

Original article

Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe

Aline Tagmann-Ioset^a, Michael Schaub^{a,b}, Thomas S. Reichlin^{a,b}, Nadja Weisshaupt^a, Raphaël Arlettaz^{a,c,*}^a Institute of Ecology and Evolution, Division of Conservation Biology, Baltzerstrasse 6, CH-3012 Bern, Switzerland^b Swiss Ornithological Institute, CH-6204 Sempach, Switzerland^c Swiss Ornithological Institute, Valais Field Station, Nature Centre, CH-3970 Salgesch, Switzerland

ARTICLE INFO

Article history:

Received 15 April 2011

Accepted 22 November 2011

Available online xxx

Keywords:

Habitat selection
 Farmland birds
 Radio-tracking
 Food availability
 Prey accessibility
 Species conservation

ABSTRACT

Most farmland birds have declined significantly throughout the world due to agricultural intensification. Agri-environmental policies could not halt the decline of ground-foraging insectivorous farmland birds in Europe, indicating a gap in knowledge of species' ecological requirements. This represents a major impediment to the development of efficient, evidence-based agri-environmental measures. Using radio-tracking we studied habitat selection by farmland Hoopoes, a rare terrestrially foraging bird in Central Europe, and assessed habitat preferences of their main prey (Molecrickets), with the aim to identify optimal foraging habitat profiles in order to guide farmland management. Hierarchical logistic regression modelling of habitat descriptors at actual foraging locations vs. random locations within the home ranges of 13 males showed that the availability of bare ground was the principal determinant of foraging activity, with an optimum of 60–70% bare ground at patch scale. This ideal habitat configuration, which facilitates birds' terrestrial hunting, was found primarily in intensively farmed fruit tree plantations which dominated the landscape matrix: this habitat offers extensive strips of bare ground due to systematic removal of ground vegetation along tree rows. In contrast, dense grassland and cropland were avoided. Another important habitat feature was the availability of nongravely soil, which enabled Hoopoes to probe the earth with their long, curved bill in search of underground invertebrates. The role of Molecrickets, however, appeared secondary to foraging patch selection, suggesting that prey accessibility was *per se* more important than prey abundance. Creating patches of bare ground within modern farmland where sufficient supplies of suitable invertebrate prey exist will support Hoopoe populations.

© 2011 Elsevier Masson SAS. All rights reserved.

Agricultural intensification after World War II has provoked a collapse of biodiversity in many regions of the world, especially in developed countries (Ehrlich and Pringle, 2008). In Central Europe, farmland wildlife has undergone a dramatic decline, especially among species that feed exclusively on invertebrates (Fuller et al., 1995; Blanco et al., 1998; Donald et al., 2001; Donald et al., 2006; Britschgi et al., 2006; Brambilla et al., 2010). This has been attributed mostly to habitat degradation caused by landscape homogenization (Benton et al., 2003), or to diminished food supply due to massive application of insecticides (Boatman et al., 2004). Habitat modifications may not only alter food abundance, but also change its availability, which is defined as abundance modified by

accessibility. Disentangling these effects is essential in order to promote efficient conservation and restoration strategies for rare, declining insectivorous species, for instance through the improvement of farming practices and agri-environment schemes. Augmenting food accessibility may merely call for simple adaptive management measures, whereas increasing food abundance may require a total change of farming practices. Fine-grained studies of a species' ecological niche may not only identify the general environmental features essential for its survival, but also enable the optimal habitat profiles for population conservation and restoration to be described, and even assess food availability (Hildén, 1965; Johnson, 1980; Schaefer and Messier, 1995).

Many birds that inhabit open and semi-open cultivated landscapes search for food on the ground, with ground vegetation structure (vegetation height and cover) dictating food accessibility (Atkinson et al., 2005; Douglas et al., 2009; Schaub et al., 2010). Several insectivorous bird species feeding on ground-dwelling

* Corresponding author. Institute of Ecology and Evolution, Division of Conservation Biology, Baltzerstrasse 6, CH-3012 Bern, Switzerland

E-mail address: raphael.arlettaz@iee.unibe.ch (R. Arlettaz).

arthropods can barely survive in today's intensive farmland owing to low food abundance, inaccessible food resources, or a combination of both. To disentangle these effects, foraging patch selection, as well as food abundance, need to be studied. It has been shown that a too dense grass sward precludes birds from accessing valuable food patches although food does occur in sufficient abundance (Schaub, 1996; Aschwanden et al., 2005; Douglas et al., 2009; Weisshaupt et al., 2011; Arlettaz et al., 2011). Since assessments of actual food availability are unfortunately missing for most species, the establishment of efficient conservation actions is considerably hampered.

