during the late nestling period. The owls were tagged with user-programmable two-stage VHF-transmitters of own construction (for further details, see Naef-Daenzer *et al.*, 2005). The transmitters had a range of c. 30 km ground to ground. The battery lasted for c. 380 days. Standard figure-8 harnesses were used to attach the tag on the owls (Kenward, 2001). The tag and harness weighed 6.9–7.2 g which represents 4–5% of bird body mass. Nine males and seven females were tracked from January 2011 until June/July 2011 and 15 males and 13 females from June/July 2011 to October 2011.

We located the birds using handheld antennas and the homing-in technique (Kenward, 2001); for further details, see Bock *et al.*, 2013; Perrig *et al.*, 2014. Locations during the night were recorded in 3-day intervals using standardized protocols (Grüebler & Naef-Daenzer, 2008) employing interval samples and focus-animal sampling (Altmann, 1974).

As an example, Fig. 1 illustrates the spatial distribution of vole sampling transects, the vole abundance and telemetry locations in a typical orchard area with two breeding pairs of little owls.

The proportions of the major habitat elements in the study area were calculated using a high-resolution land-use raster map (10 m \times 10 m) for Germany (Heuck *et al.*, 2013). We used the minimum convex polygon including all telemetry locations collected in the study as a reference (100% MCP, c. 1400 km²). The proportions of cropland, grassland, orchards, wood/shrub, urban areas, forest, vineyards and 'other' were determined using ArcGIS 9.3. These proportions were subsequently used as the available habitat in the first step of the compositional analysis (see below).

To determine the use of different habitat types on the habitat patch level, little owl home-ranges (as determined by 100% Minimum convex polygons including all telemetry locations) were mapped in the field in 2011 to assess the within-home-range available proportions of the main habitat types [cropland, grassland, orchards, urban areas, roads, forest vineyards and 'other' (i.e. all structures not attributable to one of the other seven categories)]. These proportions were used in the second step of the compositional analysis.

Individual response to vegetation height

To experimentally assess the owls' response to fine-scale structures, we offered artificial perches in six ranges used by

the tracked birds, on areas where no natural perches were available. Perches were set up in parcels of at least 50 \times 50 m of grassland and cropland during three stages of vegetation growth: (1) when vegetation was short in grassland and cropland, (2) when vegetation was high in grassland and cropland, (3) when vegetation was short in grassland and in cropland (harvested). The perches were mounted on 1.5 m wooden poles and consisted of a horizontally attached piece of branch (25 cm). To record the frequency of visits, the branch was attached to a lever operating a mechanical counter (Voltcraft Inc., Hirschau, DE, USA). The length of the lever was adjusted to trigger the counter if the load exceeded 120 g (thereby excluding visits by small birds). The artificial perches were distributed and stratified in two habitat types, hay meadows (grassland) and cereal fields (cropland). Perches were placed at least 50 m far away from natural perches and >10 m away from field borders to avoid edge effects. In each experimental home-range, one grassland and one cropland plot were selected. In each plot, we set up four perches, totalling eight perches per experimental run (for further details, see supplementary material). Half of the perches (two grassland perches and two cropland perches) were surveyed by PC 900 HyperfireTM trail cameras (Reconyx, Inc., Holmen, WI, USA). For each experimental home-range, two experimental runs were performed. For the second experimental run, one grassland and one cropland plot other than those used in the first run were selected. Half of the perches (two grassland perches

