Landscape use, foraging habitat selection and relationships to food resources in breeding little owls: recognizing the importance of scale for species conservation management

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Summary

1. Landscape use and habitat selection, which result from the behavioural response of a species to patterns of resources availability, determine the distribution of individuals within populations at several spatial scales. We investigated habitat selection of adult little owls (*Athene noctua*) in relation to landscape configuration, habitat structure and prey abundance, with the main objective to provide evidence-based conservation guidance for this rare species. More specifically, we analysed the distribution of small rodent prey, and habitat selection by foraging adults in relation to prey abundance and to factors modulating prey accessibility, particularly vegetation height.

2. Habitat selection was assessed using VHF-telemetry and by quantifying the frequency of visits to artificial perches experimentally placed in different habitat types and structures. Relative prey abundance was estimated by transect counts of signs of vole presence also in different habitat types and structures.

3. Vole prey abundance was heterogeneous, varying in relation to the type of habitat present in the intensively-used agricultural matrix. Orchards, grassland and field margins provided rich vole prey supplies whereas their abundance was almost null in cropland. Little owls typically preferred orchards and field margins over grassland and cropland, while woodland was avoided. The frequency of visits to artificial perches indicated that foraging takes place preferably above low grass vegetation, and this irrespective of prey abundance.

4. Habitat selection and resource exploitation by little owls are structured at three hierarchical levels: 1) at landscape scale, orchards were the favourite habitat; 2) at habitat patch scale, areas with higher prey abundances were used over-proportionally; 3) at the foraging site scale, little owls selected patches with low grass vegetation.

6. *Synthesis and applications*. Orchards appear to be crucial for the persistence of little owl populations in farmland, which calls for their preservation against conversion into cropland or settlements. Within orchards, an ideal mosaic of habitat patches consists of dense grassland (un-mown meadows) alternating with short grassland (pastures or mown meadows), a fine-grained habitat complex which is likely to boost small rodent populations while it also increases their availability as prey for the little owl. As crucial food suppliers, field margins further constitute an important habitat feature.

Key-words: Resource patterns, food abundance, food accessibility, habitat patch, field signs, telemetry

1 Introduction

Habitat selection patterns at the individual level determine the spatial structure of an animal population as they mostly depend on the abundance, distribution and accessibility of resources (Dolman 2012). Behavioural responses of individuals to these environmental conditions operate at different spatial scales, from landscape down to foraging site, ultimately characterizing life history traits and key demographic parameters. Understanding habitat selection at multiple scales is thus crucial for establishing species-specific ecological requirements and developing evidence-based conservation policies (Johnson 1980; Kristan 2006; Fuller 2012; Vickery & Arlettaz 2012). The cues used by animals for selecting habitat are scale-dependent, with different life history functions acting at different scales. Targeted conservation decisions are often hampered by the lack of evidence for these complementary processes operating at different scales.

Farmland across Europe has undergone fundamental changes during the last decades. Modification of farming practices has encouraged the expansion and intensification of land use. At the landscape level, patches of suitable habitat for farmland species are mostly small islands within an increasingly uniform matrix (Benton, Vickery & Wilson 2003; Vickery & Arlettaz 2012). Embedded in the matrix, these residual habitat patches are further influenced by farming practices, therefore offering varying supply of and access to resources (McCracken & Tallowin 2004). The extent and distribution of such patches are factors determining an individual's resource use within patches and movements between them (Fuller 2012). In general, the intensification of land use has affected all levels of habitat selection and ultimately also the spatial distribution of populations and their sustainability (Donald, Green & Heath 2001). Understanding how populations are affected by both the spatial configuration of habitat patches within the landscape matrix and the patterns of resources within habitat patches is particularly important in endangered and declining species inhabiting human-shaped ecosystems because these influences are crucial for their persistence.

The little owl (*Athene noctua*) is one of the many examples of farmland birds that have dramatically declined during the last decades in Europe (BirdLife International 2004; Šálek & Schröpfer 2008). Habitat loss and decreasing food availability through intensified agricultural practices are put forward as the main causes for its decline (Martínez & Zuberogoitia 2004; Šálek & Schröpfer 2008; Grzywaczewski 2009). However, quantitative evidence for the actual processes involved remains scarce. Better targeted conservation action plans are needed, which beforehand requires a good evidence base.

In central Europe, orchards are important landscape features for little owls (Van Nieuwenhuyse, Génot & Johnson 2008; Grzywaczewski 2009). Agricultural intensification resulted in a systematic removal of fruit trees, especially high trunk orchards, and decreased the number and size of such features within the agricultural landscape. As a result, habitat patches suitable for little owls remain as islands within a matrix of inhospitable habitat (Gottschalk *et al.* 2010). Within these habitat patches, little owls adjust their resource use to many ecological factors such as food availability (Żmihorski, Romanowski & Chylarecki 2012), availability of breeding or roosting sites (Martínez & Zuberogoitia 2004; Tomé, Bloise & Korpimäki 2004) and presence of predators (Tomé, Bloise & Korpimäki 2004). Habitat type and vegetation structure are furthermore likely to be important features at the habitat patch scale, which may determine the abundance and distribution of resources, but detailed information is still lacking. Decreasing habitat diversity and patchiness, and the declining extent of suitable habitats through intensified agricultural practices have an impact on such ecological factors (Żmihorski, Romanowski & Osojca 2009). In terms of food availability, for example, there is a negative effect of increased fertilization and mowing on the abundance and accessibility of small mammals (Butet & Leroux 2001), which are an important prey for little owls. Small mammals are considered as pests in agriculture, causing damages to crops (Myllymäki 1977; Jacob 2003). Small mammals constitute a staple food for many predators, determining their abundance and diversity (Baker & Brooks 1981; Butet, Paillat & Delattre 2006). Mechanical disturbance through harvesting, ploughing and tillage removes shelters, destroys nests and burrows and decrease food availability for small mammals (Tew & Macdonald 1993). Consequently, intensively cultivated agricultural fields might be inhospitable for small mammals, which might only persist within habitat patches where undisturbed areas offer refuges such as ditches, road verges, set-aside and wildflower areas (Arlettaz *et al.* 2010). However, the spatial patterns of occurrence of small mammals, especially within habitat patches and in the between-patch matrix, are poorly investigated.

At the scale of the habitat patch, fine-grained vegetation configuration such as grass cover height or density, which determines foraging efficiency, or the availability of cavities are important determinants of little owl range use. Different management regimes and differential plant growth likely shape these attributes. How such small-scale attributes affect individuals' range use receives increasing attention (e.g. Schaub et al. 2010), but is not clearly understood for little owls.

Under the general hypothesis that habitat selection of little owls is hierarchically structured as outlined above, we addressed the following specific issues. First, knowing from literature that orchards are the preferred habitat type of little owls (Glutz von Blotzheim & Bauer 1980; Van Nieuwenhuyse, Génot & Johnson 2008), we investigated whether orchards actually offer particular resource patterns at the landscape scale. These analyses provide evidence how such landscape features may differ from the surrounding matrix. Second, we analysed habitat use within habitat patches in relation to the abundance of small rodents as a staple food source. Third, we investigated the fine-grained adjustments of resource utilization in relation to foraging site-scale attributes such as vegetation height.

In brief, this study emphasizes how landscape configuration, habitat structure and prey abundance are important determinants of habitat selection of little owls and provides evidence-based guidelines for species conservation management.

2 Materials & Methods

2.1 STUDY AREA

The study was conducted in the district of Ludwigsburg, Baden-Württemberg, Southern Germany (Fig. S1). The agricultural landscape of this region is characterized by arable farmland (59%), pasture and grassland (36%), orchards and viticulture (each 1.6%). The state of Baden-Württemberg holds about 30% of the whole German stock of orchards (Küpfer & Balko 2010). The study area shows a drier and warmer climate than other parts of Germany with an average rainfall of 762 mm per year and a mean temperature of 9.7°C.

About 10 well-monitored little owl populations are dispersed in this area, totalling roughly 400 breeding pairs. The study was conducted in the subpopulation around Ludwigsburg with about 220 breeding pairs (H. Keil, pers. comm.) on an area of approximately 250 km^2. Within this population the nest sites are patchily distributed. The patches are generally inhabited by 5 - 10 breeding pairs producing 15 - 40 offspring per year. Little owls largely depend on artificial nest cavities in this region, which facilitates capture and handling of birds.

To assess regional patterns of relative vole abundance, the study area was subdivided into 4 regions (Fig. S2 & Table S1). The subdivision accounted for landscape barriers, such as the main streams of the region, namely Neckar, Enz and Murr

2.2 RELATIVE VOLE ABUNDANCE

Studies on vole abundance usually used live-trapping to monitor vole populations (Baker & Brooks 1981; Salamolard *et al.* 2000; Arlettaz *et al.* 2010; Butet *et al.* 2010). However, this method is too demanding to collect information on vole abundances at a large spatial scale. Therefore, we used an alternative method to assess the relative vole abundance through field signs, which allows quantifying vole abundance over large areas with affordable time effort (Delattre *et al.* 1990; Giraudoux *et al.* 1995; Lambin, Aars & Piertney 2001). Live trapping was carried out at two sites to collect calibration data. According to Delattre *et al.* (1990) we counted runways, holes, and molehills. Runways, holes and molehills are conspicuous signs and are visible on every type of ground. We used the sum of all superficial indices (runways, holes, molehills) as an estimate of relative vole abundance.

