Breeding territory occupancy in hoopoes: governed by habitat quality or phenotypic traits?

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ABSTRACT

1. Breeding territory selection has such a strong impact on fitness that individuals aim at choosing territories offering the most appropriate combination of resources. Assuming stable environmental conditions, the frequency of utilization of a territory over time (i.e. its occupancy rate) may indirectly inform about its quality, which might be crucial for spatially-explicit conservation management.

2. We studied the relationships between territory occupancy rate (2002-2009), habitat characteristics, prey availability (molecrickets), reproductive success, age and phenotypic traits (size, body mass, tail pattern) of territory holders in a hoopoe (*Upupa epops* L.) population in order to document habitat conservation management. Based on ideal-free distribution (IFD) theory, we predicted an absence of relationship between pairs' reproductive success and habitat occupancy and characteristics due to adjustment of local breeding density to local prey availability («habitat matching»). Based on the despotic distribution model, we predicted that phenotypically dominant individuals would occur in high-quality, densely inhabited areas.

3. Territory selection was non-random, with high quality territories being settled earlier in the season. Reproductive success did not differ strikingly with respect to territory occupancy: there was a weak, uncertain trend towards higher productivity in more frequently occupied, i.e. better quality habitats. Territory occupancy rate also appeared unrelated to habitat characteristics and molecrickets' availability. Both findings are in accordance with the IFD predictions. Male phenotypes in often occupied territories showed traits expressing dominance (i.e. larger body size and

mass, and older age) compared to males in less often occupied territories. In contrast, morphological traits of females were not related to territory occupancy. Therefore territory choice and defense seem to be essentially a male's task.

4. Our results show that average pairs’ reproductive success is a poor predictor of habitat quality in the hoopoe as it seems, conforming to the IFD model, that breeding density rules the system. Along with data on local breeding density (or area-specific breeding success), male’s quality can inform about priority areas for habitat conservation management. The determinants of habitat quality must now be studied at a finer resolution than here to better inform about best practices for habitat management.

345 words

Keywords: Arrival date; Conservation; *Gryllotalpa gryllotalpa*; Habitat selection; Individual quality; Morphological characteristics; Territory occupancy; *Upupa epops*

1. INTRODUCTION

Territory choice has a crucial impact on individual fitness since the acquisition of a good territory is essential for survival and successful reproduction (Andrén, 1990; Sergio and Newton, 2003; Sergio et al., 2007). To maximize their fitness, individuals should settle in the highest quality territories. High quality territories contain an optimal combination of essential resources needed for reproduction and survival, such as nest-sites, food, or shelter from predators (Petit and Petit, 1996). If individuals are unconstrained to move between territories, the ideal free distribution model predicts that individuals settle in the best habitats first, until the fitness benefits accrued (e.g. individual breeding success) start to become equivalent in lower quality habitats, a point in time when the latter habitats will be colonized (Fretwell and Lucas, 1969). This would result in equivalent breeding success between nests across the area, with density adjustment ultimately ruling the whole system. This mechanism has been termed habitat matching (Pulliam and Caraco, 1984), although consistent deviations from this rule have been documented in several studies (Kennedy and Gray, 1993; Tregenza, 1995). Part of these deviations stem from unequal competitive abilities among individuals. This is known as the ideal despotic distribution model which assumes that some individuals are capable of monopolizing territories; the prediction is then that territories are selected according to their quality and that subordinate individuals are excluded from the highest quality territories (Brown, 1969; Fretwell and Lucas, 1969). Both models postulate that the distribution of breeders in a heterogeneous environment is non-random in space and time: high quality territories tend to be occupied also when population density is low, while low quality territories are only occupied at high population density. Thus, the number of times a territory is occupied over a given period of time (i.e. its occupancy rate) can be used as a reliable measure for territory quality (Newton, 1991; Sergio and Newton, 2003).

Using territory occupancy rate as a measure of territory quality provides a means to identify the key habitat factors determining quality (Sergio and Newton, 2003; Mermod et al., 2009). These factors can include any resources such as food supply, nesting sites and/or structural habitat variables. The identification of these key factors is an essential step in species' conservation and management.

Migratory bird species have to select a breeding territory every year. Typically, older and thus more experienced individuals arrive first on the breeding grounds (Village, 1985; Francis and Cooke, 1986; Sergio et al., 2009). They can therefore freely select their territory. Typically, early arriving individuals also have a good body condition (Kokko, 1999). The overall outcome of this process is that when all individuals have arrived, the best territories are typically occupied by the most dominant, i.e. highest quality individuals.

Dominance per se is difficult to assess and is usually assessed through surrogate phenotypic traits, such as age, body size or coloration. Older individuals are often dominant over younger individuals, since they are physically stronger or have more experience (Sergio et al., 2007). The same holds for larger and/or heavier individuals that are physically stronger (Petit and Petit, 1996; Serrano and Tella, 2007). Finally, the pattern or intensity of feather coloration are commonly honest signals for bird’s individual quality (Fugle et al., 1984; Moller, 1992; Chaine and Lyon, 2008) and therefore correlate with dominance in many bird species

(Fugle et al., 1984; Moller, 1992; Andersson and Iwasa, 1996; Berglund et al., 1996; Chaine and Lyon, 2008). Since dominant individuals are expected to select higher quality territories, the frequency of territory occupancy must correlate positively with phenotypic traits expressing dominance in territory owners, such as age, body size or plumage characteristics.