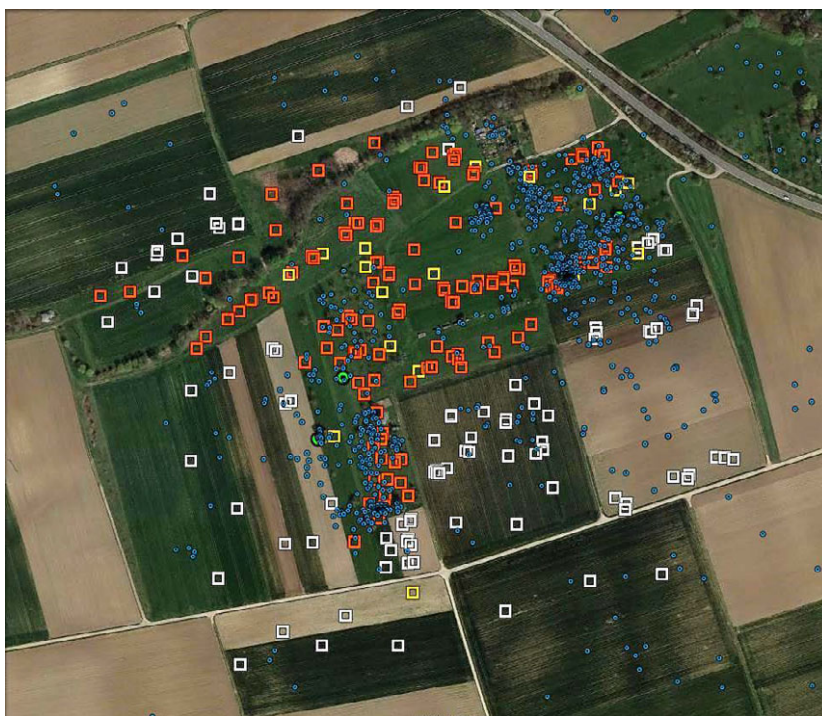


Figure 1 Illustration of an orchard area with two little owl home-ranges. Blue dots indicate bird radio-locations (individuals not discerned). Squares give the sites where vole transect counts were conducted. White squares: no vole traces recorded, yellow squares: low vole abundance index, red squares: high vole abundance index. Little owl locations were concentrated in areas with a high abundance of voles. Aerial image: © Google Earth.

and two cropland perches) were surveyed by PC 900 Hyperfire™ trail cameras (Reconyx, Inc.).

The perches and the camera traps were left three nights for habituation, followed by the sampling period of seven consecutive nights. Counters were reset daily before dawn, and read out and reset at sunset. After the session, the perches were removed from the first plot and set up in the second plot for a second run with an inverse arrangement of perches and control fields. The vegetation height in grassland and cropland was recorded at the end of each sampling period.

Data analysis

Spatio-temporal variation in vole abundance

A total of 3815 transect counts were available for the analysis of spatio-temporal variation in vole abundance; 1378 counts were in cropland, 286 in field margins, 1031 in grassland and 1120 in orchards ($N = 1426$ in the NW, 687 in the NE, 543 in the SW and 1159 in the SE). Generalised linear mixed models (GLMMs) were used to analyse patterns of vole abundance. Generalised linear mixed models were implemented in the statistical software R 2.15.1 for Windows (R Development Core Team, 2012) using the packages lme4 (Bates, Bolker & Maechler, 2012) and arm (Gelman *et al.*, 2012) for model selection and averaging.

As the data were zero-inflated, we applied logistic regression (GLMM with binomial error distribution) to analyse the general relationship of vole indices and habitat type. For the first step of analysis, count data on vole indices were transformed to binomial data, attributing transect counts with indices to 1 (voles present) and counts without indices to 0 (voles absent, for results, see supplementary information). Based on the result that voles were virtually lacking in mechanically cultivated land, only the habitat types in which voles occurred were retained to analyse the seasonal variation in vole abundance. We used GLMMs with a Poisson error distribution and logit link function (totalling 2347 counts, including zero counts).

The abundance index of voles was analysed in relation to season (month), habitat type (field margins, grassland or orchard), region (NW, NE, SW and SE) and vegetation height (continuous variable). The identity of sampling plots (of three transects each) was included as a random factor. A preliminary analysis of the seasonal trends in the vole abundance index revealed that the best fit was obtained with a fifth order polynomial ($R^2 = 0.33$; $t = 3.10$, $P < 0.002$; Table Curve 2D; Systat Software Inc., 2007). Correspondingly, a fifth-order polynomial was included into the GLMM analysis. The effect of every variable was tested with Log Likelihood ratio tests by comparing the models with and without the variable.

Habitat selection and habitat use

To identify the major habitat elements selected at the landscape scale, we performed a compositional analysis (Aebischer

& Robertson, 1994) by comparing the proportions of major habitat elements for the whole study area (available habitat) with the home-ranges estimated by the 100% Minimum Convex Polygon [MCP, (Mohr, 1947) an example is given in Fig. 2]. Major habitat elements were categorized into seven groups (cropland, grassland, orchards, urban areas, paved roads, forest and 'other'). The value of non-utilized but available habitat types was replaced by 0.01%, as recommended in (Aebischer & Robertson, 1994). We used 1000 iterations for randomization (Manly, 1997).

At the level of individual habitat patch use, compositional analysis (Aebischer & Robertson, 1994) was used to identify the preference/avoidance of structures within little owl home-ranges including all locations. We calculated the Minimum Convex Polygon (MCP; Mohr, 1947) for every individual as an estimator of the available habitat and compared it with the proportions inside the 90% isopleth of the FKC (used habitat, calculated using R-Package adehabitatHR (Calenge, 2006), see, e.g. in Fig. 2) and habitat types were categorized into six groups (cropland, field margins, grassland, orchard, road and wood/shrub).

Individual response to vegetation height

Generalised linear mixed models (GLMM) with a Poisson error distribution and a logit link function were used to analyse the factors affecting the number of visits to perches. Based on the camera data, we corrected the raw counts for the proportion of visits of other species of above 120 g. As explanatory variables, we included vegetation height, habitat type (grassland or cropland), period (nestling period from mid-May to mid-June, fledgling period from mid-June to end of July and late summer from August to the beginning of September) and distance of the perches to the breeding site in the model. The identity of the breeding site was included as random factor.