The Hoopoe *Upupa epops* is a ground-foraging bird whose populations have significantly declined throughout Central Europe during the last 50 years. Hoopoes provide the ecosystem service of eating arthropods that are pests in agriculture and forestry (Barbaro et al., 2008; Arlettaz et al., 2010b). They thus deserve conservation attention. The main cause of decline has been attributed to habitat changes after agricultural intensification, which caused losses of breeding sites due to the removal of old trees rich in cavities, denser sward in grassland due to increased fertilization, and reduction in the number of large arthropods resulting from insecticide application (Bauer and Berthold, 1997). In the present study we investigated the last two possibilities, as detailed knowledge of micro-habitat requirements of foraging Hoopoes, and of their main local prey (Molecrickets *Grylotalpa grylotalpa*; Fournier and Arlettaz, 2001) is still lacking. Schaub et al. (2010) showed that Hoopoes selected foraging patches characterized by a considerable amount of bare ground, but it is not sufficiently well known whether this preference varies within different habitat types, how it is affected by variable vegetation height, or how it is modulated by food abundance. The observation that most Swiss Hoopoes, in the south-western part of Switzerland (Valais), survive in intensively cultivated fruit tree plantations subjected to massive application of pesticides indicates that food abundance may play a lesser role than food accessibility. We used radio-tracking to assess which habitat types and vegetation structures were preferred by foraging Hoopoes, with a particular emphasis on micro-habitat features such as ground vegetation cover. We further examined what were the habitat associations of Molecrickets, which constitute more than 90% of the diet fed to chicks (Arlettaz et al., 2010a). This approach enabled us to indirectly assess the relative contribution of food abundance and food accessibility to Hoopoe's micro-habitat selection pattern, with the aim of formulating accurate conservation recommendations for Hoopoe populations.

1. Methods

1.1. Study area and data sampling

The study was carried out on the flood-plain of the Rhone river valley between Martigny and Sierre in the Canton of Valais (SW Switzerland, 46° 14' N, 7° 22' E, 460–520 m asl) in summer 2006. The plain is used intensively for agricultural purposes, especially for the cultivation of fruit trees and vineyards, but grassland, crop and vegetable cultures are also present (Arlettaz, 1984). Except in some places bordering the Rhone river, tall trees are nowadays scarce and the availability of natural cavities (hollow trees, holes excavated by woodpeckers) is therefore very limited. Since 1997, about 700 nestboxes have been installed that serve as the main nesting sites for local Hoopoes and, within a few years, have resulted in a dramatic population increase (Arlettaz et al., 2010b).

Breeding adult Hoopoes were mist-netted at their nest-box entrances. Captured birds were measured, ringed and equipped with a radio transmitter (Holohil Systems Ltd., model BD-2 P with activity sensor, 1.4 g, life span of 9 weeks). The transmitters were

fixed using a Rappole harness made of two elastic rubber lashes placed around the legs (length of open loop: 149 mm; Rappole and Tipton, 1991; Naef-Deaenzer, 2007).

Only males were radiotracked because they are more active chick-food providers than females (Arlettaz et al., 2010a). Radio-tracking began when Hoopoes started feeding their nestlings. Two people tried to collect as many visual observations of foraging Hoopoes as possible by homing-in on the birds (Harris et al., 1990). Only actual foraging activity served as a basis for habitat selection analysis. Once a ground-walking (i.e. foraging), radio-tagged bird was located visually, it was tracked with binoculars in order to precisely pinpoint foraging locations. Foraging locations were marked in the field with labelled sticks after the bird had left the foraging patch. The exact time of the sighting, and whether or not a bird had captured a prey were also recorded. To reduce spatio-temporal autocorrelation between recorded foraging locations, we used interval sampling with at least a 10 min time lapse between two relocations, unless the focal individual had left the patch in the meantime. After a radio-tracking session, which lasted about 2 h per individual, habitat characteristics were recorded within a radius of 1 m around the marked locations. A small radius was chosen as we were interested in habitat selection at the scale of the foraging habitat patch. Recorded habitat variables included habitat type, vegetation structure (vegetation height, amount of bare ground), soil structure (soil type and hardness), and the presence of Molecrickets (Table 1). Molecricet occurrence was assessed through the presence of their typical galleries dug just under the soil surface. Molecricet surveys were carried out within a larger radius (20 m) than for habitat features for maximally 15 min per location unless a Molecricet gallery had already been found before 15 min.

Our habitat selection analysis is based on a comparison of habitat characteristics at actual foraging locations vs. random locations. Minimum convex polygons (MCP) were drawn from foraging locations in order to delineate individual home ranges. Within these home ranges, but farther than 10 m from actual foraging locations, random locations were generated with the program ArcView (ArcView GIS 3.3, Environmental Systems Research Institute Inc., California, USA). The number of random locations within an individual's home range more or less amounted to the number of actual foraging locations. Habitat features were mapped similarly at both types of locations.

1.2. Statistical analyses

To evaluate foraging micro-habitat selection, we compared habitat variables recorded at actual foraging locations and at random locations, using a hierarchical logistic regression model (GLMM). Individual identity (ring number) was included as a random effect, which

Table 1
Description of recorded habitat variables with format and description of levels (if categorical).

Variable	Format	Levels
Habitat type	Categorical	Apple tree plantation, pear tree plantation, other fruit tree plantation, vineyard, grassland, cropland, unpaved road, road bank, river bank
Vegetation height	Continuous (cm)	
Bare ground	Continuous (%)	
Molecricet presence	Categorical	Yes, no
Soil type	Categorical	Loamy, sandy, gravelly
Soil hardness	Categorical	Very loose, loose, medium, hard, very hard

enabled the data of all individuals to be analysed simultaneously, while avoiding potential pseudo-replication effects (Gillies et al., 2006).

We defined several candidate models and ranked them according to their support by the data using Akaike's Information Criterion (AIC; Burnham and Anderson, 1998). Because the number of potential models was large, due to various possible combinations of explanatory variables, the selection procedure was conducted in two steps. First, we modelled Hoopoes' foraging occurrence with respect to habitat variables describing vegetation types and structure. We used different combinations of these variables, but included all soil variables and Molecricricket presence data in every model. In addition, the square of bare ground cover was systematically considered in our models in order to account for curvilinear relationships and to seek optimal habitat profile. Furthermore, we considered an interaction between vegetation height and amount of bare ground because the effect of vegetation height is expected to be more pronounced when ground vegetation cover is dense. In addition, we ran further models of Hoopoes' foraging occurrence in relation to soil variables and Molecricricket presence, but included only the best descriptors of habitat type and vegetation structure, as retained from the first step of the modelling.