Field signs of voles were counted on transects within all relevant habitat types. In each sampling area we randomly chose 3 sites where we placed a transect line of 5 m length each. The direction of a transect was chosen randomly. A zone comprising the 5 m length of the transect line and a width of 50 cm (i.e. 2.5 m^2) was meticulously scanned for vole traces. We counted the number of holes and molehills, and every runway crossing the transect was counted once. Only superficial signs showing indices of current use were counted (unused runways deteriorate within few days (own observation). We sampled 3 habitat types, cropland, grassland including hay meadows and extensive pasture (mainly horse or sheep), and orchards (fruit tree plantations with high trunks). Data for a 4th habitat type, field margins, were post-hoc extracted from ArcGIS by including counts within a buffer zone of 2 m at the boundary of every sampling area. All mechanically cultivated areas were classified as cropland. Herbaceous areas dominated by grasses (Poaceae) and forbs with maximum 5 fruit trees or other tree species were defined as grassland. Herbaceous field paths were included in this category. Areas fulfilling the criteria of grassland and containing at least 6 fruit trees, with a distance from trunk to trunk not exceeding 10-15 m were classified as orchards. Rows of trees with at least 6 trees were also included in this category. The data were collected from individual home-ranges and in 1-2-month time intervals. The data were digitised in the field using MobileMapper™ 6 computers (Magellan, MiTAC International Corporation, Santa Clara, USA), registering accurate GPS locations, number of counted indices and data attributes.

A total of 4283 transect counts were performed from February to October 2011. Altogether 17 breeding sites were sampled. 9 breeding sites were sampled 7 times, including repeat counts from February to October 2011. 2 breeding sites were sampled 6 times from February to October 2011. 6 were sampled 3 times from July to October 2011 and 1 breeding site only once in July 2011. 1426 transects were counted in the NW, 687 in the NE, 543 in the SW and 1159 in the SE. 1343 transects were counted in cropland areas, 281 in field margins, 995 in grassland and 1088 in orchards.

To test the repeatability of counts, counts were replicated once in 10 sampling areas and 2 sampling periods. Replicates were performed within 7 - 10 days after the first count. Correlations between transect counts and repeat counts were tested using linear regression. Repeat counts correlated positively and significantly with transect counts ($r^2 = 0.896$, d.f. = 574, $p < 0.001$) (for details see Appendix 1 in Supporting Information).

Both live trapping and transect counts yield relative estimates of vole abundance. Thus, it is important to calibrate the techniques. We conducted live-trappings in 2 sites within the study area. Within each site, 50 traps (Trip Trap, Humane ®) were distributed in 5 subsets containing 10 traps each. The subsets were separated at least 500 m from each other (Fig. S3). Traps were placed within the subsets with a minimum distance of 5 m between each trap.

Simultaneous to the trapping sessions, transect counts were performed right next to each trap. In addition to a correlative analysis of raw counts, we tested whether vegetation height had an effect on the relationship between trapping and transect data. Raw counts correlated positively and significantly with transect data ($r^2 = 0.15$, $t = 2.89$, d.f. 385, $p = 0.004$). Vegetation height had no significant effect on the relationship between trapping and transects data ($t = 0.03$, d.f. 94, $p = 0.97$). Both relative abundances, i.e. the number of indices and the number of trapped voles increased with increasing vegetation height (for details see Appendix S2). Moreover, other studies also calibrated vole field sign counts with live trapping and found a significant relationship between the different indices (Delattre *et al.* 1996; Lambin, Petty & MacKinnon 2000).

2.3 HABITAT PATCH USE

Data on habitat selection of adult little owls at the habitat patch level were obtained through radio-tracking. Locations of the individuals were taken during their activity phase starting generally on sunset and ending on sunrise.

Adult birds were captured 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. The transmitters emit a power of 0.4 mW which allows operational ranges of up to 40 km from elevated sites (hill top or aircraft) and 20 km ground to ground. The battery lasted for approximately 380 days. Standard figure-8 harnesses were used to attach the tag on the owls. The tag and harness total a mass of 6.9 - 7.2 g which represents 4 – 5% of bird body mass. 9 males and 7 females were tracked from January 2011 until June/July 2011 and 15 males and 13 females (comprising 7 males and 5 females of the previously tagged adults) from June/July 2011 to October 2011 (Table S5).

The tracking was carried out using handheld antennas and the homing-in technique (Kenward 2001) to allow accurate location and observation of habitat selection. Locations during the night were recorded in 3-days intervals using standardised protocols (Naef-Daenzer 2000; Grüebler & Naef-Daenzer 2008a; Grüebler & Naef-Daenzer 2008b) employing interval samples and focus-animal sampling (Altmann 1974). Two intervals of respectively 5 min were performed for each individual at each sampling night. During daytime only one location was taken per week without interval samples. The data were digitised in the field using MobileMapper® computers, registering accurate GPS locations and data attributes for radio-locations.

2.4 HABITAT MAPPING

Breeding sites of the tracked adult individuals were mapped in 2011 in order to assess the proportions of the main habitat types within the home range. This allowed the identification of habitat preferences in relation to food abundance. Habitat mapping was carried out between April and September 2011.

The area to be mapped was defined by a 500 m radius around the the breeding site of the tracked individuals. The mapped area was later adapted to the effective home range use of the corresponding individual when necessary. The type of habitat was mapped by classifying areas in either grassland, orchard or cropland areas (Table 1). Fieldways and small structures like single trees on a grass patch within a field or hedges were mapped separately and classified as either grassland or wood/bush. The habitat mapping was later digitised in the Geographical Information System ArcGIS 10. A 2 m buffer zone was added to every area border to account for field margins.

2.5 INDIVIDUAL RESPONSE TO VEGETATION HEIGHT

To assess individual response to resource accessibility, we investigated foraging behaviour of little owls in relation to vegetation height. We offered artificial perches at sites where no natural perches were available. Perches were offered in grassland and in cropland at 3 periods with different states of vegetation height. 1.50 m wooden poles were used as perches.

To count the visits, the perches were equipped with mechanical counters, operated through a lever at each visit of a bird. The lever connecting perch and counter was adjusted to operate the counter only if the load exceeded 120 g. Construction details are given in the Figs. S6. Since visits of other animals above c.a. 120 g were probable, camera traps were employed to survey the perches. The aim was to estimate the proportion of recorded visits attributable to little owls.

The artificial perches were systematically distributed and stratified in 2 habitat types, hay meadows (grassland) and cereal fields (cropland). Immediate proximity to natural perching sites like trees was avoided. Perches were placed >10 m away from the borders of the experimental area to avoid edge effects. In each experimental little owl breeding site 2 similar grassland and 2 similar cropland areas were selected. 4 perches were placed on 1 (randomly selected) of the 2 grassland areas (Fig. S5). 4 other perches were placed on 1 (randomly selected) of the 2 cropland areas, totalling eight perches per experimental run. Half of the perches (2 grassland perches and 2 cropland perches) were surveyed by trail cameras of type Reconyx™ PC 900 Hyperfire™ (Reconyx, Inc., Holmen, Wisconsin, USA).

The perches and the active trail cameras were left 3 nights for habituation. After 3 nights of habituation the sampling started for 7 consecutive nights.

Counters were reset daily before dawn, checked and reset at sunset. After one week the perches were removed from the first plot and set up in the second plot for a second run with the same setup as for the first run. During the experimental runs, the corresponding individuals were tracked longer and more frequently (every night, 4-6 intervals of 5 min).

Perches were set up in the nestling period (5 breeding sites), post-fledging period (6 breeding sites) and in late summer (5 breeding sites). During the nestling period vegetation in the grassland and cropland areas was high. During the fledging period, vegetation was low in grassland and high in cropland. Finally in late summer, vegetation was low in both grassland and cropland.

3 Statistical analyses

3.1 RELATIVE VOLE ABUNDANCE

Generalised linear mixed models (GLMMs) were used to analyse patterns of vole abundance. GLMMs 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 highly zero inflated, we applied logistic regression to analyse the general relationship of vole indices and habitat type. Count data on vole indices was transformed to binomial data, attributing transect counts with indices to 1 (voles present) and counts without indices to 0 (voles absent). Then GLMMs with a binomial error distribution were applied to this data. The presence/absence data were used as response variable and the sampling area within a sampling site was included as random factor to control for any variation within the sites. We included the 4 main habitat types (cropland, field margins, grassland and orchard). Habitat type (factor) and region (factor) were included as final predictors.

Based on the results of the first step, only the habitat types in which voles were recorded (field margins, grassland and orchard) were retained for a second step of analyses. For this part of the analysis, we used GLMMs with a Poisson error distribution and a logarithmic link function. Data were checked and corrected for overdispersion.

The relative abundance 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 sampling area within a sampling site was included as random factor. To evaluate an optimal approach to quantify the seasonal trends in relative vole abundance we used the software TableCurve 2D (Systat Software Inc. 2007) to explore non-linear relationships. The best fit was obtained with a fifth order polynomial ($R^2 = 0.33$; $t = 3.10$, $P < 0.002$). Correspondingly, a fifth order polynomial was also included into the GLMM analysis. Models were selected by using the most saturated model containing all variables and relevant interactions. The effect of every variable was tested with Log Likelihood ratio tests. Accordingly, a model without the investigated variables was tested against the saturated model containing the investigated variables.

3.2. HABITAT PATCH USE

To assess the use of habitat patches within little owl habitats, we used two home range estimators. The Minimum Convex Polygon (MCP) (Mohr 1947) and Fixed kernel contours (FKC) (Worton 1989) using the R package adehabitatHR (Calenge 2006). 100% MCPs were calculated for every study individual to determine the available habitat. FKC were applied to analyse the used habitat. We analysed habitat type preferences/avoidances at the level of the 90% and 50% FKC as compared to the availability in the full MCP. The 100% MCP's were computed in ArcGIS 10. Home range estimates based on FKC were calculated in R using the package adehabitatHR (Calenge 2006) and later imported in ArcGIS 10. We used a smoothing factor h = 20 m (cell size varied from 1.91 to 12.69 m). Habitat preferences were then analysed using Compositional analysis (Aebischer, Robertson & Kenward 1993). Habitat types were categorised into six groups (cropland, field margins, grassland, orchard, road and wood/bush). The value of non-utilized but available habitat types was replaced by 0.01% to avoid dropping habitat categories as recommended in Aebischer & Robertson 1994. We used 1000 iterations for randomisation (Manly 1997).

3.3 INDIVIDUAL RESPONSE TO VEGETATION HEIGHT

Generalised linear mixed models (GLMMs) with a Poisson error distribution and a logarithmic link function were used to analyse the factors affecting the visits to perches. Data were checked and corrected for overdispersion. Based on the camera data we used a corrected frequency of visits of little owls, correcting for visits of other nocturnal birds. GLMMs 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.