We studied the correlates and determinants of territory selection of an endangered population of hoopoe (*Upupa epops* L.) in southwestern Switzerland (Valais). Using the frequency of territory occupancy from 8 years as a surrogate for territory quality we assessed the relationships between territory quality, habitat parameters and individual characteristics. Previous studies on the same focal Swiss hoopoes have shown that they mainly feed on molecrickets (Arlettaz et al., 2010), relying very much on sparse ground vegetation for terrestrial foraging (Ioset, 2007; Barbaro et al., 2008). We therefore predicted a positive relationship between territory occupancy rate vs. molecricket abundance and amount of bare soil, respectively. We used two spatial scales for this assessment, namely a large scale radius of 300 m and a small scale radius of 200 m. Finally, we tested whether phenotypic traits of hoopoes were related with territory occupancy, predicting that larger, heavier and older individuals preferably settle in high quality territories. The main objective of the study was to provide practitioners with spatially-explicit recommendations for prioritizing areas for the conservation of the local hoopoe population. More generally, the study provides new insights into methods to assess populations’ key areas.

2. METHODS

2.1. Study species

The hoopoe preferably inhabits semi-open, dry and sunny areas of southern Europe, north-west Africa and central Asia (Glutz von Blotzheim and Bauer, 1980). In central Europe typical breeding habitat often comprises traditionally cultivated areas (Fournier and Arlettaz, 2001), but high-intensity farmland can also be inhabited provided that essential resources are available (Ioset, 2007). Hoopoes mainly feed on large soil-invertebrates which are caught by probing the ground with their long curved beak (Fournier and Arlettaz, 1998; Maumary, 2007). In Valais, food consists mostly of molecrickets (*Gryllotalpa gryllotalpa*), representing 93% of the biomass provisioned to chicks (Arlettaz et al., 2010). Hoopoes are eclectic secondary cavity breeders, occupying hollow trees and walls as well as nest boxes, provided that cavities are large enough. Hoopoes often raise two broods a year, occasionally even a third one (Portner, 2008; Arlettaz et al., 2010). Hoopoes were widely distributed in Central Europe, including Switzerland, in the 50ies (Fournier and Arlettaz, 1998; Maumary, 2007), but since then most populations have declined (Bauer and Berthold, 1997). Therefore, the species is considered to be endangered in Switzerland (Keller et al., 2001).

2.2. Study area

The study was conducted in the plain of the upper Rhône valley (46.2 °N, 7.4 °E; 480 m above sea level) (Appendix Fig. S1), where field work was performed annually from April to August 2002 to 2009. The whole study area has an extension of about 64 km^2 and is dominated by industrial farming, mainly consisting of fruit tree plantations, vineyards and vegetable crops. Pastures, meadows, vegetable gardens and wood patches are rather scarce. The whole area is interspersed with numerous roads and villages. For a more detailed description of the region see Arlettaz (1984) and Arlettaz et al. (2010). In the whole area ca 700 nest boxes for hoopoes have been installed gradually from 1997 to 2002 at 300 locations. At most locations (typically small huts and shacks) two nest boxes each have been installed.

2.3. Sampling design

2.3.1. Territory occupancy

Since the focal hoopoes now almost exclusively breed in nest boxes, we regard occupancy of nest box and territory as equivalent. Nest boxes were inspected every second week with a mirror and bulb put through the entrance hole. If a nest box was occupied it was checked every third day to collect information about clutch size, breeding success and phenology. For each of the ca 300 locations we counted in how many years they were occupied by breeding hoopoes (range 0-8).

2.3.2. Individual phenotypic traits

The majority of breeding hoopoes were caught using mist-nets, traps placed in front of the nest box or by taking brooding females from the nest box by hand. From the captured adults we determined sex, age (two classes: one year old and older), bill length, crest length, minimal wing length, length of wing feathers P5 and tail feathers R1, tarsus length and weight (body mass). All captured individuals as well as all nestlings were ringed.

Displaying hoopoes, especially receptive females, typically show their tail feathers, which have a conspicuous black-and-white pattern, to potential mates (Arlettaz, personal communication), suggesting that the pattern on the tail could carry information about individual quality. However, it is unknown which aspects of the tail pattern potentially carries the information. We therefore took several measurements (Appendix Fig. S2). The hoopoe tail consists of ten black feathers which are all quite similar in shape and size. The black coloration is interrupted by a white bar crossing the whole tail from one end to the other. This bar differs in regularity and shape between individuals. On the outer vane of the outermost feathers (R5) the stripe usually opens up to a wider area of white coloration. Furthermore it appears that some individuals have a second white area detached from the main stripe located closer to the anterior end of the R5 feathers' outer vane. To answer the question of tail pattern function we measured and compared tail characteristics on pictures taken from the tails of every adult that was caught in 2009 (Appendix Fig. S2). For this reason the tails were spread to an angle of 60°. This is a reasonable approximation to the spread when displaying (Arlettaz, personal communication). First, the linearity of the tail stripe was noted (straight; curved). Secondly the regularity of the stripe was judged and allocated to one of three classes: homogenous, medium or heterogeneous (Appendix Fig. S2 - small pictures). Thirdly because we suspected that the white areas at the outermost feathers carry a key role in signalling, we measured the length of the white area of the R5 feathers' shaft (B) and the length of the same area at the outer edge of the outer vane (A) and calculated the ratio thereof (A/B) (Appendix Fig. S2). Finally we noted if there were second white patches present on the R5 feathers.