Results

Spatio-temporal variation in vole abundance

Voies were almost completely absent from mechanically cultivated cropland (probability of presence < 0.001). The probability of presence of voles in grassland, field margins and orchards was very high, close to one (probability of presence < 0.999 ; for further information, see supplementary materials). The probability of presence of voles in the different habitat types was very similar in the four regions (Table A4, supplementary materials).

The abundance index of voles in 'vole habitats' was significantly and strongly related to season and vegetation height (Table 1). During the season, the abundance index of voles showed two peaks (in March and mid-October) (Fig. 3). Furthermore, we found a significant positive correlation between vegetation height and the vole abundance index (Fig. 4), indicating that vole abundance increases with increasing vegetation height. Finally, the analyses revealed significant differences among habitat structures. The abundance index in orchards was

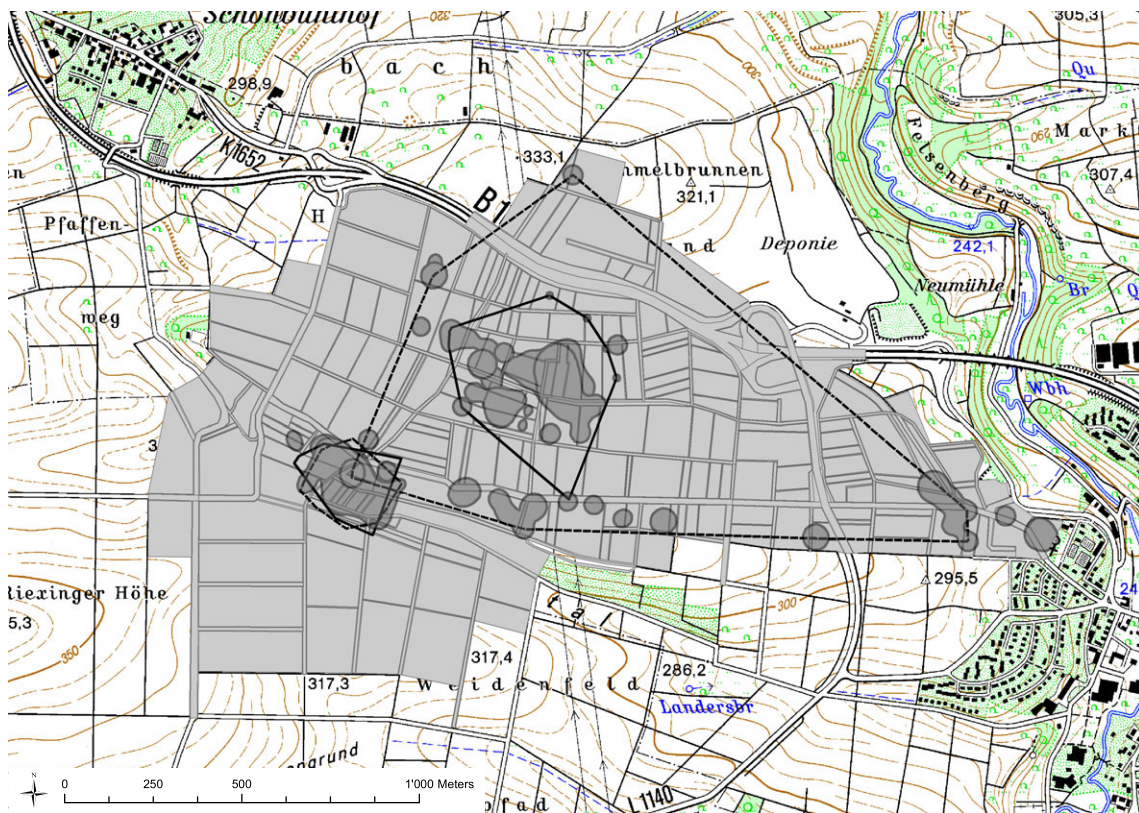


Figure 2 Example of home-ranges of two neighbouring pairs of little owls, near Schwieberdingen, Württemberg. The map indicates the area where habitat elements were mapped (light grey polygon), 90% Fixed Kernel Contours (dark grey) and 100% MCPs (female: black line, male: black dashed line). Map: © Landesamt für Topografie, Baden-Württemberg, Germany.