Finally, we used hierarchical logistic regression models (GLMM) to test whether the presence of Molecricrickets at random locations was influenced by habitat type, soil type, and soil hardness. Hoopoe identity (ring number) was fitted as a random factor, which helped to reduce possible spatial dependence of the selected locations. Model ranking was also based on the AIC values.

All analyses were performed with the statistical package R (library glmmML; R Development Core Team, 2004). Confidence intervals for predictions were obtained by non-parametric bootstrapping (1000 replicates).

2. Results

In total, 14 males were radio-tagged, of which 13 were successfully tracked while foraging (Appendix 1). For each of these 13 males between 10 and 54 foraging locations were recorded (average: 42, median: 51), resulting in 546 foraging locations in total. At 113 locations (21%) we observed prey capture.

Home range size (minimum convex polygon) increased asymptotically with the number of observations. Because it was not certain whether the number of foraging locations was sufficient to obtain a reasonable estimate of home range size, we conducted a bootstrap analysis in which home range sizes were calculated as a function of an increasing number of randomly selected locations among the actual locations of an individual. This enabled us to estimate by eye that ca. 45 locations per individual were necessary to obtain a reasonable estimate of home range size (Appendix 2). Ten out of the 13 Hoopoes fulfilled this criterion. Individual home ranges of these 10 breeding males varied between 4.4 and 72.2 ha (mean \pm SD: 39.6 \pm 25.4 ha, Appendix 3).

The first modelling step of foraging site selection by Hoopoes in relation to habitat type and vegetation structure showed that habitat type, as well as the interaction between bare ground and vegetation height, were important (Table 2). All other models performed much worse (Table 2). The second modelling step of Hoopoe foraging, with respect to Molecricricket occurrence and soil characteristics, revealed that soil type, but not soil hardness, was important (Table 3). Molecricrickets appeared only in the second ranked model, which received only about half the support by the data compared to the best model (Table 3, evidence ratio: 0.24/0.56 = 0.43).

Based on the best model, we calculated predictions using bootstrapping. Preferred foraging habitat types were unpaved roads, road banks, and Rhone river banks, while grassland and cropland were clearly avoided (Fig. 1). No clear selection was found

Table 2

Model ranking for habitat selection of 13 Hoopoes using hierarchical logistic regression models (first analytical step). The model notation shows the fixed effects. The individual identity (ring number) is included as a random effect in all models. All models also contain soil type, soil hardness and Molecricricket presence as fixed effects. Further notation: x = interaction; Bare ground²: Bare ground + (Bare ground)² (i.e. linear and quadratic effects). Also shown are the deviance, the number of estimated parameters (*K*), Δ AIC (difference in AIC value in regard to best model), and the AIC weight. The models are ranked according to the AIC weight.

Model	Deviance	K	Δ AIC	AIC weight
Bare ground ² x Vegetation height + Habitat type	896.57	22	0.00	1.000
Bare ground ² + Habitat type + Vegetation height	924.09	20	23.52	0.000
Bare ground ² + Habitat type	941.60	19	39.03	0.000
Bare ground x Vegetation height + Habitat type	960.32	20	59.75	0.000
Bare ground ² x Vegetation height	988.83	14	76.26	0.000
Bare ground + Habitat type + Vegetation height	981.98	19	79.41	0.000
Bare ground + Habitat type	999.07	18	94.50	0.000
Bare ground ² + Vegetation height	1038.65	12	122.08	0.000
Bare ground ²	1044.42	11	125.85	0.000
Bare ground x Vegetation height	1100.10	12	138.53	0.000
Bare ground + Vegetation height	1155.87	11	237.30	0.000
Bare ground	1160.53	10	239.96	0.000
Habitat type + Vegetation height	1146.00	18	241.43	0.000
Habitat type	1179.02	17	272.45	0.000
Vegetation height	1301.84	10	381.27	0.000
Intercept	1318.56	9	395.99	0.000

for fruit tree plantations and vineyards. Fruit tree plantations were the dominant habitat at the study area, whilst the highly preferred habitat types (unpaved road, road and river banks) were rare (Fig. 1).

Foraging Hoopoes showed a very clear preference for patches where bare ground amounted to 60–70% (Fig. 2). Locations with less than about 50% or more than 80% bare ground were much less likely to be selected by foraging Hoopoes. In addition, Hoopoes preferred short, rather than long swards, although this effect was much less pronounced than the effect of bare ground (Fig. 2). The interaction between bare ground and vegetation height is also clearly recognizable in Fig. 2: with short swards, Hoopoes tolerated smaller areas of bare ground. Vegetation height became irrelevant for foraging when bare ground cover was greater than about 40%. Gravelly soils were clearly avoided, while there was no clear preference for either sandy or loamy soils (Fig. 3).

Table 3

Model ranking for habitat selection of 13 Hoopoes using hierarchical logistic regression models (second analytical step). The model notation shows the fixed effects. The individual identity (ring number) is included as a random effect in all models. All models also contain the following fixed effects: Bare ground² x Vegetation height + Habitat type (best model from Table 2), but this is not shown in the table. Also shown are the deviance, the number of estimated parameters (*K*), Δ AIC (difference in AIC value in regard to best model), and the AIC weight. The models are ranked according to the AIC weight.