2.3.3. Habitat analysis

From a total of ca 300 available nest box locations, those that were occupied at least once between 2002 and 2008 by a hoopoe were identified (n = 192), from which 100 were chosen randomly. A circle of a 300 m radius [approximately corresponding to the mean home range size, ca 40 ha, (Ioset, 2007)] was drawn around each of the 100 nest box locations and 30 points within this circle were chosen randomly. Various habitat variables (see Table 1) were recorded at these points (total: n = 2130) in order to describe habitat features within territories. Points enclosed in two overlapping territories were used for both. We used a soil penetrometer to measure soil density at all sampling points. Five soil density measures were made at all sampling points. Further we used ground water table maps retrieved from the «Département des transports, de l'équipement et de l'environnement (DTEE), Service des Routes et Cours d'Eau – Projet Rhône III, Canton du Valais» and information about the molecricket abundance from the sampling described in 2.3.4. and the evaluation specified in chapter 2.4.4.

2.3.4. Molecricket occurrence

To assess the relationship between molecricket distribution and biotic factors (ground water table, soil density, soil type, vegetation cover) we sampled detection/non-detection data of molecrickets at 97 plots. These plots were selected using GIS (www.esri.com, Environmental Systems Research Institute, California), exclusively among fruit tree plantations because this is the preferred foraging habitat of hoopoes (Ioset, 2007). To ensure enough contrast, we stratified the sampling: study plots were chosen at random in areas with known high and low ground water table

(10 in each). Another 10 plots were randomly selected within areas with gravelly soil. The remaining 67 plots were chosen randomly from the remaining areas with less marginal soil type and ground water table conditions. Presence of molecrickets was determined by searching during 10 minutes their underground galleries and their entrance holes along three 10 m transects separated by three tree rows. If at least one gallery or entrance hole was found, presence of molecrickets was regarded as detected at that visit. All plots were sampled four times in June, during the peak in molecricket activity (Arlettaz et al., 2000). We recorded habitat covariates we thought relevant for molecricket occurrence (Table 1), but also took into account covariates that might have affected detectability, namely vegetation height and weather variables (precipitation on the day preceding a visit; daily average temperature; daily maximum temperature; daily sun shine duration; all obtained from the meteorological station Sion).

2.4. Statistical analyses

2.4.1. Random territory choice?

All statistical analyses except molecricket occupancy estimation were done using the software R (R Development Core Team, 2009). To test whether hoopoes selected breeding locations randomly, we compared the observed occupancy rate of all territories that were occupied at least once from 2002-2009 (n = 192) with the occupancy which would be predicted by a binomial law under a scenario of random selection of territories. To test the relationships between onset of settlement and breeding success vs. territory quality we used linear models. Average date of territory settlement was calculated as the mean of the laying dates of the first egg over the years, and territory-specific breeding success as the between-year mean number of fledglings produced on a territory. Only first broods were considered, resulting in a sample size of 186 territories. The resulting models were compared to the intercept model, and model averaged parameter estimates and AIC weights were calculated.

2.4.2. Individual phenotypic traits

The ideal despotic distribution model predicts that dominant individuals occupy the best territories (Fretwell and Lucas, 1969). To test if this hypothesis holds for the hoopoe, we fitted linear mixed effects models (normal error distribution) with different morphological traits (bill length, crest length, minimal wing size, length of P5 and first rectrix feather R1, tarsus length, body mass) as response and territory occupancy rate as explanatory variable. As the phenotypic traits of the birds occupying territories in the eight years under study were not averaged over territories we used territory as a random effect. These models were evaluated for males and females separately (males: n = 626; females: n = 758). We compared the models with the morphological traits to the intercept model and used model averaged parameter estimates and AIC weights for inference.

Second, we tested whether territory occupancy was related with the age of the individuals (two categories: one year old and older). Linear mixed effect models with a binomial error distribution and territory as random effect were used to model this binary response variable. We compared again the models including age to the intercept model and used model averaged parameter estimates and AIC weights for inference.

Modelling was performed separately for males (n = 553) and females (n = 654).

Third, we related tail patterns with occupancy. Because tail patterns were only assessed in 2009, we had to assume constancy of this character among territories over the years. For the categorical tail variables (linearity, heterogeneity and presence of a second white spot on R5, see above) we fitted general linear models with a Poisson distribution (loglinear model). To assess the influence of tail variables on the occupancy distribution we compared the saturated model to the model without interaction and calculated ΔAIC-values and AIC weights. For the continuous variable white-stripe-edge ratio A/B we used a linear regression model. Analyses were performed separately for males (n = 72) and females (n = 80).

2.4.3. Relation of occupancy and habitat characteristics

To correct for the seasonal effects of soil density measures, we measured the soil resistance once every week (n = 15) between April and August at a single plot (Swiss Grid: 592 755/118 481). Five measures each were done at every sampling occasion. We fitted a linear mixed effect model with soil density as response variable, date as explanatory fixed variable, and visit as a random effect. This model reveals that soil density increased during the season. Using the obtained parameter estimates we corrected all soil density measures for date.