Table 1 Model estimates from the analysis of vole abundance in relation to season (time) including a fifth-order polynomial (time linear – time⁵) for explaining non-linear relationships, region (NE, NW, SE, SW, see Table S1), vegetation height and the interaction between vegetation height and habitat type. $N = 2361$ transect counts

Model variables	Level	Estimate	SE	d.f.	Chi	$P(> Chi)$
Intercept		1.72	8.70	0	1391	<0.001
Habitat				2	9.28	0.010
	Edge structures	0	0			
	Grassland	4.48	7.60			
	Orchards	5.93	7.38			
Region				3	7.53	0.057
	NE	0	0			
	NW	-2.90	8.78			
	SE	-1.08	8.77			
	SW	-1.84	1.02			
Vegetation height		-2.69	1.52	2	113.59	<0.001
Vegetation height: Habitat type				2	1.23	0.267
	Vegetation height: Field margins	0	0			
	Vegetation height: Grassland	6.40	1.82			
	Vegetation height: Orchard	8.24	1.76			
Time linear		-1.38	5.72	1	-519.36	<0.001
Time ²		1.53	5.46	1	694.16	<0.001
Time ³		1.24	5.12	1	447.62	<0.001
Time ⁴		-6.47	4.85	1	141.03	<0.001
Time ⁵		-2.05	4.94	1	17.31	<0.001

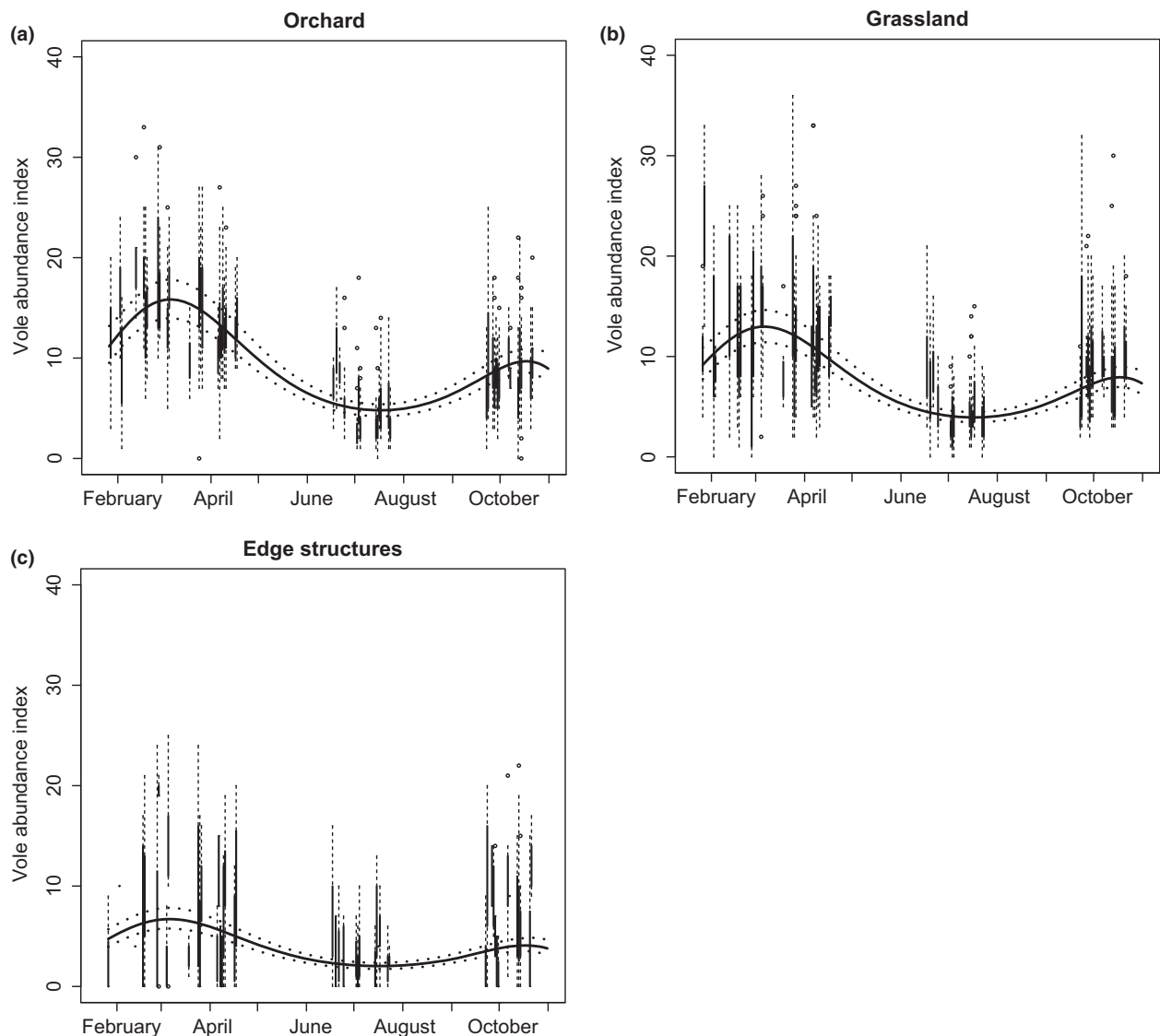


Figure 3 Seasonal variation in the vole abundance index (black line) and 95% confidence intervals (dotted lines) in the habitat structures where voles occurred (orchard, grassland and field margins). Values are based on model predictions for average values for region (NW, NE, SW and SE) and vegetation height (continuous variable). The distribution of the raw data is depicted by boxplots for each sampling date (solid line: 25–75% percentile range, broken line 5–95%: range, small circles: extremes). The abundance index is highest in orchards.

highest (5.93 ± 7.38 SE) and showed the strongest increase in relation to vegetation height (Table 1). In comparison, grassland (4.48 ± 7.6) and field edges (1.72 ± 8.70) held smaller abundance indexes of voles.

