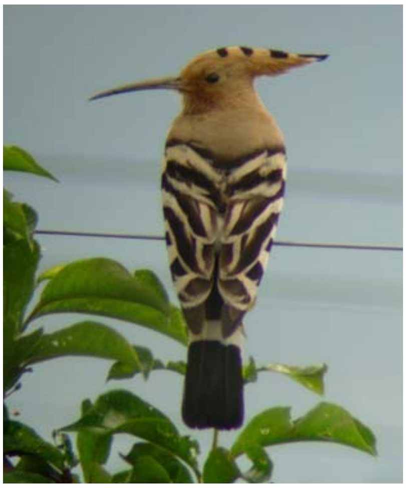
The importance of bare ground for terrestrially foraging insectivorous farmland birds: a case study of the endangered Hoopoes (*Upupa epops*)



Diplomarbeit

der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von
Aline Ioset
2007

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Abstract

1. Most farmland bird species have declined significantly throughout Central and Western Europe due to agricultural intensification. As a result of practices intensification, a denser ground vegetation cover has affected birds that search for food on the ground, reducing food accessibility by hampering bird's movements, even though food abundance tend to decrease with decreasing vegetation cover. Yet, for many ground-foraging species, quantitative assessments of optimal foraging habitat profiles such as favourite ground vegetation cover are lacking.

2. Habitat use by foraging hoopoes, a rare bird of central European ecosystems, was studied in Switzerland, testing whether ground vegetation cover is the most important factor of habitat selection, so as to identify optimal habitat profile.

3. The minimum adequate model (MAM) obtained from hierarchical binomial logistic regression analysis retained the following variables: habitat type, percentage of bare ground on the soil surface, grass management, herbicide application, soil type, and molecricket presence. Among habitat types there was a positive selection of unpaved roads, road banks, Rhone banks, vineyards, and orchards. Also positive selected were habitats with fresh cut grass and muddy or sandy ground. An optimum occurred in habitats with around 50-90% of bare ground cover. Avoided were grassland and habitats with gravely soil. Although the latter habitat is clearly unsuitable for molecrickets, prey accessibility may play a more important role in habitat selection than prey abundance.

4. Synthesis and applications: The hoopoe's preference for foraging habitats offering a high proportion of bare ground may be a characteristic shared by other typical terrestrial insectivorous birds. Farming practices ensuring microhabitats with reduced ground vegetation cover must be promoted for these threatened farmland birds.

Keywords: Hoopoe (*Upupa epops*), population decline, agricultural landscape, habitat selection, logistic regression.

1 Introduction

After dispersal or after coming back from migration a bird has first to decide where to settle for breeding (Huntingford 1984). Important cues for breeding habitat selection can be food availability, availability of nest sites, presence of mates, predation risk, or combinations thereof. Breeding habitat selection can be viewed as a hierarchical spatial process, from the choice of a potential area for breeding (home range), through to the use of certain areas within the home range (home range use) and to the choice of foraging grounds (habitat selection; Hildén 1965; Johnson 1980; Senft et al. 1987; Orians 1991; Schaefer and Messier 1995). A good breeding home range offers all kinds of resources (e.g. food, partners, nest sites, shelters from predators) in sufficient supply. If one of the required resources is lacking or insufficient, the reproductive output would be comparatively low, i.e. the home range is sub-optimal (Tye 1992, Pärt 2001). Because food is usually patchily distributed within a home range, different parts of the home range are not used evenly. Other resources being equal, places that offer high amount of food are visited more often than places where food is scarce or of lower quality. If food resources are dense and clumped, the size of the home range can be small, with an excellent costs/benefits ratio favouring reproductive output (Pasinelli et al. 2001). Properly understanding the link between patterns of food exploitation, reproductive output, and population dynamics necessitates to recognize fine-grained characteristics of foraging microhabitat as well as the tolerance of the species towards them. It is important to know the features of foraging places. Because amount of food and food accessibility are gradual (e.g. food density may vary from low to high, or accessibility may vary from difficult to easy), a combination of the two at different levels may be relevant. If the amount of food at a place is high, the bird may tolerate a more reduced accessibility than when the amount of food is low.

Many birds that inhabit open and semi-open landscapes search for food on the ground. For them, ground vegetation structure (grass height, density, and patchiness) plays a central role as regards food accessibility (Atkinson et al. 2005). As a result, several insectivorous bird species feeding on ground-dwelling arthropods can hardly survive in intensive farmland due to a too dense grass cover which precludes walking among the swards or accessing valuable food patches (Schaub

1996, Aschwanden *et al* 2005). Although food availability is one of the most important life history determinants, quantitative measures of the optimal ground vegetation structure at foraging grounds are lacking.

The hoopoe *Upupa epops* is a good example of a bird that searches food on the ground and whose populations have significantly declined throughout Europe in the last 50 years (Schaad *et al.*, in prep.). The main cause of decline has been attributed to habitat changes after agricultural intensification, which led to a loss of breeding sites (removal of old rotten trees rich in cavities), denser and higher vegetation in grassland (over-fertilization) and reduction of the number of large arthropods (insecticides) (Bauer & Berthold 1997).

Despite a well-documented preference for open and semi-open farmland, the precise microhabitat requirements of hoopoes are still poorly understood. This lack of information hampers the formulation of appropriate conservation action plans.

The main goal of this study was to assess patterns of habitat selection in an endangered population of hoopoes in Valais (Switzerland). By means of radio-tracking we assessed which habitat types and structures were preferred vs avoided, with particular attention to microhabitat features such as ground vegetation cover. Moreover, we tested whether food availability (molecrickets) was higher at foraging places than at places where no foraging activity was observed. This helped to understand whether food availability or food accessibility was more important, so as to formulate more accurate conservation action plans.