Model	Deviance	K	Δ AIC	AIC weight
Soil type	902.28	17	0.00	0.558
Soil type + Molecricricket presence	901.96	18	1.68	0.241
Soil type + Soil hardness	897.10	21	2.82	0.136
Soil type + Soil hardness + Molecricricket presence	896.57	22	4.29	0.065
Intercept	936.09	15	29.82	0.000
Molecricricket presence	934.24	16	29.97	0.000
Soil hardness + Molecricricket presence	931.94	20	35.66	0.000
Soil hardness	934.19	19	35.91	0.000

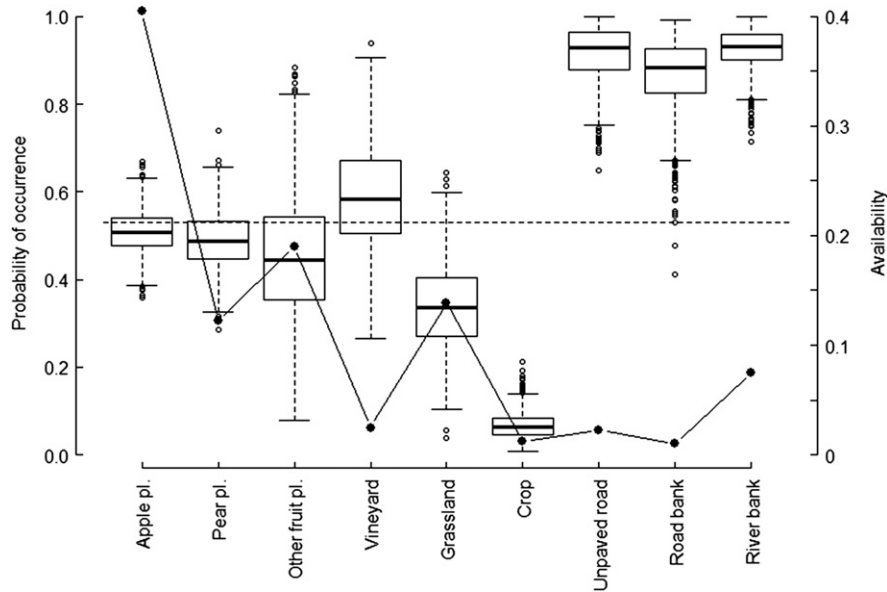


Fig. 1. Boxplot of the probability of occurrence of foraging Hoopoes in different habitat types with respect to the proportional availability of these habitat types in individual home ranges (closed dots). The estimations are based on the best model (Table 3) and calculated for sandy soil at an average amount of bare ground and vegetation height. Occurrence probabilities lower than 0.53 (broken line) indicate avoidance, probabilities larger than 0.53 indicate preference. Pl. = plantation of a fruit type.

Modelling Molecricricket occurrence at the randomly selected points within the Hoopoe home ranges showed that occurrence was affected by habitat type and soil hardness, but less so by soil type (Table 4). Molecricricket occurrence was very high in all fruit tree plantations, medium in vineyards and cropland, and very low in grassland (Fig. 4). Molecricricket presence was also low in unpaved roads, road and river banks, but the precision of these estimates was very low. Molecricricket occurrence was similar in very loose to medium soils, but then declined with increasing soil hardness (Fig. 4).

3. Discussion

Although this study took place during one year and included only 13 males, we are confident that our results reflect habitat selection patterns of Hoopoes in the study area. We have been studying Hoopoes there since the late 1990s and the year of the present radio-tracking study was not unusual in any respect, with

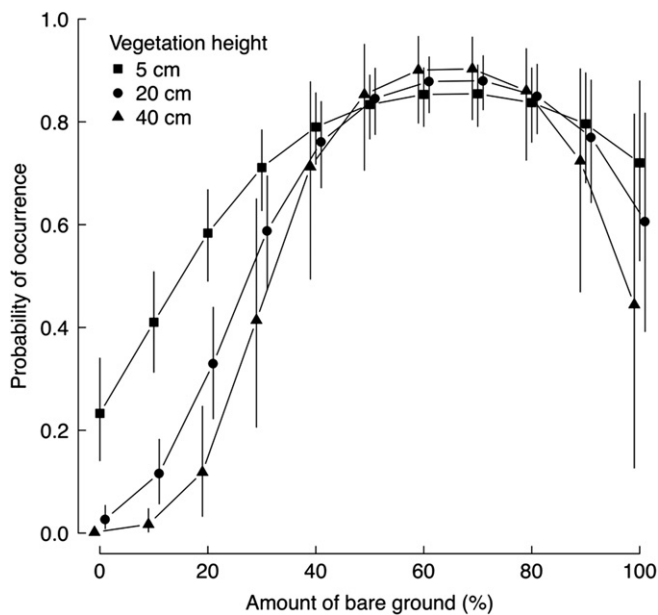


Fig. 2. Occurrence probability of Hoopoes in apple tree plantations with sandy soil in relation to the amount of bare ground and vegetation height. The estimations are based on the best model (Table 3). The vertical lines show the 95% confidence intervals.