Home-range selection and habitat use

A total of 4098 locations were available from the beginning of January 2011 to the end of October 2011. Orchards showed the highest number of locations (1957 locations, 47.8% of all locations), whereas 29.2% of the location were in cropland ($n = 1198$ locations), 9.2% in field margins ($n = 377$ locations), 10.2% in grassland ($n = 418$) and 3.5% ($n = 148$ locations) in other habitat types.

The proportions of major habitat elements over the whole study area comprised on average 33.4% cropland, 19.1% forest, 17.1% human settlements, 9.8% orchards, 9.7% open grassland, 7.1% vineyards, 2.8% wood/shrub and 1% other habitat structures. The comparison of proportions of available major habitat elements in the study area to the proportions in home-ranges as determined by the 90% FKC area revealed a significant difference ($\lambda = 0.00$; $\chi^2 = 293.69$, d.f. = 7, $P < 0.0001$ by randomization, Table 2). Orchards were by far the most preferred habitat element in the home-ranges with significantly higher average log ratios than any alternative habitat (Table 3). This indicates that little owl home-ranges were placed preferentially in areas with orchards.

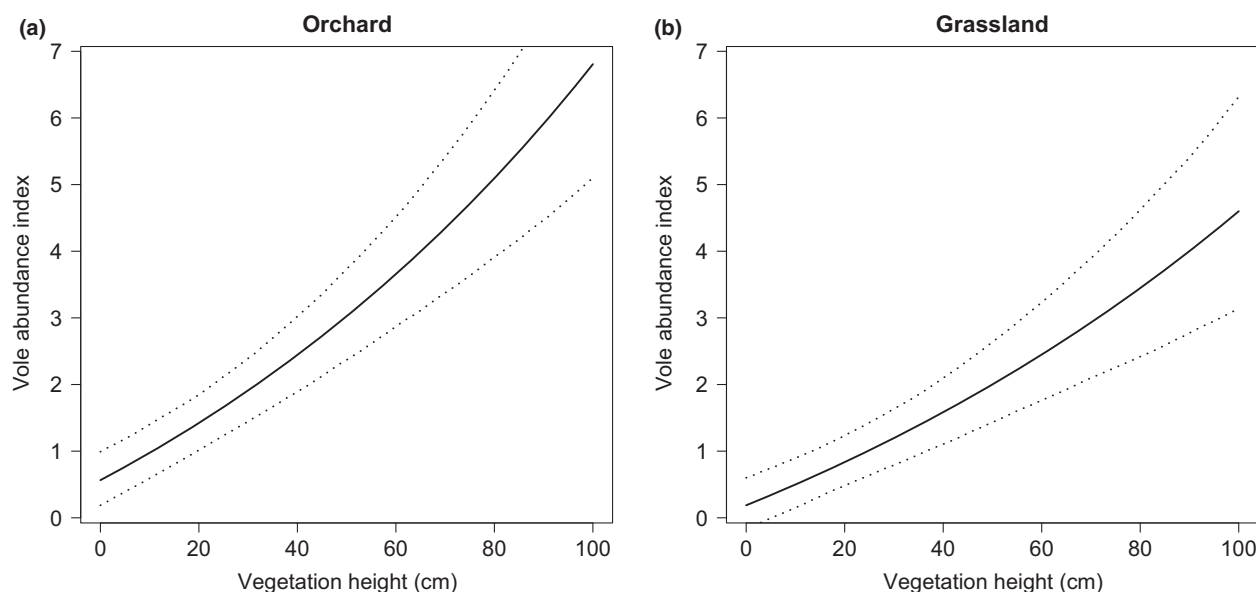


Figure 4 Relationship between the vole abundance index and vegetation height (controlling for seasonal effects) in (a) orchards and (b) grassland. For statistical details, see Table 1.

On the level of habitat patch use, on average 55.9% of the MCP home-range was cropland, 10.3% grassland, 12.2% orchard, 9.3% field margins, 6.9% roads, 2.2% wood/shrub and 3.2% other habitat types. The comparison of habitat composition in the individual MCP and the 90% FKC area revealed a significant difference ($\lambda = 0.23$; $\chi^2 = 42.66$, d.f. = 5, $P < 0.001$ by randomization, Table 3). Within the 90% FKC level, orchards were by far the most preferred habitat structure with significantly higher average log ratios than any alternative habitat. Field margins were the second most preferred habitat, followed by grassland and cropland. In contrast, the average log-ratios for roads and wooded areas show that these were used strongly under-proportionally (Table 3).