We used the model averaged parameter estimates obtained from the molecricket occupancy modelling (see chapter 2.4.4.) and point-specific habitat covariates to calculate the probability of molecrickets’ occurrence. Together with the recorded habitat variables we modelled territory occupancy of hoopoes for our 100 territories with mixed effects models (territory identity number as a random effect, habitat variables and molecrickets' occurrence probability as fixed). We modelled territory occupancy with two main steps each on two spatial scales (300 m and 200 m radius). First, we evaluated the effect of habitat type on occupancy. Since habitat type could be recorded at all points, the sample size was 3000 for the large spatial scale and 1388 for the smaller spatial scale. Second, we modelled structural habitat variables and food abundance. Since they could not be assessed at all points, sample size was lower (large scale: n = 2378; small scale: n = 1153). Structural variables were soil density, depth of ground water table, vegetation cover and soil type; molecricket occurrence probability was used as a measure of food abundance. We fitted a null model with an intercept only, a full model including all structural variables, and models that included only one structure variable. We also evaluated reasonable combinations of structural variables and models with quadratic effects for soil density and vegetation cover. As fruit tree plantations are the main local foraging habitat of hoopoes (Ioset, 2007), structural variables in that habitat may be the main determinants of overall habitat quality. Therefore, we tested the same combinations of models as in step two but this time only with structural variables measured in fruit tree plantations (large scale: n = 1182; smaller scale: n = 634).

2.4.4. Molecricket occurrence

Molecricket detection/non-detection data was analyzed using occupancy models (MacKenzie et al., 2002) with software MARK (White and Burnham, 1999). We used average daily temperature, maximum daily temperature, amount of rainfall, sunshine duration, sampling occasion, vegetation cover and vegetation height to model detection probability (p). To model occupancy probability (Ψ) we used ground water table, soil density (corrected for date, see above), soil type and vegetation cover as well as the quadratic terms of ground water table, soil density and vegetation cover and the two interactions soil type*ground water table and soil type*soil density. We performed modelling in four steps. In a first step we used the full model for occupancy including all quadratic terms and interactions and explored the effect of different combinations of covariates for detection probability. In steps two and three we investigated the importance of different quadratic terms and interactions, respectively, on occupancy. Finally we evaluated the remaining combinations of variables that were neither involved in a quadratic term nor in an interaction on occupancy. The models were ranked in every step using Akaike's Information Criterion (AIC) (Burnham and Anderson, 1998) and the best models (ΔAICc ≤ 2) were selected for the next step. To get the best predictions for extrapolation we performed a model averaging using the best models of the final step, i.e. those models for which the sum of AICc weights was ≤ 0.9.

3. RESULTS

3.1. Random territory choice?

Hoopoes did not select territories at random (χ^2_7= 76.79, *P* < 0.001, Fig. 1). The hatching date decreased strongly with occupancy rate (β = -1.85, SE = 0.43, AIC weight = 1.00), thus, territories that were occupied more often were also occupied earlier in the season. In contrast, breeding success was not or only marginally related with territory occupancy rate (β = 0.06, SE = 0.06, AIC weight = 0.67, logit scale), suggesting that more often occupied territories were not producing strikingly more fledglings than less frequently occupied territories.

3.2. Individual phenotypic traits

The average age of breeders was strongly related with territory occupancy in males (β = 0.23, SE = 0.04, AIC weight = 1.00), whilst it was very weak and at the limit of significance in females (β = 0.04, SE = 0.04, AIC weight = 0.65). The relationship was positive in both sexes, thus older individuals tended to settle in territories that were more frequently occupied.

There were clear relationships between territory occupancy and morphological characteristics in males, but not in females. The null model was often supported in females, with only one morphological trait whose estimate (negative) was non-overlapping with 0 (Table 2). By contrast, the relationships between morphological traits and occupancy were all positive in males, with four of them statistically supported: minimal wing length, P5 length, tarsus length and weight (Table 2). Thus, breeding males in territories of higher occupancy were distinctly larger and heavier (Fig. 2).

For most of the tail parameters we could not find any effects explaining the occupancy distribution of hoopoe territories. For the white-stripe-edge ratio A/B, however, we found non-conclusive results for both sexes (males: parameter estimate = 0.03, SE = 0.04, AIC weight = 0.49; females: parameter estimate = 0.01, SE = 0.02, AIC weight = 0.35). The model including tail linearity was equivalent to the intercept model in females (ΔAIC = 0.31, AIC weight = 0.46) but not in males (ΔAIC = 10.15, AIC weight = 0.01). The other tail characteristics were clearly not related with occupancy: heterogeneity (males: ΔAIC = 15.39, AIC weight < 0.00; females: ΔAIC = 19.70, AIC weight < 0.00), presence of a second white area on R5 (males: ΔAIC = 4.51, AIC weight = 0.09; females: ΔAIC = 5.42, AIC weight = 0.06).

3.3. Relation of occupancy and habitat characteristics

Model selection results for the relationship between territory occupancy and habitat characteristics are shown in Table 3. At both spatial scales, the most simple model including none of the habitat variables was the best, suggesting that the recorded habitat characteristics were not related with territory occupancy, and thus with habitat quality. This was also true when only fruit tree plantations were considered (Appendix Table S2).