2 Material and Methods

2.1 Study site

This study was carried out in the canton of Valais, in the Upper Rhone valley (south-western Swiss Alps, 46°2’N 07°4’E, 460-468 m altitude) in summer 2006. Arlettaz (1984) and Fournier (1991) have described landscape, climate and vegetation of the area. Since the 1950s and 1960s, the plain is almost exclusively devoted to industrial farming, mostly fruit tree plantations with small trees. Vineyards extensively cover the lowest parts of the adjacent south-exposed foothill, but patches of natural habitat, including steppe grassland and xeric deciduous forests also remain (see photographs in Arlettaz 1984). Human settlements extend along the contact zone between the slope and the plain.

2.2 Radiotagging

Radio transmitters (Holohil Systems Ldt., model BD-2 P with activity sensor, 1.4 g, life span of 9 weeks) were fixed on the birds using a leg-loop harness (Rappole and Tipton 1991). The total length of the open loop was about 149 mm (Naef-Daenzer in review). Hoopoes were captured with mistnets or traps directly placed in front of the nest boxes. Radio-tracking took place when hoopoes were feeding their nestlings. Only males were radio-tracked because they are more active in food providing than females (Schaad *et al.*, in prep.). An overview of the radio-tracking activity is presented in Table 1.

2.3 *Radio-tracking and habitat mapping*

Two persons tried to collect as many visual observations as possible (goal 50 locations) of foraging hoopoes by applying the homing-in on the animal (Harris *et al.* 1990). Once located visually, a tagged bird’s foraging behaviour was monitored continuously with binoculars, and its foraging area was precisely delimited. These locations were marked in the field after the bird had left the place. Time, position, and whether the bird captured a prey or not, were recorded. To reduce spatio-temporal autocorrelation between the recorded locations, a new foraging location was considered only after a time gap of at least five minutes unless the bird interrupted its research and flew away. After a radio-tracking session of about two hours, habitat parameters were recorded in a radius of 1 m around the marked locations (Table 2). Habitat variables mapped were habitat type, vegetation structure (grass height, grass management, bare ground cover, and herbicide application), soil structure (soil type and soil hardness) and presence of molecrickets (Table 2). Presence of molecricket galleries was assed in a larger radius (20 m) than for habitat features (1 m).

Within each home range (minimum convex polygon drawn from radiolocations), we selected a number of random locations corresponding to the number of actual foraging locations and mapped the same habitat characteristics as at foraging locations. A buffer zone of 20 m around each observed foraging location was set so to avoid having random points falling too close to real locations.

2.4 Statistical analysis

To compare the habitat variables recorded at foraging locations and at random locations, binomial logistic regression analyses were used, where the dependent variable was “visited” or “random” and the independent variables were the habitat descriptors listed above (Table 2). Positive parameter estimates mean that this parameter positively affected the hoopoe’s foraging selection, whereas negative parameter estimates indicate that the corresponding habitat feature was avoided. To be able to analyse the data of all tracked individuals in a single model and to avoid pseudoreplication, a mixed logistic regression model was used (Gillies et all. 2006). The individual is then a random factor, with habitat variables being fixed factors. To avoid collinearity, only habitat variables with a correlation coefficient < $|0.7|$ were included in the analysis. All analyses were performed with the statistical package R (glmmML library; R Development Core Team 2004)

Modelling strategy

To avoid the classical drawbacks inherent to stepwise modelling (Whittingham et al. 2006) several models were defined a priori and compared on the basis of the Akaike’s Information Criterion (AIC; Burnham and Anderson 1998). Because the number of potential models was very large (different combinations of all explanatory variables) the selection procedure was conducted in several steps. We used the logical regrouping of the explanatory variables into three groups: habitat, vegetation (grass height, bare ground, grass management, and herbicide application), and ground (soil type, soil hardness, and presence of molecrickets). For each group, all possible combinations of the group-specific explanatory variables were used without considering the variables of the other groups. In a next step, the explanatory variables of the best model of each group were combined, and the best combination of these blocks was retained. In a further stage, we fitted a series of models in which each model contains all explanatory variables except one, which was removed alternatively by selecting among all available variables.

Since multi-level (>2) variables weaken statistical power in binomial regression modelling, by inflating degrees of freedom, we tested whether the number of levels of explanatory variables originally consisting of more than two levels (habitat type, soil type, soil hardness and grass management) could be reduced. Because foraging location selection may vary according to food abundance we finally tested whether the interactions between presence of molecrickets and the other variables were important. This procedure resulted in a minimum adequate model (MAM). The parameter estimates of the MAM were used to show the impact of explanatory variables on the choice of foraging places.

Impact of habitat on molecricket availability

We used logistic regression to test whether presence or absence of molecricket at random locations were influenced by the habitat variables (habitat type, bare ground, grass height, herbicide use, grass cut, soil type and soil hardness; Table 1). The AIC value was also the criterion for the selection of the best model.

Home range sizes

We calculated the home range size of each individual as the Minimum Convex Polygon method (Mohr 1947), and tested whether the home range size negatively correlated with the local density of the breeding pairs. This density was calculated as the Mean Neighbour Distance (MND; Leippert 2005), which is the average distance of a given breeding site to all other active breeding sites during the breeding season.

3 Results

In total, 14 birds were radio-tagged (Table 1). One bird yielded no location, because the brood failed at an early stage. The analysis is then based on 13 individuals. Between 10 and 56 foraging locations could be recorded for each individual (average: 42.54, median: 51), resulting in 553 foraging locations in total. Out of 553 locations, 113 resulted in actual prey captures that could be directly observed, providing strong evidence that our locations concerned primarily foraging locations.

As all correlations between the various habitat variables were lower than $|0.5|$, all variables could be retained for analysis.

Hoopoe foraging places

Modelling the habitat variables within the three groups of descriptors (habitat type, vegetation and ground structures) showed that all variables were important with the exception of grass height (Table 3B, model 14). The combinations of the three groups (two by two and all three together, giving four possibilities) revealed that all three groups were important and thus were retained (Table 3D, model 28). Removing explanatory variables one by one showed that soil hardness could be eliminated (Table 3E, model 29).