Individual response to vegetation height

We recorded 711 visits to the perches during 442 sampling nights. Thirty per cent of the visits were recorded within high grass vegetation (vegetation height above 20 cm; 171 sampling nights), independently of habitat type and 70.0% of the visits within low grass vegetation (vegetation height below 20 cm; for 271 sampling nights); 29.4% of the visits were recorded in grassland areas and 70.6% in cropland. Perches were mainly visited by little owls (83.8%). Other nocturnal birds such as long-eared owls (14.7%) and barn owls (1.5%) also visited the perches. Little owls visited preferentially plots with low vegetation irrespective of habitat type. The visits to the perches decreased with increasing vegetation height (Table 4, Fig. 5). Surprisingly, the number of visits was higher in cropland than in grassland and decreased with distance to the nest. During the nestling period and late summer, the perches were more frequently visited than during the fledgling period. The explained variance

was low, which indicates that other factors not included in the model may have an effect on the frequency of visits to the perches.

Discussion

This study highlights hierarchical structures in the spatial behaviour of little owls in response to habitat structure and the abundance of a major food resource. At the landscape scale, the results support the common assumption that, in Central Europe, the occurrence of little owls strongly depends on the pattern of orchards and grassland. These offer not only the richest food resources but also cavities and perching opportunities (Aebischer & Robertson, 1994; Martínez & Zuberogoitia, 2004; Tomé *et al.*, 2004; Zmihorski *et al.*, 2012). Orchards and adjacent grassland are thus concentrations of crucial resources in the agricultural landscape (Tomé *et al.*, 2004; Parejo & Avilés, 2011; Bock *et al.*, 2013). At the habitat patch scale, areas with high average prey abundance were used over-proportionally. At the scale of individual foraging sites, little owls preferred sites with low vegetation, where prey accessibility is presumably high. This shows that the range use within the habitat islands is mainly determined by prey availability, which is prey abundance modulated by its accessibility. The abundance of voles varied highly synchronously across the study area, suggesting large-scale synchronous vole population cycles. We conclude that these characteristics created a patchy pattern with relatively small variation among habitat islands, but large annual variation in prey availability (Lambin, Petty & MacKinnon, 2000).

At the level of habitat patches, little owls clearly preferred habitat types with the highest abundance of voles. Cropland was largely avoided, probably due to the almost complete

Table 2 Results of step 1 of the compositional analysis, addressing preferences in the spatial distribution of little owl home-ranges at the landscape scale. Available proportions of habitat structures were estimated for the whole study area (c. 1400 km²). Proportions in little owl home-ranges were determined on the basis of Minimum Convex Polygon (MCP) including 100% of the individuals' locations. The table gives average log-ratio differences (\pm SE) for all pairwise comparisons between habitat elements. These were subject to pairwise t-tests and significance tests (for details, see text). Significant values (at $P < 0.05$) are indicated in bold letters

Available → ↓ Used	Cropland	Grassland	Orchard	Wood/shrub	Human settlement	Forest	Vineyard	Others
Cropland		0.112 \pm 0.134	-0.502 \pm 0.186	3.931 \pm 0.845	2.152 \pm 0.417	12.508 \pm 0.073	10.748 \pm 0.570	8.272 \pm 0.610
Grassland	-0.112 \pm 0.134		-0.615 \pm 0.162	3.819 \pm 0.862	2.039 \pm 0.451	12.395 \pm 0.104	10.635 \pm 0.601	8.160 \pm 0.584
Orchard	0.502 \pm 0.186	0.615 \pm 0.162		4.433 \pm 0.881	2.654 \pm 0.402	13.010 \pm 0.122	11.250 \pm 0.522	8.775 \pm 0.620
Wood/shrub	-3.931 \pm 0.845	-3.819 \pm 0.862	-4.433 \pm 0.881		-1.779 \pm 0.891	8.577 \pm 0.843	6.816 \pm 0.846	4.341 \pm 1.034
Human Settlement	-2.152 \pm 0.417	-2.039 \pm 0.451	-2.654 \pm 0.402	1.779 \pm 0.891		10.356 \pm 0.401	8.596 \pm 0.637	6.121 \pm 0.732
Forest	-12.508 \pm 0.073	-12.395 \pm 0.104	-13.010 \pm 0.122	-8.577 \pm 0.843	-10.356 \pm 0.401		-1.760 \pm 0.535	-4.235 \pm 0.608
Vineyard	-10.748 \pm 0.570	-10.635 \pm 0.601	-11.250 \pm 0.522	-6.816 \pm 0.846	-8.596 \pm 0.637	1.760 \pm 0.535		-2.475 \pm 0.852
Others	-8.272 \pm 0.610	-8.160 \pm 0.584	-8.775 \pm 0.620	-4.341 \pm 1.034	-6.121 \pm 0.732	4.235 \pm 0.608	2.475 \pm 0.852	