The number of visits of perches were analysed in relation to vegetation height, habitat type (grassland or cropland), period (nestling period, fledgling period, late summer) and distance of the perches to the breeding site. Vegetation height (continuous variable), habitat type (factor), distance to breeding site (continuous variable) were used as predictors. The sampled breeding site was included as random factor. The effect of every variable was tested with Log Likelihood ratio tests.

4 Results

4.1 RELATIVE VOLE ABUNDANCE

3815 transects including repeat counts (n = 900) were included in the final data set for binomial analyses. 1378 counts were in cropland, 286 in field margins, 1031 in grassland and 1120 in orchards. 1426 transects were located in the NW, 687 in the NE, 543 in the SW and 1159 in the SE.

The analysis at the level of presence/absence of voles showed that voles were almost completely absent from homogenous and mechanically cultivated cropland (probability of presence < 0.001). The probability of presence of voles in grassland, field margins and orchards was close to one in all three habitat types, with the highest probability in orchards. (Fig. 1). A log likelihood ratio test revealed no significant differences between the regions (NW, NE, SW, SE) in this pattern (Table 1). This indicates a similar spatial pattern over all regions for the presence/absence of vole indices in the 4 main habitat types

For the second step of analyses on relative abundance of vole indices, 2361 transect counts were included in the dataset (vole habitats, including zero values). 286 transect counts were sampled in field margins, 1031 transects in grassland and 1120 transects were sampled in orchards. 856 counts were grouped in NW, 426 in NE, 342 in SW and 737 in SE. The results reveal that the relative abundance of voles in 'vole habitats' was strongly related to season and vegetation height (Table 2). Log likelihood ratio tests showed a highly significant effect of date, which suggests strong seasonal variation in the relative abundance of voles over the sampling period (Fig. 2). The relative vole abundance peaked in March, whereas the abundance dropped down towards the breeding season in Mai and June and reached its lowest level towards July. Thereafter the relative abundance of voles increased slightly towards autumn. Log likelihood ratio tests also revealed a highly significant effect of vegetation height as a main factor. This result indicates that the relative abundance of voles increased with increasing vegetation height (Fig. 3). The effect of vegetation height was not significantly different between habitat types, suggesting that the increase was similar in all habitat types. Finally, the analyses revealed a significant effect of habitat type, suggesting a difference of relative abundance of voles between grassland, field margins and orchards (Table 2).

4.2 HABITAT PATCH USE

A total of 4098 locations were taken from the beginning of January 2011 to the end of October 2011. Orchards had the highest number of locations with 1957 locations (47.8% of all locations). 1198 locations were in cropland (29.2%), 377 in field margins (9.2%), 418 in grassland (10.2%), 28 on roads (0.6%), 99 in wood/bush (2.4%) and 21, i.e. 0.5% in other habitat types (Table S4).

On average 55.9% of the 100% MCP home range was cropland, 10.3% grassland, 12.2% orchard, 9.3% field margins, 6.9% roads, 2.2% wood/bush and 3.2% other habitat types (Table S4). All home ranges contained orchard as habitat type.

The overall comparison of habitat use from the 90% FKC compared to habitat availability in the 100% MCP gave $\lambda = 0.23$ ($\chi^2 = 42.66$, d.f. = 5, $p < 0.001$ by randomization), i.e. habitat use significantly differed from proportionality according to availability (Tables 3a and S6a). The overall comparison of habitat use from the 50% FKC compared to habitat availability in the 100% MCP gave $\lambda = 0.1228$ ($\chi^2 = 60.81$, d.f. = 5, $p < 0.001$ by randomization). Again, little owls did clearly not use habitat proportionally to the available percentages (Tables 3b and S6b).

At the 90% FKC level orchards were by far the most preferred habitat type with significantly higher average log ratios than any alternative habitat. Field margins were the second most preferred habitat, followed by grassland and cropland with significantly higher average log-ratios than roads and wooden areas. Roads and wooden areas were the most avoided habitats (Tables 3a and S6a). At the 50% FKC level orchards were also the most preferred habitat structure and habitat field margins the second most preferred, followed by grassland and cropland. Cropland had a significantly higher average log-ratio than woody areas and roads that were the most avoided habitats (Tables 3b and S6b).

4.3 INDIVIDUAL RESPONSE TO VEGETATION HEIGHT

We recorded 711 visits to the perches during 442 sampling nights. 213 visits were recorded within high grass vegetation (for 171 sampling nights), independently of habitat type and 498 visits within low grass vegetation (for 271 sampling nights). 209 visits were recorded in grassland areas and 502 in cropland. We collected data from 5 breeding sites during the breeding period in Mai and beginning of June. A second sampling session in 5 breeding sites was conducted during the fledgling period in June and July. A third sampling session took place in august during the post-fledgling period in 6 breeding sites. Based on the camera data, 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. 4). Cropland was more visited than grassland. Perches were less visited with increasing distance to the nestbox. During the first and the third sampling session, the perches were more frequently visited than during the second sampling session. The explained variance was not very high, which indicates that other factors not included in the model may have an effect on the frequency of visits to the perches.

5 Discussion

This study highlights how habitat selection of little owls is structured in response to spatial patterns of occurrence of their major food resource, voles. These behavioural adjustments occurred at three hierarchical levels: 1) at landscape scale, orchards were the preferred habitat: the spatial pattern of little owl occurrence is largely congruent with the spatial pattern in vole occurrence; 2) at the habitat patch scale, areas with potentially high abundance of prey were used overproportionally; 3) at the foraging site scale, little owls concentrated activity onto sites with low grass vegetation, where prey accessibility is presumably high.

In the study area, orchards are embedded within a landscape matrix which is dominated by high-intensity agriculture. Orchards showed similar patterns of abundance and seasonal variation of prey over the whole study area, which suggests that these habitat patches fluctuate synchronously at a regional scale. Compared to the matrix, orchards offer richer food supplies, which contrasts with other habitats and provides an explanation why orchards are the favourite landscape features for little owls. Orchards furthermore offer cavities, perches, and hiding places, contrary to other habitats (Bock *et al.;* Tomé, Bloise & Korpimäki 2004; Parejo & Avilés 2011).

At the habitat level the distribution of voles was clearly heterogeneous. Orchards, grassland and field margins all hold important stores of prey, whereas the abundance of voles was near null in cropland. Moreover, prey abundance increased with increasing vegetation height in suitable vole habitats. These results show that the availability of voles varies within habitat patches and amongst habitat types. Agricultural land use is likely an important determinant of these patterns. As shown in several studies (Tew & Macdonald 1993; Butet & Leroux 2001) agricultural land use negatively influences the abundance of voles directly through mechanical disturbance and indirectly through a decrease of heterogeneity. Mowing generally leads to a temporary decrease in the abundance of small mammals and the abandonment of mown patches by small mammals (Garratt, Minderman & Whittingham 2012), but common voles do not leave recently mown patches (Tew & Macdonald 1993). Furthermore, field margins are less affected by tillage or mowing as they are linear structures along patch borders, and are usually not mechanically cultivated or mown.

At the level of individual range use, orchards and field margins were preferred over grassland and cropland. Woody areas were strongly avoided. Therefore, little owls did not use habitat at random and the significant preference for orchards indicates that little owls intensively use patches offering the highest potential prey abundance. Furthermore, in comparison to grassland, orchards offer many natural perches, which may facilitate access and detection of prey.

At the level of small-scale responses to resource patterns, we found that little owls preferred foraging sites with low grass vegetation, irrespective of potential prey abundance. It may be expected that little owls prefer patches of grassland as this habitat type presented a high prey abundance. Additionally, patches with high vegetation in grassland were richer in voles than low vegetation patches. The preference for patches with low vegetation was therefore probably due to a better accessibility to food resources compared to high vegetation. These results suggest that prey accessibility and/or detectability play an important role in addition to prey abundance, similar to other raptor species feeding on small rodents (Aschwanden, Birrer & Jenni 2005; Arlettaz *et al.* 2010). The importance of accessibility and/or detectability of prey was also shown for insectivorous birds searching for food on ground (Schaub *et al.* 2010; Tagmann-Ioset *et al.* 2012). Moreover, little owls rely more on vision than other nocturnal birds (Van

Nieuwenhuyse, Génot & Johnson 2008). They mostly hunt by a "perch and pounch" technique and by walking on ground (Van Nieuwenhuyse, Génot & Johnson 2008). To better disentangle the relationships between food abundance, access and detectability, further experimental research may independently vary the abundance and accessibility of prey.

This study further establishes that habitat selection of little owls is hierarchically structured, hence improving the evidence base with respect to the different scales addressed. It also provides an explanatory base for interpreting existing habitat suitability models (Gottschalk *et al.* 2010). Habitat type and vegetation structure affect the spatial distribution of resources and their abundance. These in turn are important features at the habitat patch scale but also at the foraging-site scale. This study suggests that all levels of habitat selection were related to agricultural land use. Land use affects the spatial configuration of habitat patches within the landscape matrix, resource patterns within habitat patches and, finally, vegetation structure. Agricultural intensification may therefore be the ultimate driver of the dynamics and persistence of little owl populations.

To our knowledge this study is one of only few (e.g. Lambin, Petty & MacKinnon 2000; Arlettaz *et al.* 2010) providing evidence that the abundance of small mammals varies also during the season and not only in annual cycles. The landscape scale spatial patterns were virtually identical over the whole study area. This suggests that the landscape scale variation in vole populations is related to fundamental ecological factors rather than to variation in habitat components at a local scale. However, such factors were not focus of this study.

In general, all observed patterns of habitat selection may result in variation in breeding success and individual survival (Thorup *et al.* 2010). At the landscape scale, configuration and abundance of landscape features are of high importance for population persistence as the owls' decisions on settlement and breeding concern this scale. The habitat patch scale determines how little owls cover their daily energy needs. Additionally, the offer of shelter and protection from predators might be crucial at this scale. At the foraging site scale, little owls decide how they achieve physiological balance by optimizing the ratio between energy intake and expenditure.