3.4. Molecricket occurrence

Molecricket occupancy models with interactions got weak support by the data (best model: ΔAICc = 13.72 compared to overall best). The best 15 models are presented in Table 4. The quadratic terms of soil density and ground water table seem to be important and are included in the best 15 models. The parameter estimates of the best models showed that detection probability of molecrickets was dependent on ground vegetation cover, sunshine duration and to a lesser extent sampling occasion. The parameters most relevant for molecricket occurrence were soil type, soil density, ground water table and vegetation cover as well as the same two above-mentioned quadratic terms. As regards detection probability, the estimates for the best models were negative for vegetation cover (β = -0.63; SE = 0.16) and positive for sun shine duration (β = 0.43; SE = 0.14). For occupancy we found a quadratic relationship with soil density (β1 = -17.32, SE = 8.37; β2 = 29.53, SE = 13.76) and a negative for ground water table (β = -0.29; SE = 0.27).

Fig. 3 shows the model-averaged relationships between molecricket occupancy probability and the covariates included in the best 15 models. It is striking that the molecricket occupancy probability was similar in all soil types except in soil type 3 (silty soil embedded in a matrix dominated by gravel, stones or pebbles), in which molecrickets had a considerably lower occurrence probability. Soil type 6 (vegetal soil, decomposed litter) did not occur in any sampled fruit tree plantation and was therefore not included. Molecricket occurrence probability declined with increasing depth of the ground water table (Fig. 3A). The relationship with soil density was more complex (Fig. 3B); molecricket occurrence was higher in soft and hard soils compared to medium soils. This was most pronounced with soil type 3. As expected, vegetation cover only had a very weak impact on molecricket occupancy (Fig. 3C).

4. DISCUSSION

This study shows that hoopoes select their territories in a non random fashion, indicating spatial heterogeneity in the availability of crucial resources. According to the ideal free distribution model, breeding success did not relate (or if so only very marginally) to territory occupancy rate, which suggests a process of spatial adjustment of breeding density to local habitat quality across the study area. However, our models were unable to identify the determinants of habitat quality: neither habitat type, nor vegetation characteristics, nor molecricket availability correlated with territory occupancy rate. Further evidence that habitat quality varies spatially is provided by the male (but not female) holders of high-occupancy rate territories reproducing earlier in the season, being older and/or phenotypically larger and heavier than in territories occupied only sporadically; this is in line with the predictions of the ideal despotic distribution model (Fretwell and Lucas, 1969).

These findings generally provide support to the view that territory occupancy rate effectively reflects habitat quality (Sergio and Newton, 2003). Knowledge about territory occupancy over the years may thus efficiently deliver information about spatially-explicit prioritization for conservation management.

The fact that we could not establish a clear link (only a weak, uncertain trend was noticed) between breeding success and territory occupancy would be in conformity with the ideal free distribution model. This contrasts with findings of earlier studies where such a link could be evidenced. It may well be that hoopoes, due to their very short life cycle (Reichlin et al., unpublished data) and to a loose territorial behavior (only direct nest surroundings are defended against conspecific intruders; (Arlettaz, 1984) – contrary to most other above study species (e.g. raptors) – readily adjust their local density to local habitat conditions so that any arising discrepancies in the breeding ability between pairs are simply obliterated by density-dependent regulating factors acting upon fecundity. But other factors could also play a role and contribute to explain the pattern observed. First, reproductive success in the study area has a strong stochastic component due to sensitivity to short-term weather variation (Arlettaz et al., 2010), which may blur the detection of any possible relationship. Second, we considered only first broods for the evaluation of a territory's breeding success, whilst the latter actually results from a trade-off between investments in the first and second (if not third) brood (Lindén, 1988). In this respect, it is possible that the habitat quality of the territory where the first brood was raised influenced the outcome of the second brood, through so called carry-over effects: raising the first brood in a high quality territory might require less energy from parents inhabiting prey rich habitats, providing them with more scope for successfully engaging in a second reproductive attempt. Finally, the number of fledglings may be a too crude estimate of a breeder's fitness: both post-fledging and adult survivals might be more important in a rapid generation turnover species like the hoopoe (Reichlin et al., unpublished data). Interestingly, Mermod et al. (2009) who carried out in the same study area a similar study on wryneck (*Jynx torquilla* L.), another rather short-lived bird, also found no influence of occupancy on number of fledglings.

We could not evidence a relationship between frequency of territory occupancy and habitat characteristics and food availability, contrary to our expectations. However, a clustered spatial distribution of territories within the study area, along with a non-random occupancy pattern and evidence for despotic distribution of male phenotypes indicates that spatial heterogeneity in habitat quality actually occurs. Approximately 700 nest boxes were homogeneously installed across the study area. Potential breeding sites thus by far outnumber the yearly number of broods, which peaked in 2007 with 118 successful broods (Arlettaz et al., in press). Nest opportunities currently being unlimited, molecricket availability is the only possible limiting resource, as this prey constitutes more than 90% of the food provisioned to chicks (Arlettaz et al., 2010). The possibility that we have not considered the correct habitat type and variables is very unlikely because our descriptors were chosen from the same detailed radiotracking studies of habitat use (Ioset, 2007). Changes in the farmland matrix during the course of the study also cannot be inferred because fruit tree plantations, predominant in the study area, have a low rotation. There are, however, other methodological caveats that probably operate here. According to radiotracking data obtained by Ioset (2007), we assumed average home range sizes of 40 ha and thus modeled virtual circular foraging territories within a radius of 300 and 400 m around nests (territory centre), although breeding hoopoes have been observed to forage as far as 1.1 km from nest (Arlettaz, 1984). This crude approach would work well only if molecrickets have homogenous spatial distributions within these surface areas and if hoopoes would exploit the habitat in an isotropic and regular manner. From the same radiotelemetry study, however, we know that hoopoes recurrently return to the same foraging patches (Ioset, 2007), which points towards highly scattered and possibly molecricket hotspots of restricted extension. Varying modeling scales would thus only marginally contribute to overcome this caveat. Only very fine-grained mapping of molecricket availability over wide areas could solve this sampling problem, but they would imply strenuous field surveys.