We then tested whether the foraging locations differed from random locations with respect to specific habitat categories. First, there was no differential preference for the various orchard types (AIC of the model with different orchard types: 831.2; AIC of the model without different orchard types: 827.5). In addition, there was no differential preference for the habitat types woodland, cropland, vegetable garden, and built/aquatic habitats (AIC of the model with the different types: 827.5; AIC of the model without these different types: 823). Level reduction with the other habitat variables (unpaved road, road bank, vineyards, Rhone bank, and grassland) did not lead to a better model. The levels of the soil type could also be reduced to gravel and muddy/sandy (AIC: 821.1). Soil hardness was already eliminated in a former step.

At the next step, only herbicide application was found to interact with molecricket gallery finding: AIC 790.7 (Table 4). In contrast, no interaction was found between molecricket presence and bare ground, soil type, habitat type, or grass cut. The parameter estimates of the minimum adequate model (MAM) are shown in Table 5.

Parameter estimates

Based on the MAM (Table 5), hoopoes tend to select foraging places preferably on unpaved roads, road banks, Rhone bank, in vineyards, and orchards (Fig. 1). Built/aquatic habitats were avoided, while grassland was neutral. The availability of the different habitat types was dominated by orchards and unsuitable habitats; the highly preferred habitat type, i.e. unpaved road, was very rare (Fig. 1). The microhabitat structure of the selected foraging places was characterized by the following relationships: Hoopoes preferred foraging locations with around 70% of open ground (Fig. 2a), that were either freshly mown (Fig. 2c), or muddy or sandy (Fig. 2e), and where molecricket galleries occurred in the absence of herbicide application (Fig. 2h). Indeed, if molecricket galleries do occur no herbicide use is better. If no molecricket is detected, the probability to observe a hoopoe is higher at places where herbicide is used. Avoided were locations with gravel, places that were not regularly mown, and that either had no bare ground or were fully bare.

Does the selection of foraging place depend on ground prey accessibility or on prey density?

Five hundreds fifty-three (random) locations were suitable for this test. We found that the probability to find molecricket galleries depended mostly on habitat type and on herbicide application (Table 6). The occurrence probability was highest in orchards (all types) followed by vegetable gardens, Rhone bank and vineyards (Fig. 1). In all other habitat types the occurrence probability of molecrickets was much lower. Freshly mown and early cut grass raise the probability to find molecricket galleries (Fig. 2c). There was a positive effect of herbicide application on the probability to find molecricket galleries (Fig. 2d). Soil hardness seems to play a more important role in molecrickets than in hoopoes, as middle soil hardness increases the probability to find molecricket galleries (Fig. 2f).

Home range area

Because the home range size increases asymptotically with the number of observations, bootstrap in the program ArcView was used to estimate how many locations were necessary to estimate the home range size reliably. As more than 46 locations per individual were needed, we could use 10 hoopoes for this analysis. Home ranges averaged 39.6 ha (SD: 25.4 ha; range 4.4 – 72.2 ha). 102 nesting sites were identified during the breeding season 2006. Home range size was not affected by brood density (test statistics, df: 8, p = 0.6).

4 Discussion

The favourite foraging habitats of hoopoes in the upper Rhone valley were unpaved roads, road banks, Rhone bank, vineyards, and orchards. Avoided were unsuitable foraging habitats such as human settlements, woodlands, and croplands. An optimal foraging habitat profile consisted of 50 – 90 % (optimum 70 %) bare ground, mown grass, muddy or sandy soils, and presence of molecrickets combined with no herbicide application. Very low and high vegetation density, not mown grass, and gravely soils negatively impacted upon foraging habitat selection.

The preference for unpaved roads, road banks, and Rhone banks is particularly striking because their availability is extremely low. In contrast, orchards appeared much less selected although they made up almost 50 % of the overall habitat availability within all home ranges pooled together. This apparent low selection is mostly artefactual given the high prevalence of that habitat type.

A principal reason for the attractiveness of these preferred habitats may be their patchy configuration. Indeed, the most important parameter among the vegetation variables was clearly the fraction of bare ground (with a quadratic relationship), showing a distinct peak around 70 %. Foraging hoopoes like to walk on low ground vegetation, bare ground, sandy soil, or even on tarred roads. At a local scale, grass height does not play a significant role in foraging habitat selection as long as there is enough bare ground to permit walking around stalks. Extensive grassland is not appreciated at all. This finding contrasts with the study by Atkinson et al. (2005) who established that grass stalks height was the most important determinant of insectivorous terrestrial songbirds. As the intensification of farming practices has generally led to large areas with a denser ground vegetation cover, this may have contributed to the decline of terrestrial insectivorous birds (Bechard 1982) such as the hoopoe.

Woodland, cropland, and vegetable garden were classified as not suitable habitats. We can imagine that cropland in general is not attractive, both because of exposure to predators and lower arthropod food availability in regularly ploughed soils. This may be especially crucial as regards molecrickets, hoopoes’ favourite prey, which dig a complex network of galleries under the soil surface. Although scarce within our hoopoe home ranges, local forests are riparian stands with a dense understorey hampering access to the ground.

Hoopoes avoid gravely soils but seem to be indifferent to a muddy or sandy soil. Soil hardness thus does not have a notable importance. We may expect, however, that very hard soil is difficult to penetrate for a hoopoe bill, and difficult to drill galleries in for molecrickets, whilst too soft soils may cause molecricket gallery networks to collapse. The presence of molecricket (estimated though their galleries) seems to have a positive effect on the probability to find a hoopoe. Interesting is the significant interaction found between herbicide application and molecricket gallery occurrence. Indeed, if molecricket galleries are found, no herbicide application appears to favour hoopoes' occurrence, whereas where no gallery is found, the probability to observe hoopoes will be higher in places with herbicide application. We believe, however, that this strange pattern can be explained in terms of molecricket gallery detection probability, which is largely habitat dependent (in this case detectability is higher where herbicides are applied).