Ranked variable sequence (most to least used, >>> denoting significant preference over subsequent category): Orchard >>> Cropland > Grassland >>> Human settlement > Wood/shrub >>> Others >>> Vineyard >>> Forest.

lack of voles (however, these patches may occasionally offer alternative prey such as earthworms and large insects). Despite similar vole abundances, orchards were preferred over open grassland. This indicates that perching opportunities and cover against potential predation provided by fruit trees might strongly influence the range use. Furthermore, field edges were attractive (foraging) sites. These structures appear also to be more promising foraging grounds compared to plain grassland or crop areas. This finding is in line with earlier research reporting a preference of little owls to breed in areas with small field sizes (which therefore offer more edges; Gottschalk, Ekschmitt & Wolters, 2011). Therefore, at the habitat-patch level, food-rich sites were generally preferred over places with low food abundance. Additionally, structural features improving the access to prey such as low vegetation, bare ground and perching sites modulated the range use within home-ranges.

At the level of small-scale behavioural patterns, little owls preferred sites with low vegetation, irrespective of prey abundance. Although cropland offers almost no voles, it was slightly preferred over open grassland, especially when vegetation was low. Cropland may harbour other prey types like ground-dwelling insects that could be easier to detect for the owls when vegetation is low, and the higher proportion of accessible bare ground in the cropland plots (cereals) may also have attracted the birds (Coudrain, Arlettaz & Schaub, 2010; Schaub *et al.*, 2010; Arlettaz *et al.*, 2012; Tagmann-Ioset *et al.*, 2012). This and the preference for habitat edges suggest that the selection of foraging sites is not only determined by prey abundance, but also by the accessibility of the prey (Arlettaz *et al.*, 2010; Schaub *et al.*, 2010; Tagmann-Ioset *et al.*, 2012), the combination of these two factors determining prey availability. Thus, the short-term selection of foraging sites is similar to that of other raptor species feeding on small mammals (Aschwenden, Birrer & Jenni, 2005; Arlettaz *et al.*, 2010). To better disentangle the relationships between food abundance and the detectability and accessibility of food, further experimental research may independently vary the abundance and accessibility of prey. Given the similar prey abundance in orchards and grassland, we hypothesize that little owls will increase the use of grassland in the presence of artificial perching sites.

In summary, the abundance of food was a main determinant of habitat selection and use at all three spatial scales. However, the results suggest that the access to resources was an additional key factor in habitat selection at all spatial scales. At the landscape scale, the pattern of elements providing important resources – orchards and grassland – within the agricultural matrix was the crucial condition for settlement. At the habitat patch scale, preferences depended on the relative abundance of voles and on structures facilitating foraging. At the scale of the foraging site, the use of sites within habitat patches depended on vegetation height, probably because low vegetation increases prey accessibility.

An important conservation implication of the findings is that the distribution and range use of little owls is influenced by habitat changes occurring at different temporal scales. While landscape features change over decades, habitat patch

Table 3 Results of step 2 of the compositional analysis, addressing preferences in habitat use within individual home-ranges. Proportions of habitat elements available to each individual were determined on the basis of the minimum convex polygon including all radio-locations. These were compared to the proportions in the 90% isopleth of the fixed kernel utilization distribution (details see text). The table gives average log-ratio differences (\pm SE) for all pairwise comparisons between habitat elements. These were subject to pairwise t-tests and significance tests (for details, see text). Significant values (at $P < 0.05$) are indicated in bold letters

Available → ↓ Used	Cropland	Grassland	Orchard	Field margins	Road	Wood/Bush
Cropland		-0.096 ± 0.125	-0.689 ± 0.179	-0.165 ± 0.084	0.509 ± 0.277	1.455 ± 0.614
Grassland	0.096 ± 0.125		-0.593 ± 0.189	-0.069 ± 0.134	0.614 ± 0.305	1.591 ± 0.641
Orchard	0.689 ± 0.179	0.593 ± 0.189		0.524 ± 0.144	1.233 ± 0.305	2.074 ± 0.694
Field margins	0.165 ± 0.084	0.069 ± 0.134	-0.524 ± 0.144		0.714 ± 0.273	1.679 ± 0.629
Road	-0.509 ± 0.277	-0.614 ± 0.305	-1.233 ± 0.305	-0.714 ± 0.273		1.247 ± 0.671
Wood/shrub	-1.455 ± 0.614	-1.591 ± 0.641	-2.074 ± 0.694	-1.679 ± 0.629	-1.247 ± 0.671	

Ranked variable sequence (most to least used, >>> denoting significant preference over subsequent category): Orchard >>> Field margins > Grassland > Arable land >>> Road >>> Wood/shrub.