Regarding molecrickets' occurrence, the model confirmed our field impressions. Detection of molecrickets was decreasing with increasing vegetation cover, increasing with sun shine duration and to some extent dependent on sampling occasion. We believe that this is first because dense vegetation hinders the fine recognition of ground structure (i.e. location of galleries), while sunshine enhances visibility of the ground structure, i.e. the detection of molecricket galleries just below the soil surface. Furthermore, endothermic organisms usually reduce their activity in bad weather conditions which makes them more difficult to detect and render them unavailable to predators (Taylor, 1963; Veistola et al., 1997; Arlettaz et al., 2010). Finally, molecrickets have a distinct abundance peak around mid and late June (Arlettaz and Sierro, unpublished data). Molecrickets' occurrence depended on soil structure as shown by Portner (2008): this study confirmed, firstly, that small-grained soils with lots of sand in the matrix were preferred over gravelly soils or soils with limited amounts of sand. Secondly, we could establish that molecrickets prefer wet soils, as shown by a preference of molecrickets for water table levels close to the soil surface. The pattern arising from our soil density evaluation is difficult to interpret. We expected molecrickets to prefer soils with medium density because too soft soil might cause molecricket galleries to collapse while in too hard soils it would be difficult to drill galleries. Instead we observed high occurrence probability in very soft and hard soils. The reason for this remains unknown. Finally, we observed a slight decrease in molecricket occupancy with increasing vegetation cover. This may in part be due to a preference of molecrickets for sun-exposed bare ground patches where they lay clutches of eggs just below the soil surface to activate embryonic development (own unpublished data).

The relationships between individual characteristics (age, size, weight) and territory occupancy differed between males and females. This suggests that males and females use different cues for territory selection. It is common that males judge territory quality and try to monopolize the best territories (Francis and Cooke, 1986; Jacot et al., 2009) while females evaluate the quality of males rather than the quality of territories (Andersson and Iwasa, 1996). The patterns observed in hoopoes seem to match this view. Breeding dispersal of hoopoes is higher in females than males and higher in one year old compared to older individuals (Bötsch, 2010). Together with the results of the present study, this indicates that dominant males monopolize the best territories and avoid dispersal, probably because there are too high costs entailed with dispersal and the acquisition of a new territory. Our results also suggest that territory securing is exclusively a male’s job (Francis and Cooke, 1986; Jacot et al., 2009), as is food provisioning to the incubating female and nestlings (Arlettaz et al., 2010).

As predicted by the ideal despotic distribution model (Fretwell and Lucas, 1969), high quality territories were occupied earlier in the season by older males. This is in complete accordance with the findings for painted buntings (*Passerina ciris*) and black kites (*Milvus migrans*) (Lanyon and Thompson, 1986; Sergio et al., 2007). There are two mechanisms that could explain this pattern: on the one hand, the hierarchical status of older birds is usually higher in general because they are simply more experienced, which allows them to monopolize the best territories (Smith et al., 1980; Lanyon and Thompson, 1986; Newton, 1991; Holmes et al., 1996; Petit and Petit, 1996; Sergio et al., 2007; Serrano and Tella, 2007; Sergio et al., 2009). On the other hand, older individuals of migrating birds usually arrive on the breeding grounds before younger individuals and are therefore free to choose the best territories first (Village, 1985; Francis and Cooke, 1986; Sergio et al., 2007; Sergio et al., 2009).

The hypothesis that individuals breeding in territories with higher occupancy (high quality territories) are larger and/or heavier (Petit and Petit, 1996; Serrano and Tella, 2007) was supported for hoopoe males. Since theory states that dominant individuals should occur in more frequently occupied territories (Fretwell and Lucas, 1969), we can conclude that there is a tight relation with hierarchical status, with large body size and mass expressing dominance. It is, however, not clear, whether body size is directly beneficial in terms of agonistic conflicts for territory acquisition or indirectly via an effect of the arrival date (Sergio et al., 2007; Serrano and Tella, 2007). Body size traits of females were not positively correlated with territory occupancy. In contrast to males, females are losing body mass while brooding (Dafond, 2008). Because breeding females were not all captured during the same nesting stage, with respect to chicks’ age, an existing relationship may have been overlooked. For the other female traits, spurious findings are unlikely because of the low values of estimates and their large errors.

There was considerable uncertainty about the relationship between occupancy and tail parameters linearity and the white-stripe-edge ratio.

Despite the weak statistical support, we think that there could still be an effect. The sample size was relatively small (males: n=72 / females n=80) rendering the confirmation of possibly existing subtle relationships difficult. Evaluating the tail patterns of previous years and increasing the sample size might help to clarify the importance of the tail pattern for mate choice and dominance. It is also possible that other traits than the measured parameters are decisive to signal individual quality. For example, the strength of ultraviolet (UV) reflection is an important signal in other birds (Griggio et al., 2010). More studies are required to be more conclusive.