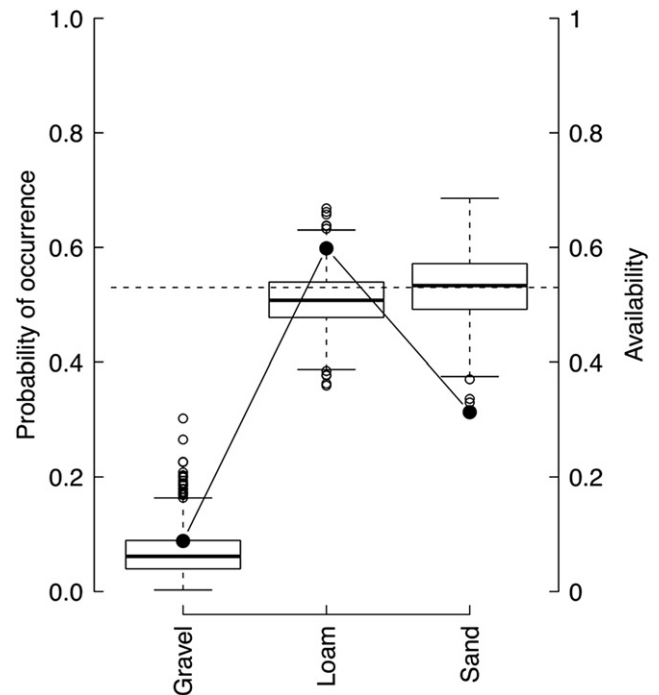


Fig. 3. Boxplot of the probability of occurrence of foraging Hoopoes in relation to different soil types. The estimations are based on the best model (Table 3) and calculated for vineyards at an average amount of bare ground and vegetation height. Occurrence probabilities lower than 0.53 (broken line) indicate avoidance, probabilities larger than 0.53 indicate preference.

Table 4

Model ranking for the presence of Molecrickets using hierarchical logistic regression models at 484 randomly selected locations. The model notation shows the fixed effects, while the random effect individual is included in all models but not shown. Also shown are the deviance, the number of estimated parameters (K), ΔAIC (difference in AIC value in regard to best model), and the AIC weight. The models are ranked according to the AIC weight.

Model	Deviance	K	ΔAIC	AIC weight
Soil hardness + Habitat	322.29	14	0.00	0.653
Soil type + Soil hardness + Habitat	319.79	16	1.50	0.308
Habitat	336.90	10	6.61	0.024
Soil type + Habitat	333.75	12	7.47	0.016
Soil type + Soil hardness	538.46	8	204.17	0.000
Soil hardness	550.26	6	211.97	0.000
Soil type	587.99	4	245.70	0.000
Intercept	607.01	2	260.72	0.000

radio-tagged individuals showing no apparent marginal behaviour. We also believe that the foraging patterns evidenced in this study apply to several Central European populations – many of which, like ours, rely on molecrickets as their staple diet (studies cited in Fournier and Arlettaz, 2001) – if not beyond this geographic area (Barbaro et al., 2008).

Our study illustrates that the typical foraging locations of Hoopoes are characterized by a sparse ground vegetation cover, a short vegetation, and a fine-grained, non-stony soil. Unpaved roads, as well as road banks and river banks, although rare in the study area, were the preferred foraging habitat types. In contrast, densely vegetated habitats such as grassland were avoided. Yet, as

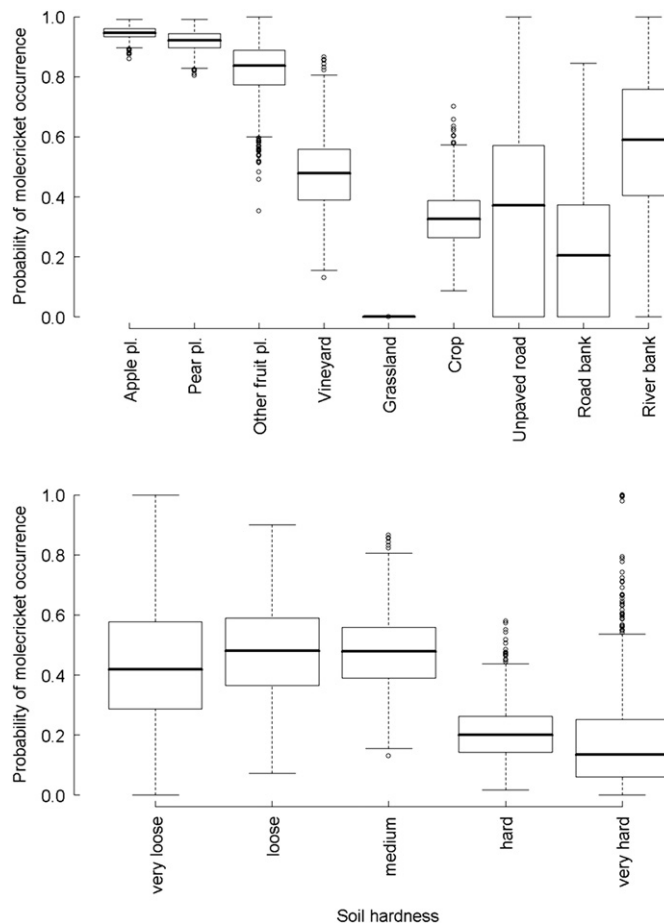


Fig. 4. Boxplot of the occurrence probabilities of Molecrickets in relation to habitat type (upper plot) and soil hardness (lower plot). The estimations are based on the best model (Table 4). Pl. = plantation of a fruit type.

the preferred habitat types only cover small areas they are unlikely to be the habitat types where Hoopoes capture most prey items. By contrast, fruit tree plantations dominate the landscape matrix and this habitat type was used according to its availability by foraging Hoopoes. It is thus likely that Hoopoes collect the largest amount of prey in fruit tree plantations, which is corroborated by numerous field observations. As such, this habitat type is of prime importance for the presence of Hoopoes in our study area.