Our estimation of selection patterns can be considered as conservative since random locations may in the end have been as suitable as actual foraging locations, a problem called „contamination" by Johnson *et al.* (2006). The same author also demonstrated that, although contamination reduces the magnitude of the coefficients, this diminution in the contrast of the underlying ecological signal does not exceeded sampling variation if more than 20 % of the observed locations were confirmed use locations. Although the contamination level is not known in our case, our sampling deign was probably robust enough in this respect.

Molecrickets are not evenly distributed and their occurrence pattern correlates with habitat type, soil hardness, and soil type (granulometry). These variables are probably not affected by different detection probabilities among the different levels within variables. On the other hand, vegetation variables could influence detection probability of molecricket galleries, negatively affecting it when the grass is dense or high. Indeed, it is unlikely that there are effectively fewer molecrickets where the grass is dense and high as these orthopterans feed on plant roots and other soil organisms such as earthworms (Baur *et al.* 2006).

The occurrence probability of molecrickets and foraging hoopoes showed very similar patterns (Figs. 1 and 2). However, due to the problem of detectability of molecrickets mentioned above, it is difficult to conclude whether it is prey abundance or prey accessibility, which is more crucial for the selection of foraging ground by hoopoes. Yet, the over-exploitation, compared to availability, of unpaved roads and banks of tarred roads would suggest that prey accessibility is more important than prey occurrence. The preference for mown grass also supports this view. Soil hardness seems to play a more important role for molecrickets than for hoopoes, as middle hardness increases the occurrence probability of molecricket galleries. This again supports the prey accessibility hypothesis, because hoopoes forage in hard and lose soils although the probability of finding molecricket galleries at these places is lower. We can also notice the positive effect of herbicide application on the probability to find molecricket galleries. If the assumption that herbicide application does not influence the distribution of molecricket is true (a detectability bias), this positive effect also would support the importance of accessibility. Indeed, the second factor explaining hoopoe preferences was herbicide application in the absence of molecricket galleries. But preferred over all is when there are molecricket galleries and no herbicide is applied. This interaction supports the priority of prey abundance. The irrelevance of grass height and the crucial importance of bare ground can be interpreted in two ways. First, if we assume that there is no difference in the molecricket gallery distribution between sites with middle and high grass height and/or cover, hoopoes should systematically choose middle grass height and middle bare ground, which enhance prey accessibility. Second, the low probability to find hoopoes and molecricket galleries at low grass height and low vegetation cover is likely to be due to low molecricket density where too few roots are available to feed on.

The aim of this study was to draw an optimal foraging habitat profile for the hoopoe so as to propose targeted habitat management measures for species conservation. The availability of bare ground (optimum around 50 – 90 % with peak at 70 %) is the most important feature of hoopoe's foraging habitat. Low vegetation cover on the ground is often achieved in intensively cultivated orchards and vineyards, either through the application of herbicides (Conventional or biological control production) or through a mechanic removal of grass along tree rows (bio-organic production). Another technique used in both farming regimes is frequent mowing of grass, which, when vegetation is kept very short, offers another suitable structure for optimal foraging. The combination of these various agricultural practices also warrants the existence of an heterogeneous, patchy habitat, which may well play a crucial role for terrestrial insectivorous birds, as illustrated here for he hoopoe.

5 Acknowledgments

I am grateful to Prof. Dr. Raphaël Arlettaz for his supervision and for communicating his knowledge about the species of interest and to Dr. Michael Schaub for his co-supervision and his grand support during the fieldwork and the statistical analysis. I specially thank Nadja Weisshaupt for her precious collaboration during all the study time. Thanks also to Paul Mosimann for showing how to install the transmitter on the birds, to Tomas Reichlin and Michael Schaad for catching the birds, to Dr. Fabio Bontadina for his advices in radio telemetry, to Antoine Sierro for showing how to control the nest boxes and to the Swiss Ornithological Institute for the material support and the allowance to ring hoopoes. Thanks as well to Dr. Patrick Patthey for GIS aid, to Olivier Roth for the access to the library, to Dr. Adrian Aebischer, and Natalina Signorell for their helpful advises and to Marcel Moser for PC-support. Thanks also to Bundesamt für Umwelt BAFU for providing the aerial photographs. Finally, I want to cordially thank my family and my fiancé, Christoph Tagmann, as well as my friends for their remarkable encouragement.

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Table 1: Overview of radio-tracking activity in 14 hoopoe males.

Ring number	Nest box	Radio-tracking period	Number of visual locations	Home range size (ha)	Reason for incomplete data
H 85153	A35	03.05 – 11.05.2006	13	Insufficient data	Predated (06.05.2006)
H 80195	A42	09.05 – 22.05.2006	54	44.98	
H 86134	B4	10.05 – 14.05.2006	10	Insufficient data	Bad signal
H 90056	B35	10.05 – 24 .05.2006	56	11.45	
H 96003	C38	16.05 – 28.05.2006	52	52.71	
H 95737	D49	23.05 – 02.06.2006	51	72.24	
H 90278	B36	25.05 – 28.05.2006	0	Insufficient data	Clutch abandoned (26.05.2006)
H 86180	D55	31.05 – 08.06.2006	51	4.35	
H 90278	B48	30.06 – 06.07.2006	51	62.67	
H 90112	D21	06.07 – 12.07.2006	50	23.61	
H 95623	A30	07.07 - 07.07.2006	12	Insufficient data	Bird disappeared (08.07.2006)
H 86129	A05	14.07 – 19.07.2006	51	19.19	
H 90270	A110	19.07 – 27.07.2206	50	30.59	
H 95417	A114	21.07 – 26.07.2006	52	74.24	
		Total:	553	Average: 39.60 ha	

Table 2: Variables recorded for the study of habitat selection with format and levels (if categorical).