With respect to conservation, the results suggest the following options that are easy to implement. The strong contrast in food abundance between orchards or grassland and the remaining cultivated matrix suggests that these habitat patches are crucial elements in the agricultural landscape, and that they have to be promoted as such. Withstanding the increasing pressure to transform orchards into cropland or settlement areas is thus a first important conservation issue. Second, regarding the management of the grass layer within grasslands, especially orchards, alternating patches of high vegetation and high prey abundance with areas of low/cut vegetation offering high prey accessibility may markedly improve access and exploitation of food resources, which will translate into enhanced productivity. Recent evidence emphasises that the supply of food to the growing broods has a pervasive effect on nestling survival and fledgling condition (Thorup *et al.* 2010). Therefore, measures to improve access to resources may address a crucial habitat quality to ensure successful reproduction and population persistence. Third, increasing the number of field boundaries, e.g. field margins, could also improve matrix heterogeneity (Vickery & Arlettaz 2011). Homogenization of habitat patches through a reduction of habitat types and cultures but also the increase of the area of crop fields should be avoided, and a fine-grained mosaic promoted. Applied on a wide scale, these measures may enable reconnecting presently isolated populations and re-instate a positive metapopulational dynamics of little owls across their former distribution range.

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Table 1: Model parameters from the analysis of vole presence/absence in the 4 main habitat types (cropland, field margins, grassland and orchards) over the 4 main regions (NE; NW, SE, SW; see Table S1), with estimates and standard errors (SE), n = 3815 observations.

Variables	Levels	Estimate	SE	Df	Chi	P(>|Chi|)
Intercept		3.55	0.35	0	825.46	<0.001***
Habitat				3	836.78	<0.001***
	Cropland	0	0			
	Field margins	13.88	1.40			
	Grassland	18.69	2.72			
	Orchards	19.31	2.90			
Region				3	1.02	0.80
	NE	0	0			
	NW	-0.50	2.09			
	SE	-0.90	2.19			
	SW	-0.95	2.50			

Table 2: Model parameters from the analysis of vole abundance within vole habitats in relation to season (time) including a fifth order polynomial (time linear – time^5) for explaining non-linear relationships, region (NE, NW, SE, SW, see Table S1), vegetation height and the interaction between vegetation height and habitat type, with estimates and standard errors (SE), n = 2361 observations.

Model variables	Level	Estimate	SE	Df	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 ***

Table 3: Compositional analysis: simplified ranking matrix based on a comparison of proportional habitat use (90% fixed kernel contours (FKC) A) and 50% FKC B)) within 100% minimum convex polygon (MCP) home ranges with proportions of available habitat types. Each mean element in the matrix was replaced by a sign indicating the direction of selection, with a triple sign representing a significant deviation from random at an alpha rejection level of 0.05.

A

	Cropland	Grassland	Orchard	Field margins	Road	Wood/Bush	Rank
Cropland		**-**	**---**	**---**	**+++ (+)**	**+++**	2
Grassland	**+**		**---**	**-**	**+++**	**+++**	3
Orchard	**+++**	**+++**		**+++**	**+++**	**+++**	5
Field margins	**+++**	**+**	**---**		**+++**	**+++**	4
Road	**--- (-)**	**---**	**---**	**---**		**+++**	1
Wood/Bush	**---**	**---**	**---**	**---**	**---**		0

B

	Cropland	Grassland	Orchard	Field margins	Road	Wood/Bush	Rank
Cropland		-	---	---	+++	+++	2
Grassland	+		---	-	+++	+++	3
Orchard	+++	+++		+	+++	+++	5
Field margins	+++	+	-		+++	+++	4
Road	---	---	---	---		-	0
Wood/Bush	---	---	---	---	+		1

Table 4: Model parameters of the analysis of perch visits by little owls in relation to vegetation height, habitat type (cropland or grassland), season (period1, period 2, period 3) and distance to the breeding site, with estimates and standard errors (SE) and number of observations n = 417.

Variables	Levels	Estimate	SE	Df	Chisq	P(>|Chi|)
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***

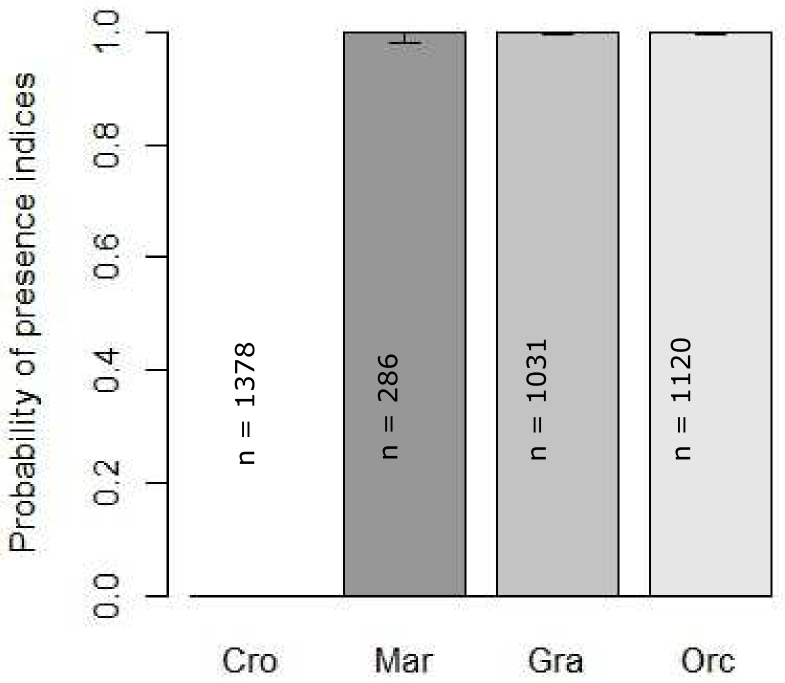
Figure captions

Fig. 1: Probability of presence/absence of voles in the four main habitat types (Cro = cropland, Mar = field margins, Gra = grassland, Orc = orchard), based on predictions of the binomial model. Voles are virtually absent in cropland. The probability of vole presence is highest in orchard, grassland and field margins, approaching a ratio of 1.

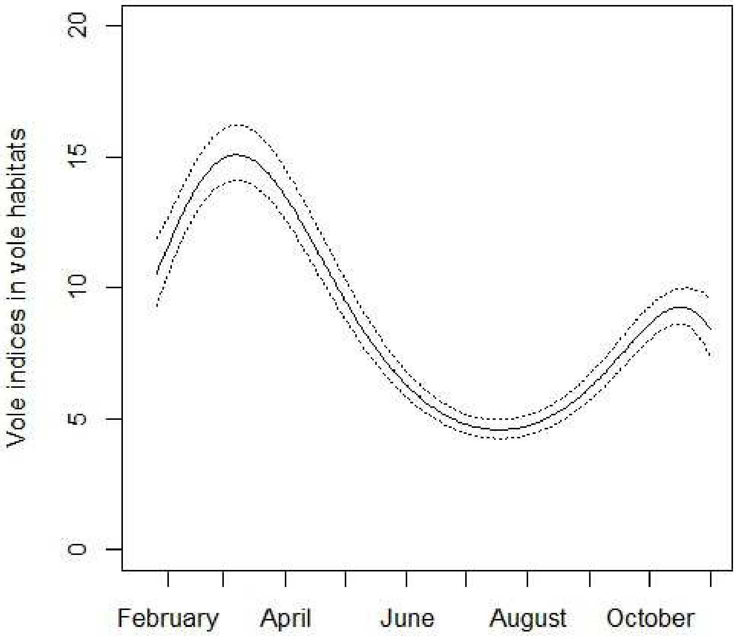
Fig. 2: Seasonal variation of the relative vole abundance index in the three habitat types harbouring high vole abundance (orchard, grassland and field margins). The abundance increases slightly at the beginning of the year towards spring and then drops down towards summer; it increases again towards autumn.

Fig 3: A) Relationship between the relative abundance index for voles and vegetation height (excluding seasonal effects) in orchards (significant trend). B) Relationship between the vole abundance index and vegetation height (excluding seasonal effects) in grassland (significant trend). For statistical details see Table 1.

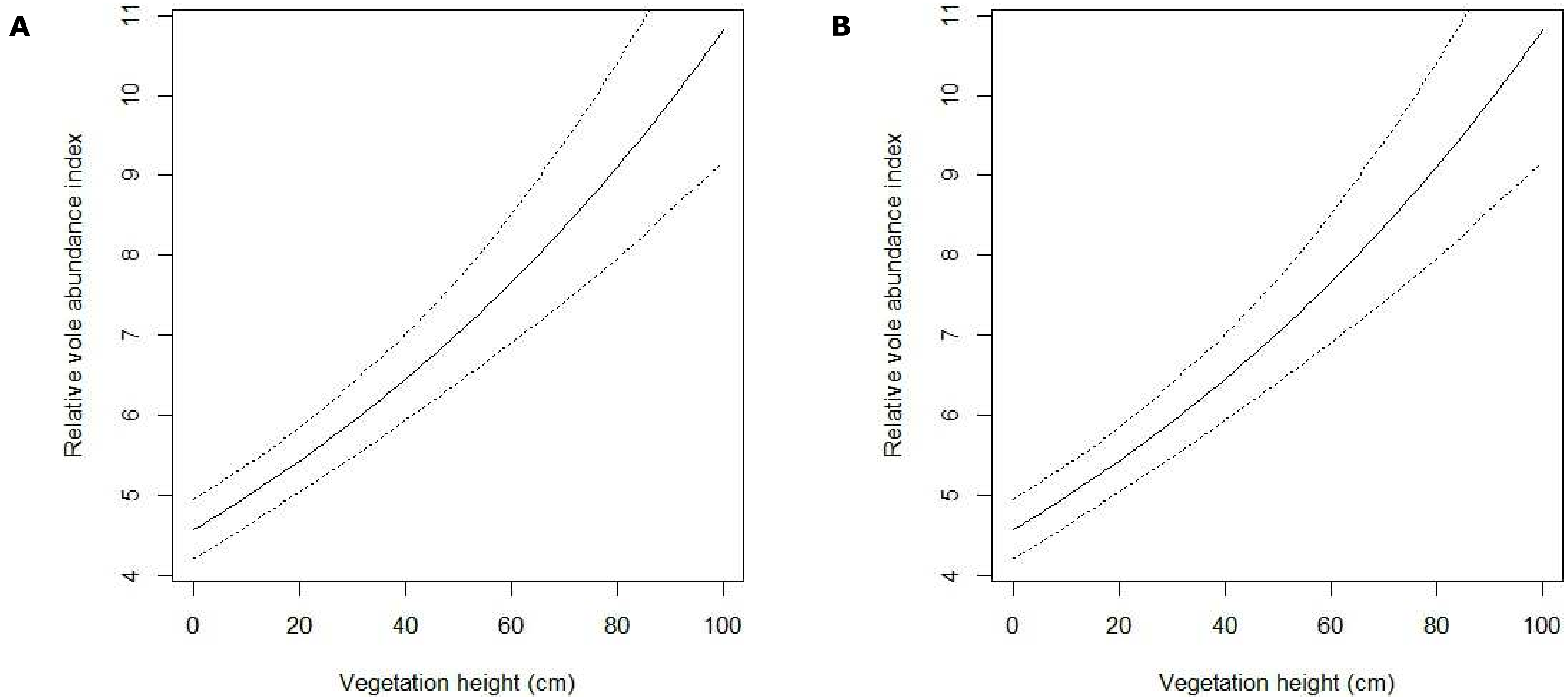
Fig. 4: A) Number of perch visits by little owls over all the sampling period in grassland, for a nestbox distance arbitrarily fixed at 50 m for the model projection. B) Number of perch visits by little owls over all sampling periods for cropland with a nestbox distance arbitrarily fixed at 50 m for the model projection. The perches are visited more frequently with lower vegetation height Statistical details see Table 4.