The preference of foraging Hoopoes for patches of bare soil is most probably attributable to enhanced access to their main ground-dwelling prey, because Molecricet presence did not appear in the best model for foraging patch selection. Thus, accessibility of prey may play a more important role than its presence. Schaub et al. (2010) and Barbaro et al. (2008) also provided evidence that Hoopoe foraging patches are characterized by sparse vegetation, and similar conclusions concerning the importance of bare ground for foraging has been obtained for a range of insectivorous birds that search for their food on the ground (Perkins et al., 2000; Moorcroft et al., 2002; Atkinson et al., 2004; Devereux et al., 2006; Donald and Morris, 2005; Menz et al., 2009; Coudrain et al., 2010; Martinez et al., 2010; Weisshaupt et al., 2011; Arlettaz et al., 2011). The presence of bare ground thus appears as an important, common habitat feature for ground-foraging insectivorous farmland birds (Schaub et al., 2010). However, another aspect not investigated here might also explain the observed habitat selection pattern: Hoopoes may prefer to forage in bare and short grass habitats because this increases anti-predator vigilance (Schaub et al., 2010). We believe, however, that this situation does not apply in the study area. Farmland in the Rhone valley is too intensive to harbour populations of diurnal predators; the only local predator likely to prey on foraging Hoopoes is the Sparrowhawk *Accipiter nisus*. Though it frequently breeds on the woody slopes adjacent to the plain occupied by Hoopoes, it rarely visits nearby farmland during the breeding season.

Our model projections showed that an ideal foraging habitat profile consisted of 50–80% (optimum ~60–70%) of bare ground at the scale of a foraging patch. The vegetation configuration found along roads and rivers, as well as within fruit tree plantations, is close to that ideal habitat profile. In fruit tree plantations, the removal of ground vegetation at trunk base leaves about 30–60% of a parcel area bare most of the time (Fig. 5). In addition, the permanently vegetated strips between the tree rows are regularly mulched by farmers, which further enhances suitable conditions, since Hoopoes also show a preference for short grass, with a higher tolerance towards an absence of bare soil the shorter the grass. However, the presence of short grass is secondary compared to the availability of bare ground. This finding differs from the conclusion reached by Atkinson et al. (2005) that grass stalk shortness is the principal determinant of habitat selection in terrestrially feeding British songbirds. However, the wet climatic conditions in the UK, with its lush grass vegetation, are far from offering suitable breeding conditions to species with population strongholds in the Mediterranean, such as the Hoopoe. The avoidance of cropland, a habitat with extensive bare soil, may be explained by a low density of Molecrickets and of other large underground invertebrates. Ploughing destroys the gallery systems of Molecrickets. In addition, insufficient vegetation cover and lack of invertebrate biomass deprive Molecrickets of their principal food sources such as plant roots and earthworms (Baur et al., 2006). It thus seems that cropland in Central Europe may offer the only alternative habitat to (mostly) Mediterranean birds requesting bare ground if their main diet is epigeous, i.e. if prey is not living deep in the soil and can thus simply be picked up from the soil surface. The Stone curlew (*Burhinus oedipnemus*) in England is a good example (Green et al., 2000).



Fig. 5. Typical configuration of fruit tree plantations on the plain of the Rhone in Central Valais (SW Switzerland). Ground vegetation has been removed around the tree trunks (application of herbicides) to avoid competition for water between trees and ground vegetation. This provides accessible foraging patches for Hoopoes.

Hoopoes preferred to forage in sandy and loamy soils, but avoided gravelly soils, although soil hardness *per se* did not appear in the best model. The latter exclusion may be due to the situation that soil type, with its three gradations, already sufficiently characterizes Hoopoe's preference for a given substrate, masking the effect of the more subtle gradient of soil hardness. Hoopoes use their long curved bills to systematically probe the upper soil layers in search of mostly underground invertebrates. This foraging tactic requires relatively soft, penetrable soil substrates, as described for Common snipes (*Gallinago gallinago*, Green, 1988). The same holds for Molecrickets which need soft and medium soils in order to dig their underground galleries.

Soil softness played an important role for Molecrickets, with softer soils showing a higher probability of occurrence of Molecricket galleries. Soil moisture, which is likely to increase soil softness, may also have played a role in habitat selection, but this study did not quantify it. Further work is necessary to see whether the presence of a permanent ground water table, typical of alluvial plains, may enhance soil surface moisture, indirectly benefitting Molecrickets. It may be claimed that our model does not account for detection probability of Molecricket galleries, which is likely to vary with respect to ground vegetation cover. We believe, however, that the intensive search for galleries within a small area (circle of 20 m radius) greatly reduced the risk of missing them. In actual fact, the occurrence pattern of Molecrickets provides further support to the prey accessibility hypothesis, because Hoopoes forage extensively on habitat patches characterized by hard soils such as unpaved roads, which cannot harbour Molecrickets. Along unpaved roads, Hoopoes may have foraged for alternative prey (e.g. caterpillars, Fournier and Arlettaz, 2001; Arlettaz et al., 2010a) or benefitted from Molecrickets spilling over from adjacent fields, but our field observations provided no information on this point.