Variables	Format	Levels
Habitat type	Categorical	Apple, pear, other orchard, cropland, vegetable garden, unpaved road, road bank, vineyard, Rhone bank, grassland, woodland, built/aquatic
Grass height	Continuous (cm)	
Grass cut	Categorical	Fresh, old, not cut
Bare ground	Continuous (%)	
Herbicide	Categorical	Yes, no
Molecricket presence	Categorical	Yes, no
Soil type	Categorical	Muddy, sandy, gravel
Soil hardness	Categorical	1 to 5, 1 is very loose (e.g. sand) and 5 is very hard

Table 3: Comparison of the different models tested. Firstly, the best variable combination within the three groups (habitat type, vegetation structure and soil structure) was identified. Secondly, the combinations of the resulting three best models are assesses. Finally, each variable was once removed. The best model at each modelling step is bold printed. (D.f. = degrees of freedom) 1: the corresponding variable is included in the model, 0: the corresponding variable is not included in the model.

	Habitat variables										
Model number	Habitat type	Bare ground^2	Grass height	Grass cut	Herbicide	Molecricket presence	Soil type	Soil hardness	D.f.	Deviance	AIC
A. Habitat											
1	1	0	0	0	0	0	0	0	965	1157	1179
B. Vegetation											
2	0	1	0	0	0	0	0	0	972	1034	1042
3	0	0	1	0	0	0	0	0	973	1325	1331
4	0	0	0	1	0	0	0	0	971	1324	1334
5	0	0	0	0	1	0	0	0	973	1345	1351
6	0	1	1	0	0	0	0	0	970	1028	1038
7	0	1	0	1	0	0	0	0	968	985.6	999.6
8	0	1	0	0	1	0	0	0	970	998.3	1008
9	0	0	1	1	0	0	0	0	969	1315	1327
10	0	0	0	1	1	0	0	0	969	1314	1326
11	0	0	1	0	1	0	0	0	971	1312	1320
12	0	1	1	1	0	0	0	0	967	984.1	1000
13	0	1	1	0	1	0	0	0	969	985.5	997.5
14	**0**	**1**	**0**	**1**	**1**	**0**	**0**	**0**	**967**	**936.4**	**952.4**
15	0	0	1	1	1	0	0	0	968	1302	1316
16	0	1	1	1	1	0	0	0	966	936.1	954.1

Table 3 (continued)

	Habitat variables										
Model number	Habitat type	Bare ground^2	Grass height	Grass cut	Herbicide	Molecricket gallery	Soil type	Soil hardness	D.f.	Deviance	AIC
C. Ground											
17	0	0	0	0	0	1	0	0	972	1285	1291
18	0	0	0	0	0	0	1	0	972	1330	1338
19	0	0	0	0	0	0	0	1	970	1315	1327
20	0	0	0	0	0	1	1	0	970	1267	1277
21	0	0	0	0	0	1	0	1	968	1260	1274
23	0	0	0	0	0	0	1	1	967	1301	1317
24	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**966**	**1248**	**1266**
D.											
25	1	1	0	1	1	0	0	0	956	836.6	874.6
26	0	1	0	1	1	1	1	1	960	895.4	925.4
27	1	0	0	0	0	1	1	1	955	1112	1152
28	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**1**	**949**	**779.2**	**831.2**
E. Elimination of one											
29	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**0**	**953**	**782.8**	**826.8**
30	1	1	0	1	1	1	0	1	951	831.3	879.3
30	1	1	0	1	1	0	1	1	949	781.8	831.8
32	1	1	0	1	0	1	1	1	950	848.3	898.3
33	1	1	0	0	1	1	1	1	952	810.5	856.5
34	1	0	0	1	1	1	1	1	951	1046	1094
35	0	1	0	1	1	1	1	1	960	895.4	925.4

Table 4: Results of logistic regression tests for interaction between molecricket finding and the other habitat variables remaining after level reduction test.

Interaction of molecricket finding with	**D.f.**	**Deviance**	**AIC**
Habitat	953	776	820
Bare ground	958	783.6	817.6
Grass cut	956	781.9	819.9
Herbicide use	**958**	**756.7**	**790.7**
Soil type	958	784.6	818.6
Model without interaction	959	784.7	816.7

Table 5: Parameter estimates of the habitat variables with the minimum adequate model. Given are the point estimates, the standard errors, the z-statistics and the p-value. The intercept refers to habitat type “orchard”, to no herbicide use, to no grass cut, to absence of molecrickets and to a gravel containing soil.

Habitat variables	Estimates	Standard error	z	Pr(>|z|)
Intercept	-6.801115	0.7304519	-9.3108	< 0.001
Habitat type (Built/aquatic)	-3.409187	0.5662821	-6.0203	< 0.001
Habitat type (Unpaved road)	3.010167	0.6437535	4.6760	< 0.001
Habitat type (Grassland)	-0.498820	0.5224931	-0.9547	0.340
Habitat type (Road side)	1.908144	0.6307416	3.0252	0.003
Habitat type (Rhone bank)	1.081955	0.6332132	1.7087	0.087
Habitat type (Vineyard)	0.838669	0.4961886	1.6902	0.091
Bare ground	0.152712	0.0139821	10.9220	< 0.001
Bare ground^2	-0.001125	0.0001432	-7.8620	< 0.001
Herbicide (yes)	0.417114	0.5548176	0.7518	0.452
Grass cut (yes)	0.946754	0.5166471	1.8325	0.067
Grass cut (yes fresh)	1.851924	0.3373666	5.4894	< 0.001
Grass cut (yes old)	0.671543	0.2733722	2.4565	0.014
Molecricket presence (yes)	1.514189	0.3494960	4.3325	< 0.001
Soil type (muddy/sandy)	3.371826	0.5759395	5.8545	< 0.001
Herbicide (yes) x Molecricket gallery (yes)	-3.002637	0.5921152	-5.0710	< 0.001

Table 6: Logistic regression models for the occurrence of molecrickets in relation to different habitat variables. Shown are the degrees of freedom, the residual deviance and AIC value for each model.