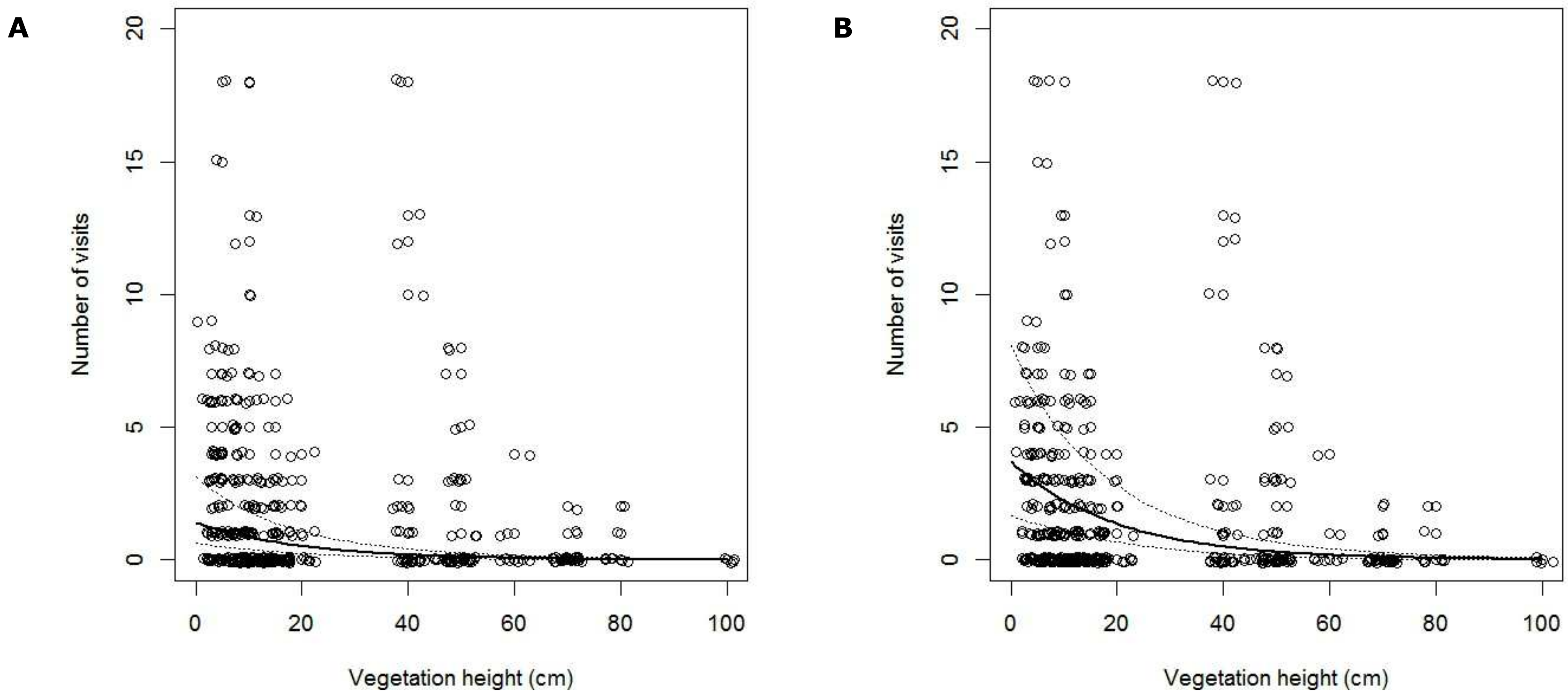
Apolloni, Figure 1



Apolloni, Figure 2



Apolloni, Figure 3



Apolloni, Figure 4

Supporting Information

Appendix 1: Repeatability of field sign counts

In order to test the repeatability of counts, counts were replicated once in 10 sampling areas and at 2 sampling periods. Replicates were performed within 7-10 days after the first count.

Altogether 900 repeat counts were carried out during the sampling period. Repeat counts were performed twice over the sampling period. 323 repeat counts were realized in 15 little owl breeding sites in July and 576 counts in September and October over 16 breeding sites. Only the 576 repeat counts of the September and October session were retained for the final analysis. These repeat counts were performed in a 7 to 10 day time interval from the transect counts. 195 repeat counts were performed in cropland areas, 192 in grassland and 189 in orchard. The correlations for index counts in general and for runways, holes and heaps counts in particular, were all highly significant (Table S2 & Fig. S3). This result points out that repeat counts were very close to the corresponding transect counts, which indicates a high repeatability of the method and moreover a high detectability of all indices in only one transect count passage.

Appendix 2: Calibration of transect counts

Both live trapping and transect counts yield relative estimates of vole abundance. Thus, it is important to calibrate the techniques to ascertain that they yield reliable estimates. Both indices for relative abundance of voles correlate positively, independent of the vegetation height (Table S3). Moreover, other studies also calibrated vole field sign counts with live trapping and found a significant relationship (Delattre *et al.* 1996; Lambin, Petty & MacKinnon 2000). Transect counts of field signs allowed to record a complete range of relative abundances, i.e. from complete absence to extremely high densities of voles (range indices 0 to 0.99). Live trapping probably may not have the same resolution.

Appendix 3: Camera Traps

Five trail cameras of type "Reconyx™ PC 900 Hyperfire™" (Reconyx, Inc., Holmen, Wisconsin,USA) provided by the division of Conservation biology of the University of Bern were tested during October and November 2010. Additionally to the Reconyx cameras, 3 Bushnell® trophy cam cameras were tested. The cameras were placed at breast level or lower in different angles, surveying different sample areas. Pictures of voles in open areas were successfully taken. The trigger-speed was higher in the Reconyx cameras compared to the Bushnell cameras. A problem in both models was the passive infrared (PIR) detection fields which are designed to detect larger objects (in most camera types the detection 'windows' point to the lower field of vision of the optics). The effective detection area for small animals is restricted to less than 15% of the area that is covered optically. To overcome this problem, the Bushnell cameras were equipped with alternative PIR lens originally designed for ceiling-mounted devices (Kube Electronics ® Gossau Switzerland, Type TR248, 13 radial detection windows). Although the alternative lens have a circular detection field, the single 'detection windows' were c.a. 20 x 30 cm (camera at 1.5 m above ground), covering about 25% of the optical view. Thus, the alternative lens left also much of the area uncovered and the probability to miss a subject smaller than the between-window distance (20-40 cm) was high.

For data collection 20 modified trail cameras were used to assess vole activity. For surveys, cameras were spread over the three main habitat types (cropland, grassland and orchards) in order to obtain a good cover of the sampling area. Home range sizes of common voles are supposed to be around 350 - 400 m^2 and individual movements should be small according to literature (Delattre *et al.* 1996; Brügger, Nentwig & Airoldi 2010). Six cameras (two in each of the three habitat types) were thus placed in each sampling area. A minimum distance of 50 m was put between the cameras. Cameras were checked after 4 days and 3 nights. The sampling was repeated three times per sampling period in each sampling site with a 3 - 4 day interval.

More than 100’000 pictures were analysed to investigate the visibility of voles. The “trapping” rate of the cameras was very low (very few voles were visible on the pictures in comparison to the huge amount of pictures) (Tables S8a & b). Moreover, the rate of empty pictures was higher than the rate of mice pictures, which increases the uncertainty of the data. We renounced to further analyse the camera trap data set.

Table S1: Subdivision of breeding sites into four major regions within the district of Ludwigsburg with codes for each breeding site in the respective regions: North-West (NW), North-East (NE), South-West (SW) and the South-East (SE) of the district of Ludwigsburg (see Fig S2), Kleinsachsenheim (KS), Enzweihingen (EN), Vaihingen (VA), Rosswag (RW), Grossbottwar (GB), Ottmarsheim (OT), Heimerdingen (HD), Schöckingen (SO), Rutesheim (RU), Remseck (RE), Markgröningen (MG), Münchingen (MU), Schwieberdingen (SC).