Our results have implications for the conservation of this species that provides a valuable ecosystem service by eating Molecrickets which are considered a pest in market vegetable production (Arlettaz et al., 2010b). It may well be that the absence of Hoopoes in today's modern farmland of Central Europe is caused more by unfavourable micro-habitat structure, especially dense ground vegetation cover affecting prey accessibility, than by prey abundance itself. The intensification of farming practices has generally led to extensive areas with a much denser ground vegetation cover than in the past, which may have contributed to the decline of terrestrial insectivorous birds such as the Hoopoe. If so, measures to

encourage open ground vegetation cover could prove a simple, beneficial management option to support many ground-foraging farmland birds (Schaub et al., 2010). In the case of Hoopoes, we suggest the creation of patches of bare ground in areas of Central Europe known to harbour good Molecricket populations, or other large underground invertebrates. Providing that the necessary habitat complementation, such as trees with cavities or nestboxes is available nearby (Barbaro et al., 2008), Hoopoes may readily react to these simple habitat management measures. The optimal farmland matrix for applying these measures probably consists of orchards, fruit tree plantations, vineyards and/or semi-open grassland, where patches of bare ground can be created. Our optimal thresholds for bare ground cover (60–70%) at the foraging patch scale may provide the necessary guidance for conservation and restoration action plans, although a smaller amount of bare ground is certainly sufficient at the level of the whole territory. The required structure can be achieved either through a moderate application of herbicides (conventional or biologically controlled production) or through a mechanical removal of grass (organic production). It is paradoxical that Hoopoe survival in commercial fruit tree plantations may depend on the combination of both relaxed management practices that provide good conditions for the survival of their main underground prey (Molecrickets) and chemical or mechanical reduction of the grass cover in order to provide access to crucial prey. The removal of the grass cover on a large proportion of the ground surface would further guarantee the existence of heterogeneous, patchy habitats for many other endangered terrestrial insectivorous birds (e.g. Weisshaupt et al., 2011; Arlettaz et al., 2011), if not other flora and fauna inhabiting farmland.

Acknowledgments

We would like to thank P. Mosimann-Kampe, M. Schaad, A. Siervo and F. Bontadina for their support in the field. P. Patthey, O. Roth, A. Aebischer, N. Signorell and M. Moser offered valuable help with data analyses and provided computer support. Aliko Buhayer corrected the English. We would also like to thank the Ministry of Environment for providing aerial photographs.

Appendix 1

Table A1

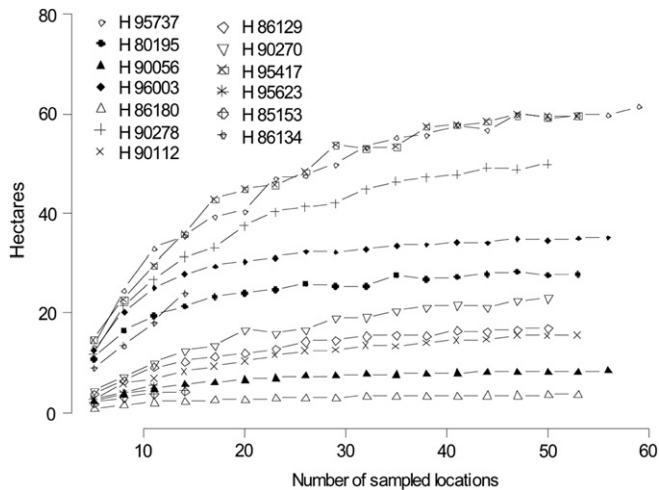
Details of the 14 Hoopoe males radio-tagged in Central Valais in 2006, with individual ring code, tagging time period, home range size (minimum convex polygon) and number of recorded visual locations.

Ring number	Radio-tagging period	Home range size (ha)	Number of visual locations
H 85153 ^a	3–11 May	–	11
H 80195	9–22 May	44.98	54
H 86134 ^a	10–14 May	–	10
H 90056	10–24 May	11.45	54
H 96003	16–28 May	52.71	52
H 95737	23 May – 2 June	72.24	51
H 90278 ^b	25–28 May	–	0
H 86180	31 May – 8 June	4.35	51
H 90278	30 June – 6 July	62.67	50
H 90112	6–12 July	23.61	48
H 95623 ^a	7 July	–	12
H 86129	14–19 July	19.19	51
H 90270	19–27 July	30.59	50
H 95417	21–26 July	74.24	52

^a No estimate of home range size due to insufficient data (see Methods).

^b This individual disappeared after tagging, but was later found again at a replacement brood although not radiotracked then.

Appendix 2. Home range size in relation to the number of available locations for each individual. 80 bootstrap replications were performed for each chosen number of locations.



Appendix 3. Example of the home range of Hoopoe male H 95417, which had the largest home range in our study. The nest-box A 114 is indicated by a star. Black line: minimum convex polygon; black dots: foraging locations; white dots: random locations; light circles: buffer zone of 20 m radius around the foraging locations.



References

Arlettaz, R., 1984. Ecologie d'une population de Huppes, *Upupa e. epops*, en Valais: répartition spatiale, biotopes et sites de nidification. *Nos Oiseaux* 37, 197–222.

Arlettaz, R., Reichlin, T.S., Schaad, M., Schaub, M., 2010a. Impact of weather and climate variation on Hoopoe reproductive ecology and population growth. *J. Ornithol.* 151, 889–899.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M., Braunisch, V., 2010b. From publications to public actions: when conservation biologists bridge the gap between research and implementation. *BioScience* 60, 835–842.

Arlettaz, R., Maurer, M.L., Mosimann-Kampe, P., Nusslé, S., Abadi, F., Schaub, M., 2011. New vineyard cultivation practices create patchy ground vegetation, favouring Woodlarks. *J. Ornithol.* doi 10.1007/s10336-011-0737-7.