Habitat variables	**D.f.**	**Deviance**	**AIC**
Habitat type	443	307.39	331.39
Herbicide use	453	357.52	361.52
Grass cut	451	544.89	552.89
Soil hardness	450	546.77	556.77
Grass height	452	499.27	505.27
Bare ground	453	590.38	594.38
Soil type	452	602.01	608.00
0-Model	454	616.27	618.27

Figure captions

Figure 1: Occurrence probability of both foraging hoopoes (based on best model predictions for freshly mown grass, bare ground 70%, no herbicide application, muddy/sandy soils, and presence of molecricket galleries) and molecrickets (logistic regression) in different habitat types (left axis), compared to relative availability of habitat types within the home range of 10 hoopoes with sufficient data (right axis).

Figure 2: Occurrence probability of hoopoes and molecrickets according to different ground vegetation structures and soil variables (within orchards, for freshly mown grass, when bare ground is fixed to 70%, in the absence of herbicide application, when the soil is muddy/sandy, and molecricket galleries are recorded, if not mentioned otherwise). (a) Probability to find a foraging hoopoe, respectively molecrickets, at places with different bare ground percentages. (b) Probability to find molecrickets at places with different grass height (cm). (c) Probability to find a foraging hoopoe, respectively molecrickets, at places with different grass management (mown, freshly mown, mown earlier, and not mown). (d) Probability to find foraging hoopoes, respectively molecrickets, at places with and without herbicide application. (e) Probability to find a foraging hoopoe, respectively molecrickets, in different soil types (gravel vs mud or sand). (f) Probability to find molecrickets at places with different soil hardness (from very soft to very hard). (g) Probability to find a foraging hoopoe at places with or without molecrickets. (h) Probability that a hoopoe searches for food with respect to different management types vs prey occurrence probability.

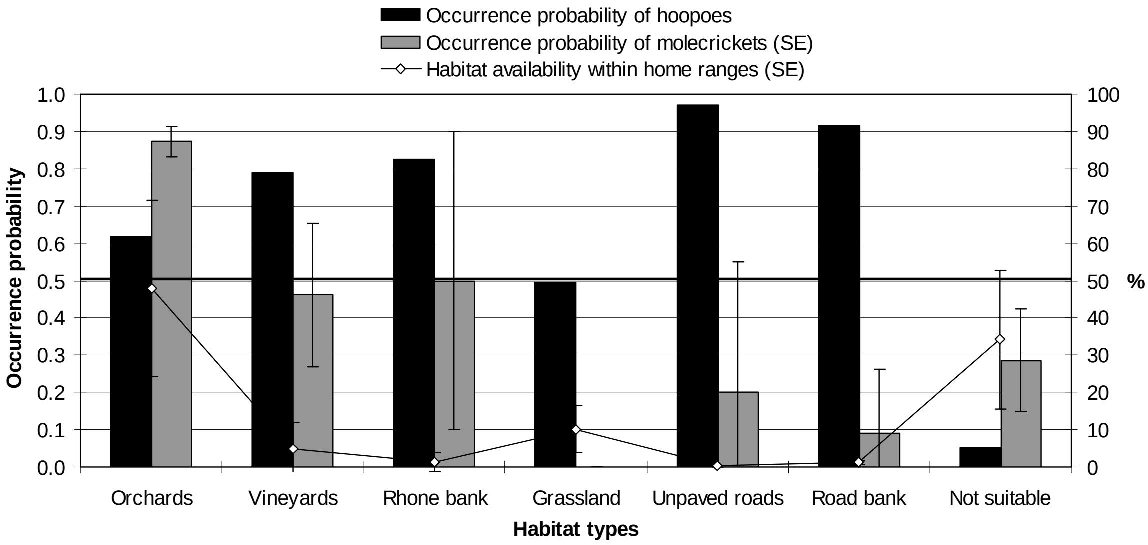

Occurrence probability of hoopoes
Occurrence probability of molecrickets (SE)
Habitat availability within home ranges (SE)
Occurrence probability
%
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
100
90
80
70
60
50
40
30
20
10
0
Orchards
Vineyards
Rhone bank
Grassland
Unpaved roads
Road bank
Not suitable
Habitat types