NW	**NE**	**SW**	**SE**
KS14	GB83/81	HD9/0	RE47
EN97/98	OT96	HD8	MG106/108
VA21	OT99	SO71	MU104/103
RW7		RU1	SC2/SC9

Table S2: Results of the linear regression testing whether transect counts correlate with corresponding repeat counts, with estimate and standard error (SE), n = 574 repeat counts.

	t	df	Estimate	SE	p (>|t|)
Intercept	3.99	1	0.51	0.13	<0.001
Repeat counts	56.66	574	0.90	0.16	<0.001

Table S3: Results of the linear regression testing whether indices counts correlates with trapping data, with estimates and standard errors (SE), n = 94 observations, residual SE = 0.76. Both indices for relative abundance of voles correlate positively. Vegetation height has no significant effect on this relationship.

	Estimate	df	SE	t-value	p (>|t|)
Intercept	-0.12	2	0.16	-0.74	0.46
Indices	0.03	94	0.01	2.89	0.00
Vegetation height	0.00	94	0.00	0.03	0.97

Table S4: Percentage of habitat type for each tracked individual and their corresponding 100% MCP home range. The mean percentages are given at table bottom.

Individual	Cropland	Field margins	Grassland	Orchard	Road	Wood/Bush	Human settlement	River	Forest	Vineyard
EN97m	46.5	8.5	15.9	**22.1**	4.5	2.4	0	0	0	0
EN98f	70.5	7.6	12.1	**1.9**	6.0	1.9	0	0	0	0
EN98m	69.0	6.6	8.9	**2.0**	7.2	1.2	5.1	0	0	0
GB81f	54.3	10.3	10.2	**20.1**	3.8	1.3	0	0	0	0
HD8m	64.7	8.2	4.2	**11.7**	8.8	0.6	1.8	0	0	0
HD9m	59.5	9.1	4.4	**16.0**	10.9	0.2	0	0	0	0
KS14f	70.8	8.7	6.3	**3.9**	5.4	0.3	4.6	0	0	0
KS14m	70.1	8.1	8.4	**3.7**	6.5	0.3	3.0	0	0	0
MG106f	49.6	12.1	25.0	**8.7**	1.0	3.6	0	0	0	0
MG108f	45.3	9.8	17.4	**17.4**	6.5	3.6	0	0	0	0
MG108m	60.4	8.6	14.2	**9.7**	4.8	2.4	0	0	0	0
MU103f	36.7	9.3	10.2	**14.2**	13.7	0.6	15.4	0	0	0
OT96f	56.0	8.4	17.8	**13.9**	3.0	0.3	0	0	0	0
OT96m	51.3	8.6	12.2	**18.7**	7.2	1.1	0.5	0.4	0	0
OT99f	58.6	10.6	11.5	**12.8**	3.9	1.6	0	1.0	0	0
OT99m	57.6	10.6	13.1	**12.5**	3.5	1.5	0.2	1.0	0	0
RE47f	50.5	10.2	4.8	**12.2**	11.7	5.1	5.5	0	0	0
RE47m	47.0	9.5	4.1	**16.2**	11.5	6.8	4.9	0	0	0
RU1m	28.9	10.9	41.1	**7.3**	8.5	3.4	0	0	0	0

RW7f	78.2	9.4	5.3	**2.3**	1.7	3.1	0	0	0	0
RW7m	72.3	10.2	4.9	**9.0**	2.3	1.3	0	0	0	0
SC2f	75.8	9.8	6.8	**2.6**	4.0	1.0	0	0	0	0
SC2m	62.9	9.2	8.9	**7.1**	9.5	1.6	0.7	0	0	0
SC9f	45.7	10.6	7.7	**25.0**	7.9	3.0	0	0	0	0
SC9m	63.9	8.7	9.3	**7.4**	7.4	3.3	0	0	0	0
SO71f	66.0	9.9	3.1	**11.7**	9.2	0	0	0	0	0
SO71m	41.0	12.9	5.3	**22.4**	10.0	0	8.4	0	0	0
VA21f	26.0	8.1	2.7	**34.8**	7.3	5.2	0.4	0	0.1	15.5
VA21m	43.0	6.3	1.7	**7.6**	11.3	6.6	0	0	0	23.5
Average	55.9	9.3	10.3	**12.2**	6.9	2.2	1.7	0.1	0.0	1.3
Locations	29.2	9.2	10.2	**47.8**	0.6	2.4	≥0.1	≥0.1	≥0.1	≥0.1

Table S5: Tagged and tracked individuals

Individual	Tagged on	Retagged on	Followed from…to
EN97.M	23.06.2010	06.07.2011	January-October 2011
EN98.F	23.06.2011	21.06.2011	January–October 2011
2011EN98.M	21.06.2011		
GB83.F/GB81.F	13.06.2010	10.06.2011	January–October 2011
HD9.M/HD0.M	10.06.10	04.07.2011	January–October 2011
2010HD0.F	10.06.10[1]		July–October 2011
2011HD0.F	25.05.2011		
HD8.M		26.06.2011	January–October 2011
KS14.M	11.06.2010	17.07.2011	January–October 2011
2011KS14.F	22.07.2011		July–October 2011
MU104.M	08.06.2010		January-April 2011
MU103.F	20.06.2011		January–October 2011
2011OT96.M	25.06.2011		July–October 2011
2011OT96.F	17.06.2011		July –October 2011
OT99.M	19.06.2010	17.06.2011	January–October 2011
OT99.F	19.06.2010		January–September 2011
RE47.F	30.05.2011		July-October 2011
RE47.M	04.06.2011		July–October 2011

RU1.M	08.07.2011		July–September 2011
2010RW7.F	18.06.2011[2]		January–February 2011
2011RW7.F	28.06.2011		July-August 2011
RW7.M	23.06.2010	14.06.2011	January-October 2011
SC2.F	17.06.2010	28.06.2011	January-October 2011
2011SC2.M	28.06.2011		July-October 2011
SC9.F	16.06.2010	15.06.2011	January-October 2011
SC9.M	16.06.2010	15.06.2011	January-August 2011
SO71.F	02.07.2011		July-October 2011
SO71.M	28.06.2011		July-October 2011
VA21.F	18.06.2011		July-October 2011
VA21.M	11.06.2010		January-July 2011

Table S6: Matrix of means and standard errors for 90% A) and 50% B) Fixed Kernel Contours (FKC) as reference, ranking the habitat types in order of use. At each position in the matrix, the mean and standard error of the elements were calculated over all 29 individuals, and the significance of the ratio evaluated by randomization tests.

A

	Cropland	Grassland	Orchards	Field margins	Road	Wood/Bush
Cropland		-0.198 ± 0.107	-0.889 ± 0.109	-0.296 ± 0.070	0.614 ± 0.332	2.288 ± 0.753
Grassland	0.198 ± 0.107		-0.691 ± 0.108	-0.098 ± 0.088	0.812 ± 0.339	2.483 ± 0.763
Orchards	0.889 ± 0.109	0.691 ± 0.108		0.593 ± 0.070	1.503 ± 0.327	3.186 ± 0.769
Field margins	0.296 ± 0.070	0.098 ± 0.088	-0.593 ± 0.070		0.909 ± 0.313	2.601 ± 0.765
Road	-0.614 ± 0.332	-0.812 ± 0.339	-1.503 ± 0.327	-0.909 ± 0.313		1.638 ± 0.745
Wood/Bush	-2.288 ± 0.753	-2.483 ± 0.763	-3.186 ± 0.769	-2.601 ± 0.765	-1.638 ± 0.745	

B

	Cropland	Grassland	Orchard	Field margins	Road	Wood/bush
Cropland		-1.105 ± 0.544	-2.352 ± 0.628	-1.681 ± 0.355	2.130 ± 0.547	2.044 ± 0.599
Grassland	1.105 ± 0.544		-1.246 ± 0.571	-0.576 ± 0.369	3.235 ± 0.720	2.905 ± 0.690
Orchard	2.352 ± 0.628	1.246 ± 0.571		0.670 ± 0.396	4.482 ± 0.562	4.029 ± 0.559
Field margins	1.681 ± 0.355	0.576 ± 0.369	-0.670 ± 0.396		3.811 ± 0.478	3.559 ± 0.482
Road	-2.130 ± 0.547	-3.235 ± 0.720	-4.482 ± 0.562	-3.811 ± 0.478		-0.300 ± 0.682
Wood/bush	-2.044 ± 0.599	-2.905 ± 0.690	-4.029 ± 0.559	-3.559 ± 0.482	0.300 ± 0.682	

Table S7: Home range dimensions in ha for each tracked individual obtained through the computation of the 100% Minimum Convex Polygon (MCP), with the number of locations indicated in brackets.

ID	MCP 100% area (ha) male	MCP 100% area (ha) female
EN98	56.22 (n = 128)	17.94 (n = 241)
KS14	45.44 (n = 166)	45.98 (n = 82)
MG108	42.91 (n = 124)	21.51 (n = 130)
OT96	36.83 (n = 98)	19.69 (n = 127)
OT99	46.95 (n = 141)	43.19 (n = 129)
RE47	12.97 (n = 124)	19.32 (n = 128)
RW7	25.06 (n = 138)	9.27 (n = 51)
SC2	108.48 (n =99)	24.93 (n = 172)
SC9	20.10 (n = 230)	13.89 (n = 280)
SO71	8.23 (n = 98)	11.36 (n = 87)
VA21	11.72 (n = 68)	35.10 (n = 98)
EN97	48.49 (n = 315)	na
GB81	na	46.41 (n = 186)
HD8m	37.63 (n = 121)	na
HD9	18.21 (n = 279)	na
MG106	na	9.94 (n = 78)

MU103	na	26.73 (n = 111)
RU1	11.95 (n = 70)	na

Table S8: Percentage of pictures with voles taken by trail cameras for the survey of vole activity A) and total number of pictures per habitat taken with trail cameras to survey vole activity B).

A

	Cropland	**Grassland**	**Orchard**
January/february	na	3.92	1.80
March	na	0	4.36
April/Mai	0	0	0
July/August	0	0.05	0
October	0	0	0

B

Period	**Cropland**	**Grassland**	**Orchard**
January/February	na	1098	1889
March	na	296	527
April/Mai	245	6593	7783
July/August	10333	59041	9118
October	151	6607	4106

Figure captions

Fig. S1: Map of the study area with breeding sites. Abbreviations: Enzweihingen (EN), Grossbottwar (GB), Heimerdingen (HD), Kleinsachsenheim (KS), Markgröningen (MG), Münchingen (MU), Ottmarsheim (OT), Remseck (RE), Rutesheim (RU), Rosswag (RW), Schwieberdingen (SC) and Schöckingen (SO), and numbers for individual codes.