Aschwanden, J., Birrer, S., Jenni, L., 2005. Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*)? *J. Ornithol.* 146, 279–286.

Atkinson, P.W., Buckingham, D., Morris, A.J., 2004. What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? *Ibis* 146 (Suppl. 2), 99–107.

Atkinson, P.W., Fuller, R.J., Vickery, J.A., Conway, G.J., Tallwin, J.R.B., Smith, R.E.N., Haysom, K.A., Ings, T.C., Asteraki, E.J., Brown, V.K., 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *J. Appl. Ecol.* 42, 932–942.

Barbaro, L., Couzi, L., Bretagnolle, V., Nezan, J., Vetillard, F., 2008. Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. *Biodivers. Conserv.* 17, 1073–1087.

Blanco, G., Tella, J.L., Torre, I., 1998. Traditional farming and key foraging habitats for chough *Pyrrhocorax pyrrhocorax* conservation in a Spanish pseudosteppe landscape. *J. Appl. Ecol.* 35, 232–239.

Bauer, H.-G., Berthold, P., 1997. *Die Brutvögel Mitteleuropas. Bestand und Gefährdung*, second ed. Aula, Wiesbaden.

Baur, B., Baur, H., Roesti, C., Roesti, D., Thorens, P., 2006. *Sauterelles, Grillons et Criquets de Suisse*. Editions Haupt, Berne.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188.

Boatman, N.D., Brickle, N.W., Hart, J.D., Milsom, T.P., Morris, A.J., Murray, A.W.A., Murray, K.A., Robertson, P.A., 2004. Evidence for the indirect effects of pesticides on farmland birds. *Ibis* 146 (Suppl. 2), 131–143.

Brambilla, M., Casale, F., Bergero, V., Bogliani, G., Crovetto, G.M., Falco, R., Roati, M., Negri, I., 2010. Glorious past, uncertain present, bad future? Assessing effects of land-use changes on habitat suitability for a threatened farmland bird species. *Biol. Cons.* 143, 2770–2778.

Britschgi, A., Spaar, R., Arlettaz, R., 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: lessons for overall Alpine meadowland management. *Biol. Conserv.* 130, 193–205.

Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer, New York.

Coudrain, V., Arlettaz, R., Schaub, M., 2010. Food or nesting place? Identifying factors limiting wryneck populations. *J. Ornithol.* 151, 867–880.

Devereux, C.L., Vickery, J.A., Fernández-Juricic, E., Krebs, J.R., Whittingham, M.J., 2006. Does sward density affect prey availability for grassland birds? *Agric. Ecosyst. Environ.* 117, 57–62.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Biol. Sci. Ser. B* 268, 25–29.

Donald, P.F., Morris, T.J., 2005. Saving the Sky Lark: new solutions for a declining farmland bird. *Br. Birds* 98, 570–578.

Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agric. Ecosyst. Environ.* 116, 189–196.

Douglas, D.J.T., Vickery, J.A., Benton, T.G., 2009. Improving the value of field margins as foraging habitat for farmland birds. *J. Appl. Ecol.* 46, 353–362.

Ehrlich, P.R., Pringle, R.M., 2008. Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. *Proc. Natl. Acad. Sci. U. S. A.* 105 (Suppl. 1), 11579–11586.

Fournier, J., Arlettaz, R., 2001. Food provision to nestlings in the Hoopoe *Upupa epops*: implications for the conservation of a small endangered population in the Swiss Alps. *Ibis* 143, 2–10.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* 9, 1425–1441.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., Jerde, C.L., 2006. Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898.

Green, R.E., 1988. Effects of environmental factors on the timing and success of breeding of common snipe *Gallinago gallinago* (Aves: Scolopacidae). *J. Appl. Ecol.* 25, 79–93.

Green, R.E., Tyler, G.A., Bowden, C.G.R., 2000. Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *J. Zool.* 250, 161–183.

Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., Wray, S., 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* 20, 97–123.

Hildén, O., 1965. Habitat selection in birds: a review. *Ann. Zool. Fenn.* 2, 53–75.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.

Martinez, N., Jenni, L., Wyss, E., Zbinden, N., 2010. Habitat structure versus food abundance: the importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*. *J. Ornithol.* 151, 297–307.

Menz, M.H.M., Mosimann-Kampe, P., Arlettaz, R., 2009. Foraging habitat selection in the last Ortolan Bunting *Emberiza hortulana* population in Switzerland: final lessons before extinction. *Ardea* 97, 323–333.

Moorcroft, D., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., 2002. The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *J. Appl. Ecol.* 39, 535–547.

Naef-Deaenzer, B., 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *J. Avian Biol.* 38, 404–407.

- Perkins, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Barnett, P.R., 2000. Habitat characteristics affecting use of lowland agricultural grassland by birds in winter. *Biol. Conserv.* 9, 279–294.
- R Development Core Team, 2004. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small passerines. *J. Field Ornithol.* 62, 335–337.
- Schaefer, J.A., Messier, F., 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18, 333–344.
- Schaub, M., 1996. Jagdverhalten und Zeitbudget von Rotkopfwürgern *Lanius senator* in der Nordwestschweiz. *J. Ornithol.* 137, 213–227.
- Schaub, M., Martinez, N., Tagmann-loset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLoS ONE* 5, e13115.
- Weisshaupt, N., Arlettaz, R., Reichlin, T.S., Tagmann-loset, A., Schaub, M., 2011. Habitat selection by foraging wrynecks *Jynx torquilla* during the breeding season: identifying the optimal habitat profile. *Bird Study* 58, 111–119.