Hoopoe territories clearly differ in quality, as inferred from the non-random pattern of occupancy over the years and from the despotic distribution of male phenotypes. Both territory occupancy pattern and male hierarchical status estimated from phenotypic traits provide spatially-explicit information for setting conservation priorities: emphasis should be placed on those areas in which territories are more frequently occupied and that are inhabited by dominant males. Further studies are now needed to determine habitat features related with territory quality. The resolution and scales used in the present study could not address this question appropriately as molecricket hotspots are likely to be scattered and small. This information would be essential to inform best habitat management practices. More generally, combining information on local breeding density, territory occupancy rate and territory holders' hierarchical status may provide crucial information for improving management decisions for species of conservation concern.

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TABLES

Table 1: Description of habitat variables that were recorded at all sampling points for modelling hoopoe territory occupancy and molecricket occupancy.

Parameter	Levels	Description
Habitat type	apple tree plantation apricot tree plantation pear tree plantation arable field vineyard grassland river bank wood non-tarred road unsuitable area	habitat surrounding the sampling point (unsuitable area = building, tarred road, open water)
Vegetation cover	continuous (to next 10%)	in fruit tree plantations for both: underneath trees and in tractor driving track; and as average in other habitats
Mowing	yes or no	regular mowing of the driving track (only for fruit tree plantations)
Ground management	mowing herbicide mechanical veg. removal no treatment	management of the vegetation strip underneath plantation trees (only for fruit tree plantations)
Soil type	1) silty soil with no-till-limited presence of sand 2) silty soil with obvious presence of sand 3) silty soil embedded in a matrix dominated by gravel, stones or pebbles 4) sandy soil where large structures such as gravel and pebbles are absent 5) sand embedded in a matrix dominated by gravel, stones or pebbles 6) all kind of vegetal soil (decomposed litter)	characterisation of top soil layer
Soil density	continuous (0-15 in steps of 0.5)	Five measures using a soil penetrometer

Table 2: Model averaged parameter estimates of the effect of territory occupancy on different morphological measures, evaluated by linear mixed effects model. Given are the estimates, their standard errors (SE), as well as the AIC weights compared to the intercept model (w_i) and sample size (n). The parameters are shown for males and females separately.

	Males				Females			
Morphological trait	Estimate	SE	w_i	n	Estimate	SE	w_i	n
Bill length	0.01	0.08	0.70	468	0.00	0.01	0.27	527
Crest length	0.00	0.02	0.27	578	0.00	0.02	0.27	641
Minimal wing length	0.19	0.09	0.92	575	-0.01	0.03	0.31	646
P5 length	0.17	0.09	0.90	566	0.00	0.02	0.27	634
R1 length	0.02	0.05	0.34	551	-0.07	0.09	0.51	634
Tarsus length	0.03	0.02	0.82	577	-0.03	0.02	0.86	650
Weight	0.35	0.09	1.00	609	0.03	0.06	0.33	735

Table 3: Model selection summary of 1) the effects of habitat type on frequency of territory occupancy for a radius of 300 m (n = 3000) and 200m (n = 1388) and 2) of the structural variables (300 m radius, n = 2378; 200 m radius, n = 1153). Shown are the differences between the best and the current model (ΔAIC), the AIC weight of the current model (w_i), the number of estimated parameters (K) and the deviance.

	radius = 300 m				radius = 200 m			
Model	ΔAIC	w_i	K	Deviance	ΔAIC	w_i	K	Deviance
1) Evaluation of habitat type:								
intercept	0.00	1.00	2	593.96	0.00	1.00	2	594.87
habitat type	17.86	0.00	11	593.81	17.89	0.00	11	593.76
2) Evaluation of structural variables:								
intercept	0.00	0.40	2	567.05	0.00	0.40	2	482.76
molecrickets	1.99	0.15	3	567.04	1.97	0.15	3	482.73
dens	2.00	0.15	3	567.05	1.98	0.15	3	482.74
gw	2.00	0.15	3	567.05	2.00	0.15	3	482.76
veg	2.00	0.15	3	567.05	2.00	0.15	3	482.76
soilt	9.99	0.00	7	567.04	9.94	0.00	7	482.70
dens+gw+veg+mcrickets+soilt	17.97	0.00	11	567.02	17.90	0.00	11	482.66

Covariates: molecrickets = molecricket occurrence probability, dens = soil density, gw = ground water table, veg = vegetation cover, soilt = soil type.

Table 4: Model selection summary for molecricket occupancy- (Ψ) and detection probability (p), in response to habitat parameters. Shown are the differences between the best and the current model (ΔAICc), the AIC weight of the current model (w_i), the number of estimated parameters (K) and the deviance for the best 15 models ($\sum w_i = 0.9$).