Fig. S2: Map of the study area showing the four regions and the investigated breeding sites.

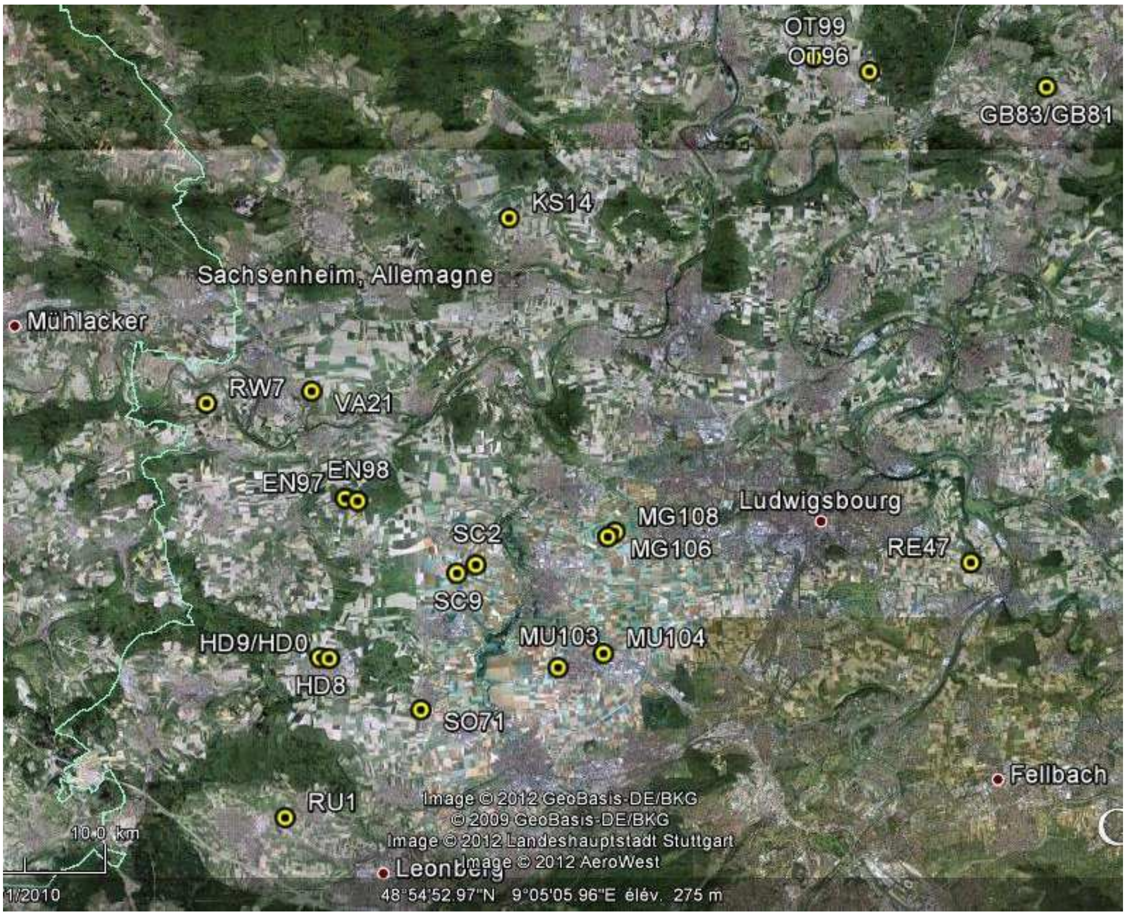
Fig. S3: Correlation between transect counts and repeat counts. The number of relative vole abundance indices found on transect counts and on repeated counts correlates significantly. Statistical results are given in Table S2.

Fig. S4: Maps of the first A) and the second mousetrapping site B) showing the five subsets of 10 traps each.

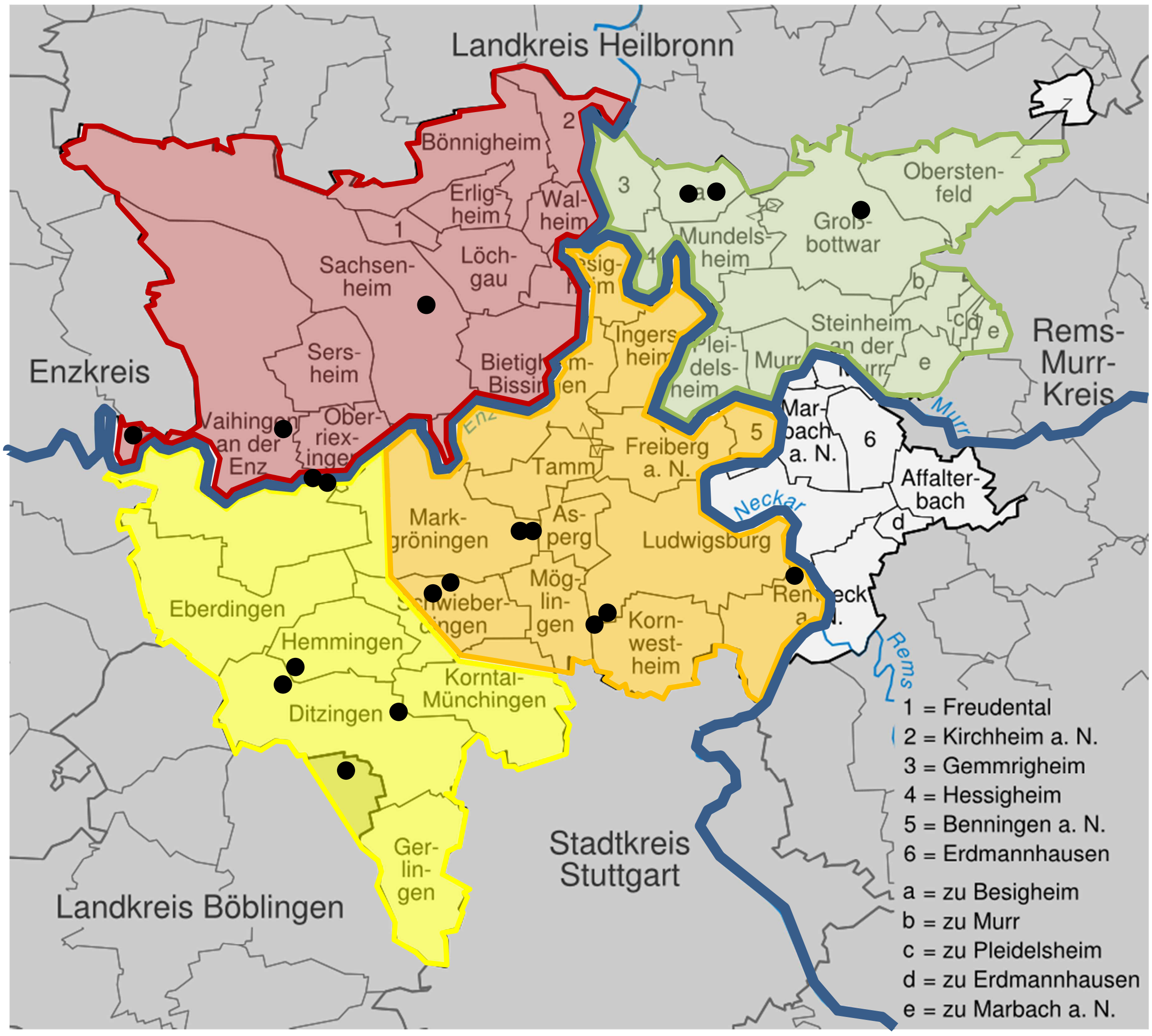
Fig. S5: Schematic representation of the set up for the investigation on the use of perches by little owls. The figure shows a breeding site with two similar grassland areas and two similar cropland areas. Four perches were set up in one grassland areas and one cropland area A) for 10 days and then set up in the other grassland and cropland area B) for another 10 days. G: experimental grassland areas, C: experimental cropland areas.

Fig. S6: Construction details of devices mounted on perches for counting the visits of birds exceeding a load of 120 g.

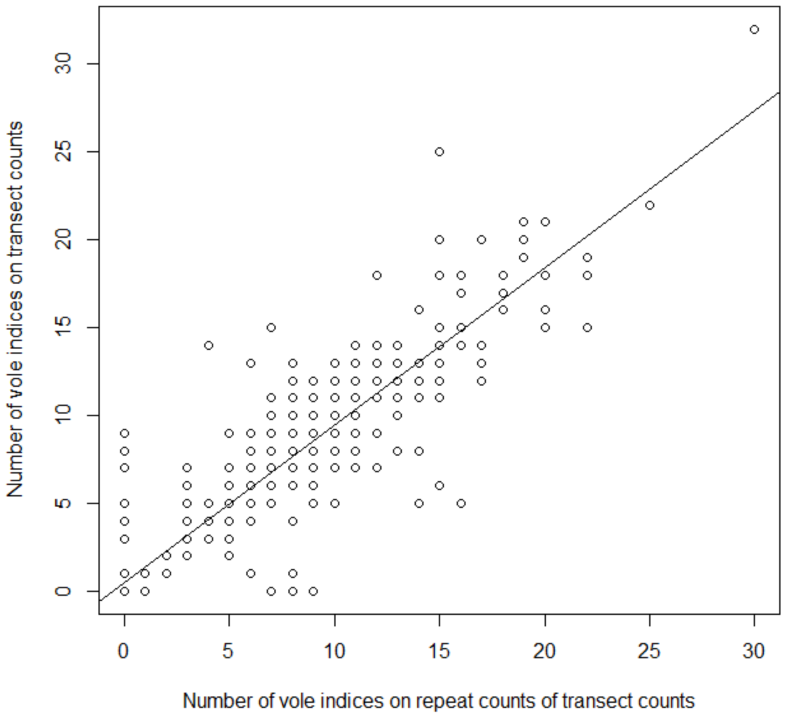
Fig S7: Example of a breeding site in Markgröningen A) and Rosswag B) where relative vole abundance was sampled by transect counts of field signs. The pictures highlight the high spatial resolution of the method. Red squares indicate sampling points with a high (> 5 signs) occurrence of field signs, orange squares an intermediate (1 – 5 signs) occurrence of field signs. Number of field signs n = 218 A) and n = 248 B). White squares indicate absence of field signs.