Figure 1

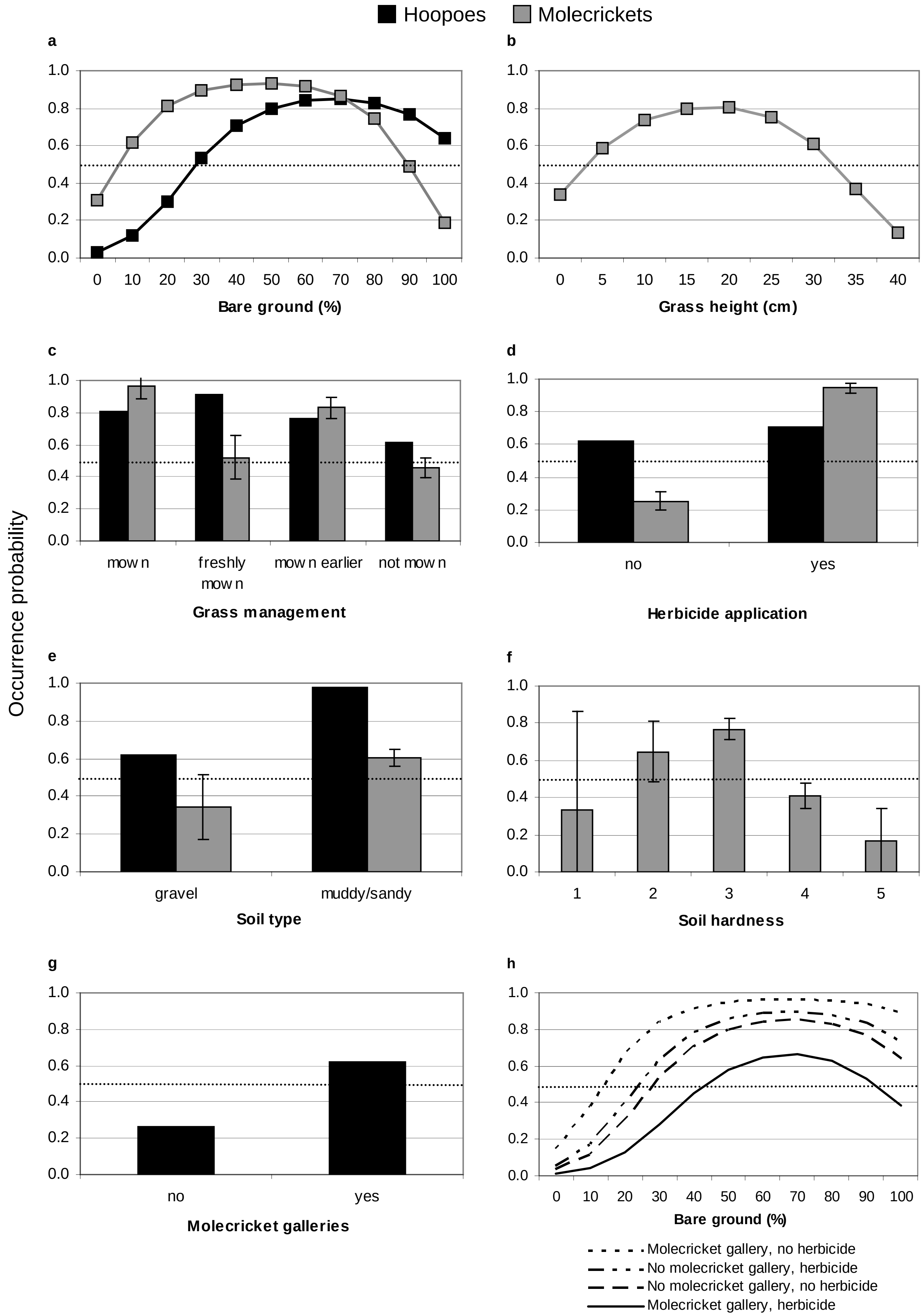
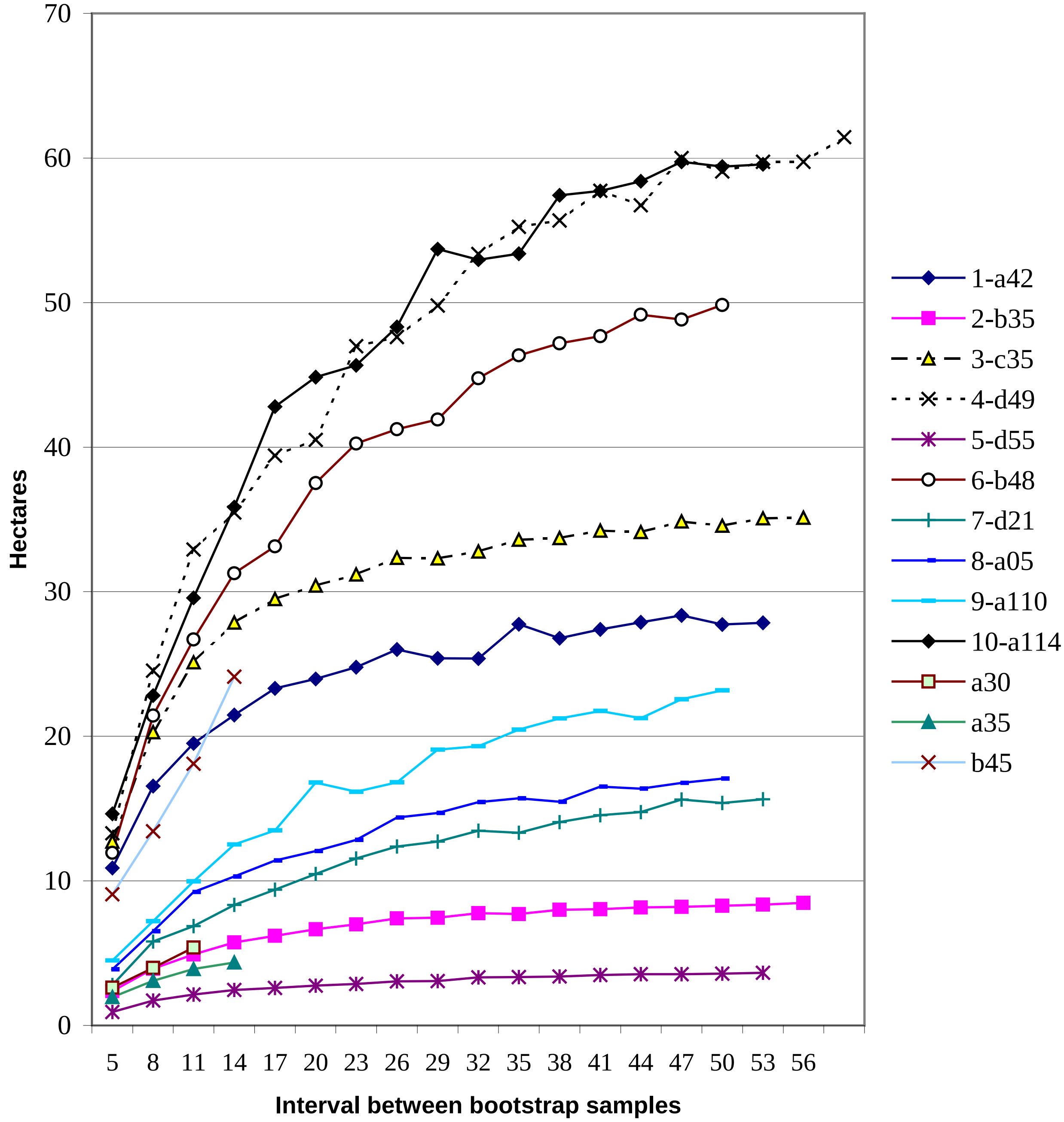

Hoopoes
Molecrickets
Occurrence probability
a
Bare ground (%)
b
Grass height (cm)
c
mown
freshly mown
mown earlier
not mown
Grass management
d
no
yes
Herbicide application
e
gravel
muddy/sandy
Soil type
f
Soil hardness
g
no
yes
Molecricket galleries
h
Bare ground (%)
Molecricket gallery, no herbicide
No molecricket gallery, herbicide
No molecricket gallery, no herbicide
Molecricket gallery, herbicide