Table 4 Model estimates of the analysis of the number of perch visits by little owls in relation to vegetation height, habitat type (cropland or grassland), season (period 1, period 2, period 3) and distance to the breeding site. Number of observations $n = 417$ visits

Variables	Levels	Estimate	SE	d.f.	χ^2	P
Intercept				0		<0.001
Vegetation height		-0.05	0.01	1	56.881	<0.001
Habitat type				1	25.375	<0.001
	Cropland	0	0			
	Grassland	-0.95	0.19			
Period				2	17.905	<0.001
	Period 1	0	0			
	Period 2	-1.35	0.32			
	Period 3	-1.35	0.44			
Distance to breeding site		-0.01	0.002	1	13.618	<0.001

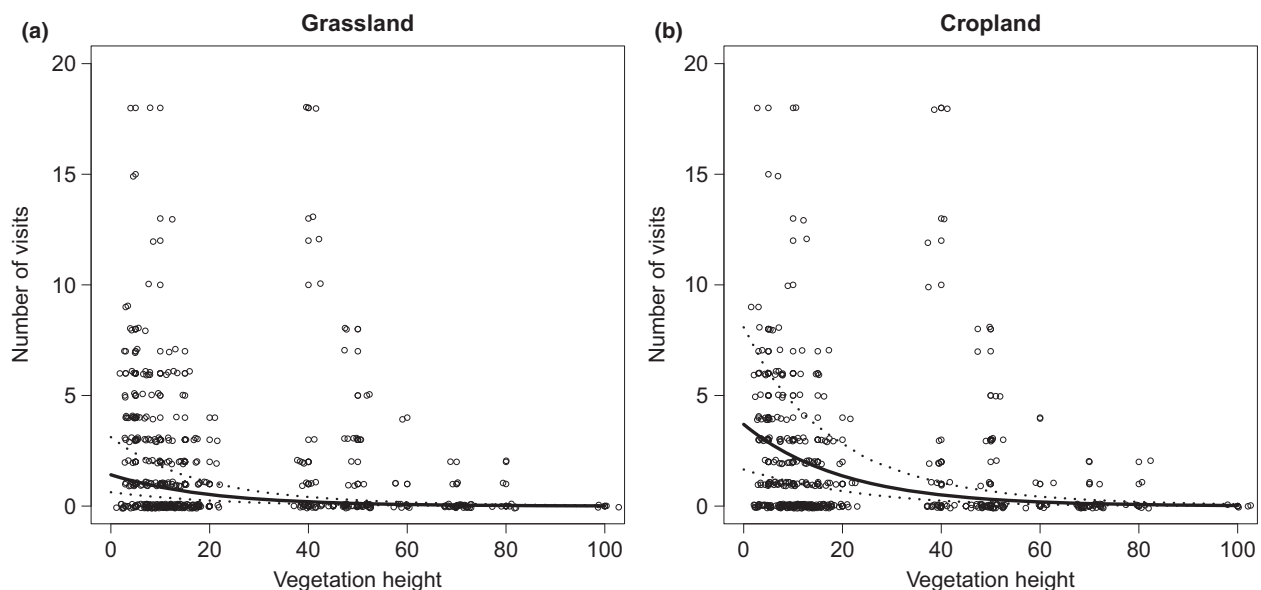


Figure 5 Number of perch visits by little owls (points = raw counts; line = model estimates with 95% CrI) in (a) grasslands and (b) in cropland. Model-predicted values are given for the whole sampling period and for a distance from the nestbox of 50 m. For statistical details, see Table 4.

features may change annually in relation to farming concepts, and characteristics of foraging patches may change within weeks in relation to the farming process. To mitigate demographic bottlenecks due to food limitation (particularly during breeding; Thorup *et al.*, 2010), conservation measures may also address this hierarchy. At the level of the Central European landscape, orchards are mandatory for the occurrence of little owls and long-term measures should focus on their conservation and restoration. At the scale of habitat patches, grasslands are important as main prey providers. But as shown in this study, many farmland birds need to have not only abundant food supplies but also habitat structures that facilitate the accessibility of prey (Coudrain *et al.*, 2010; Schaub *et al.*, 2010; Arlettaz *et al.*, 2012). Habitat management measures creating a mosaic with patches of tall grass acting as food producers and patches of short grass enabling the access to food might highly improve these habitat patches. Moreover, wildflower areas which are a kind of unmanaged grassland are even better providers of small mammals (Arlettaz *et al.*, 2010). Added to the matrix together with a mosaic of short grass and unmanaged structures like field margins and perches to increase the accessibility of food, the quality of such patches would be highly improved in terms of food availability.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Repeatability of field sign counts.

Appendix S2. Correlation between transect counts and live-trapping.

Appendix S3. Setup of the perch experiment.

Appendix S4. Probability of presence/absence of voles in the four main habitat types (cropland, field margins, grassland and orchards).

Appendix S5. Compositional analysis of habitat use.