Apolloni, Figure S1

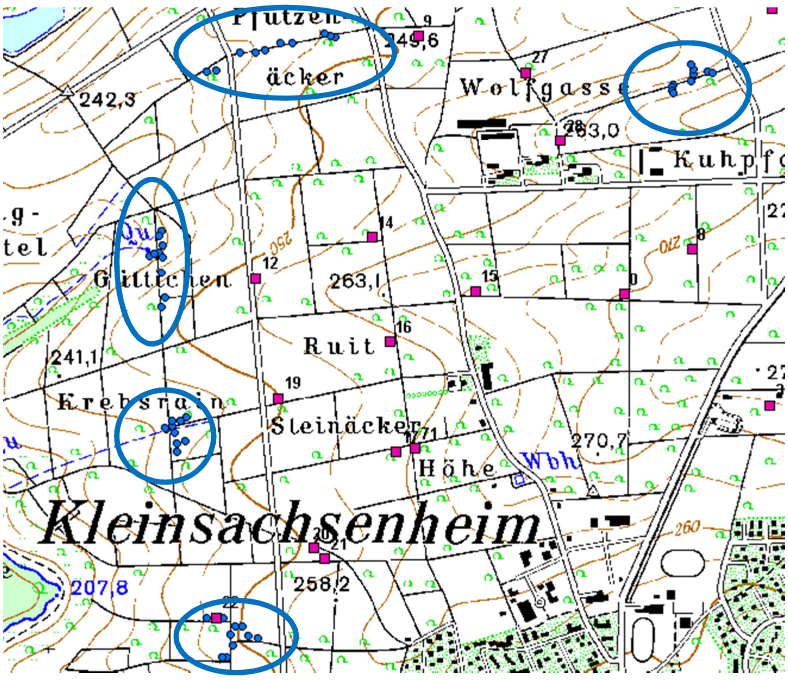


Apolloni, Figure S2



Apolloni, Figure S3

A



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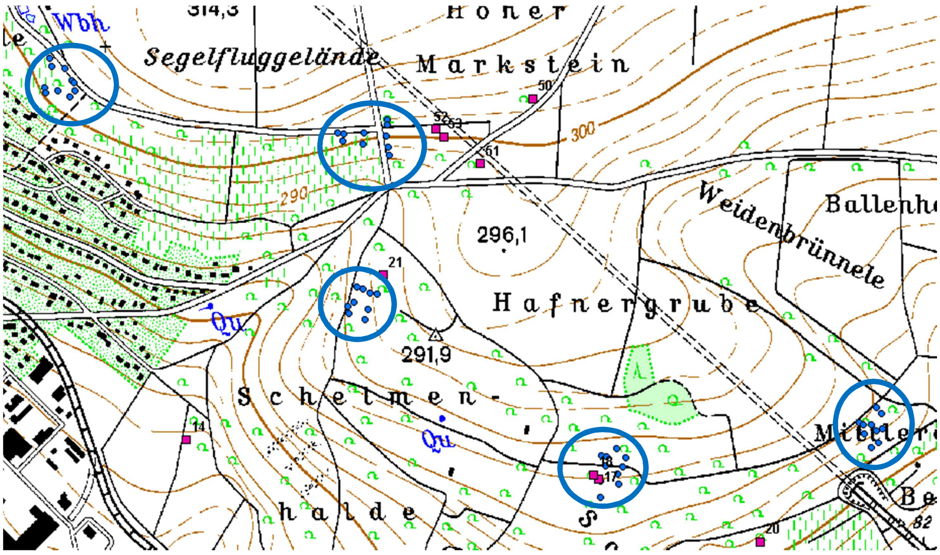

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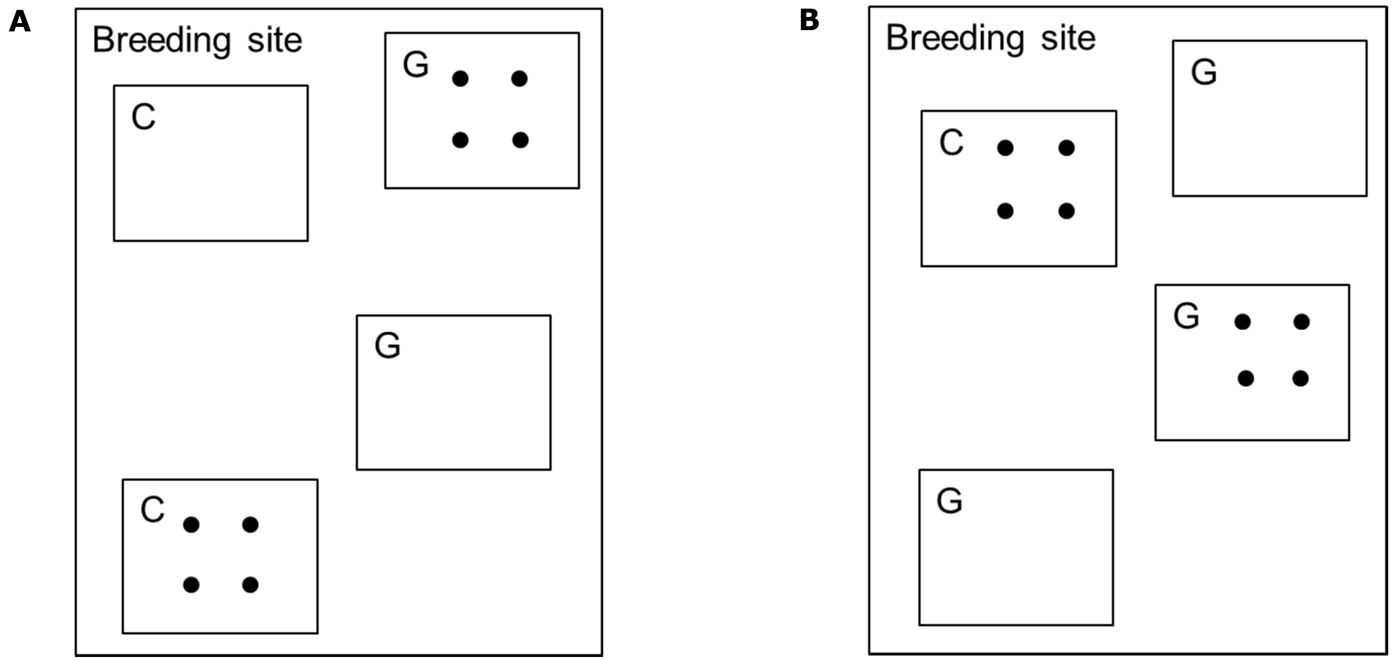
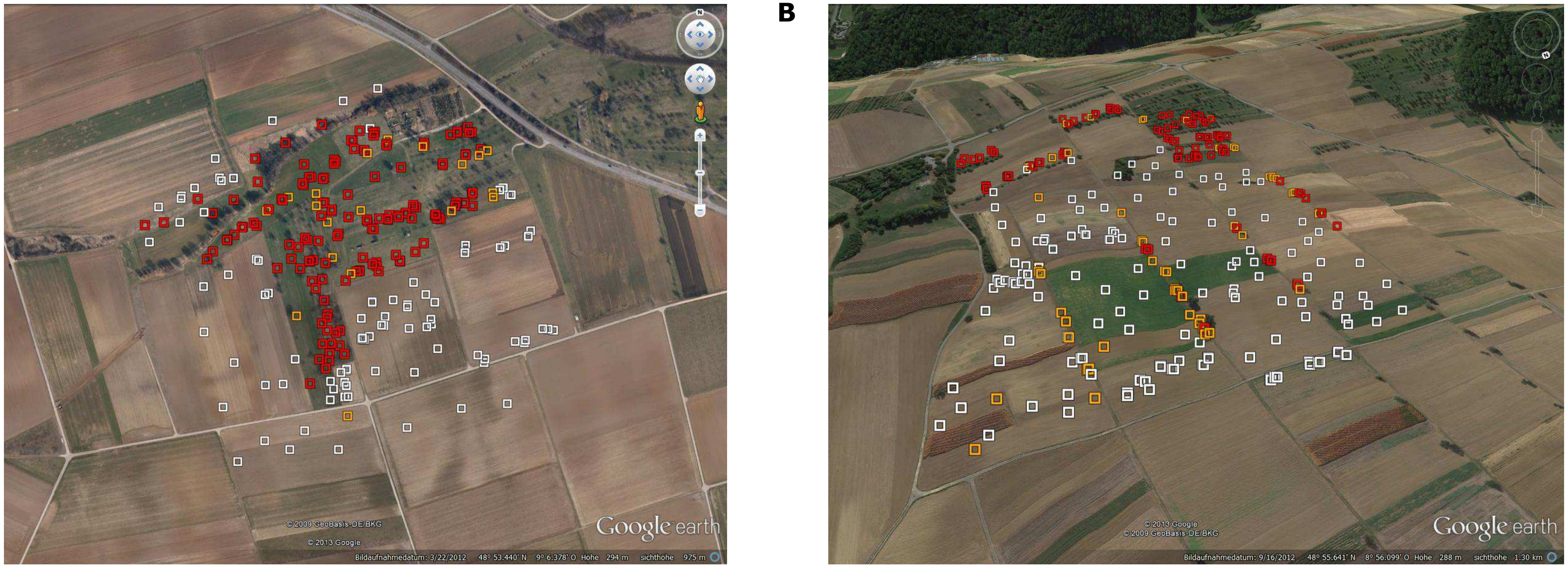


Apolloni, Figure S5

Apolloni, Figure S6

A **B**



Apolloni, Figure S7