Figure 2

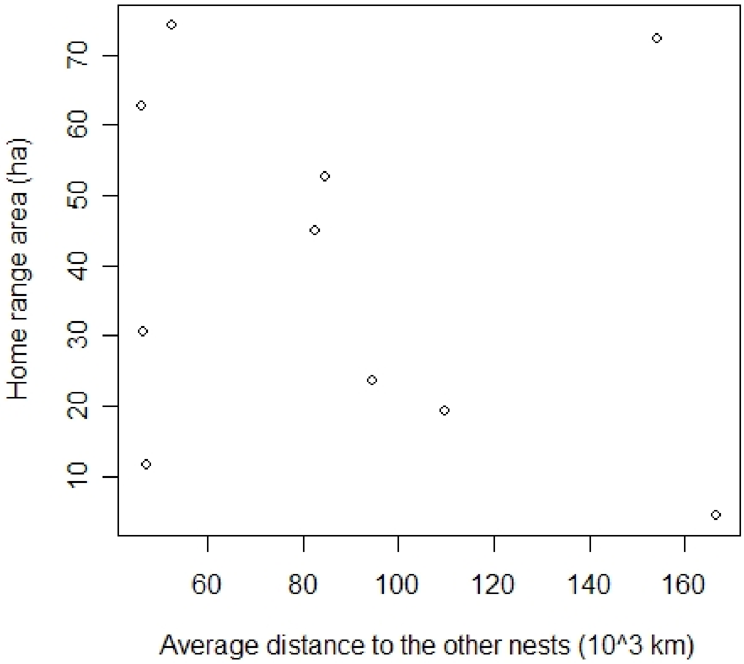
Appendix 1: Home range size in relation to the number of available locations for each individual. 80 bootstrap replications were performed for each chosen number of locations.



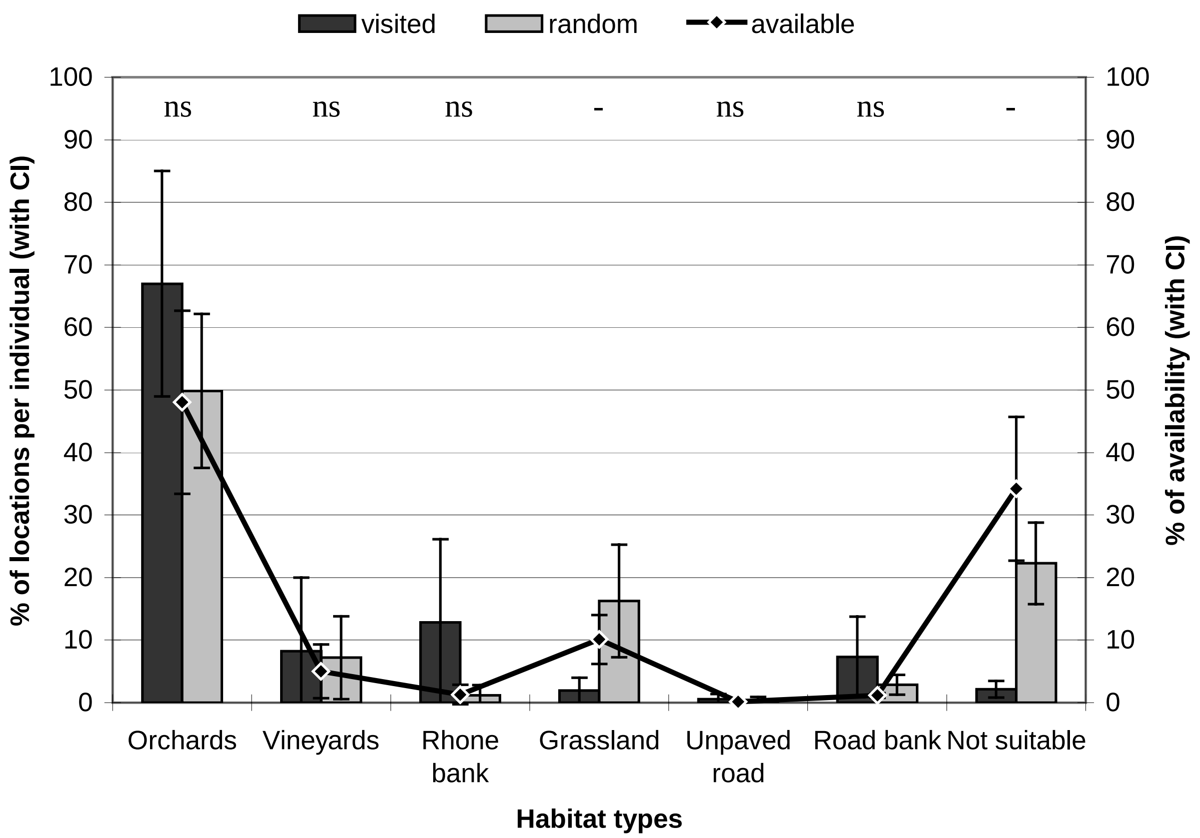
Appendix 2: Home range measurements (n = 10)

	Average	**Standard deviation**
Area (ha)	39.60	25.35
Maximal distance to nest box (m)	839.39	283.20
Maximal distance within the home range (m)	1134.83	400.12

Appendix 3: Linear regression between the home range sizes of 10 hoopoes with enough data and the hoopoe brood density (expressed as the average distance to the other occupied nest boxes) using the statistical package R (lm library; R Development Core Team (2004); $p = 0.60$).



Appendix 4: Comparison of habitat type use vs availability for 13 individuals using confidence intervals (CI; Neu et al. 1974). The results of the mixed model analysis (visited and random; left axis) are compared with the available area of the habitat types (calculated with ArcView using aerial photographs; right axis).



Appendix 5: Example of a home range (nest box A 114). Black line: Minimum Convex Polygon, black dots: visited locations, white dots: random locations, light circles: buffer zone of 20 m radius around the visited locations.