Model	ΔAICc	w_i	K	Deviance
Ψ (soilt+dens+gw+dens^2) p (veg+sun)	0.00	0.46	11	401.15
Ψ (dens+gw+dens^2) p (t+veg+sun)	3.35	0.09	10	407.05
Ψ (dens+dens^2) p (t+veg+sun)	4.51	0.05	9	410.72
Ψ (soilt+dens+dens^2) p (t+veg+sun)	4.79	0.04	13	400.62
Ψ (soilt+dens+veg+dens^2) p (t+veg+sun)	5.01	0.04	14	398.09
Ψ (dens-veg+gw+dens^2) p (t+veg+sun)	5.06	0.04	11	406.21
Ψ (dens+gw+dens^2+gw^2) p (t+veg+sun)	5.11	0.04	11	406.26
Ψ (dens+gw+dens^2) p (veg+sun)	5.51	0.03	7	416.55
Ψ (dens+veg+dens^2) p (t+veg+sun)	5.86	0.02	10	409.57
Ψ (soilt+dens+dens^2) p (veg+sun)	6.31	0.02	10	410.02
Ψ (soilt+dens+veg+dens^2) p (veg+sun)	6.45	0.02	11	407.60
Ψ (soilt+dens+gw+dens^2+gw^2) p (t+veg+sun)	6.46	0.02	15	396.71
Ψ (soilt+dens+veg+gw+dens^2+gw^2) p (t+veg+sun)	6.66	0.02	16	394.01
Ψ (soilt+dens+gw+dens^2) p (t+veg+sun)	6.72	0.02	14	399.80
Ψ (dens+dens^2) p (veg+sun)	6.75	0.02	6	420.12

Covariates: dens = soil density, gw = height of ground water table, soilt = soil type, sun = daily sunshine duration, t = sampling occasion, veg = vegetation cover, dens^2 = quadratic term of soil density, gw^2 = quadratic term of ground water table.

FIGURE CAPTIONS

Fig. 1: Observed and expected (under a random selection scenario) frequency of territory occupancy.

Fig. 2: Relationship between minimal wing length, P5 length, tarsus length and body mass (from upper left to lower right) of territory owners and territory occupancy rate (2002-2009). Males: open circles; females: closed circles. The regression lines refer to males.

Fig. 3: Occupancy probability of molecrickets in response to depth of the ground water table (A), soil density (B) and surface vegetation cover (C). Predictions are shown for five different soil types occurring at the sampling sites (Table 1). Closed circles represent soil type 1, open circles represent soil type 2, open squares represent soil type 3, open diamonds represent soil type 4 and open triangles represent soil type 5.

FIGURES

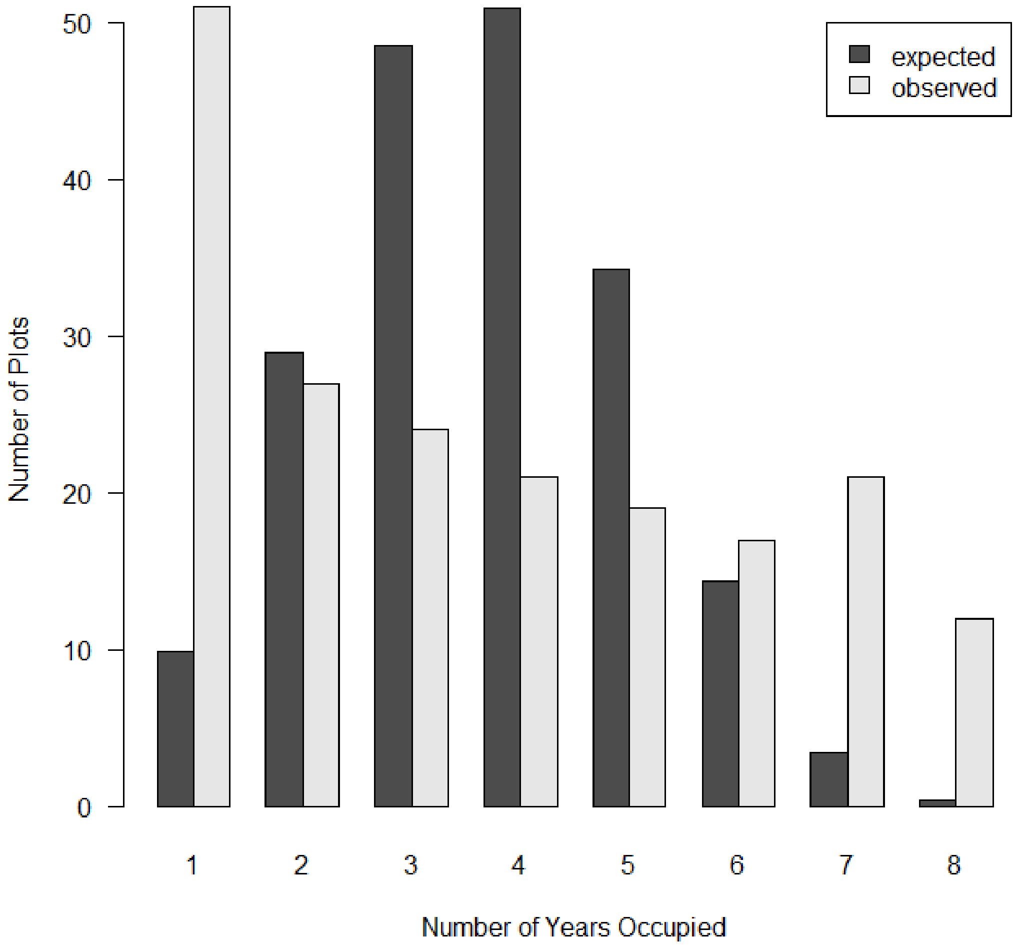

Fig. 1

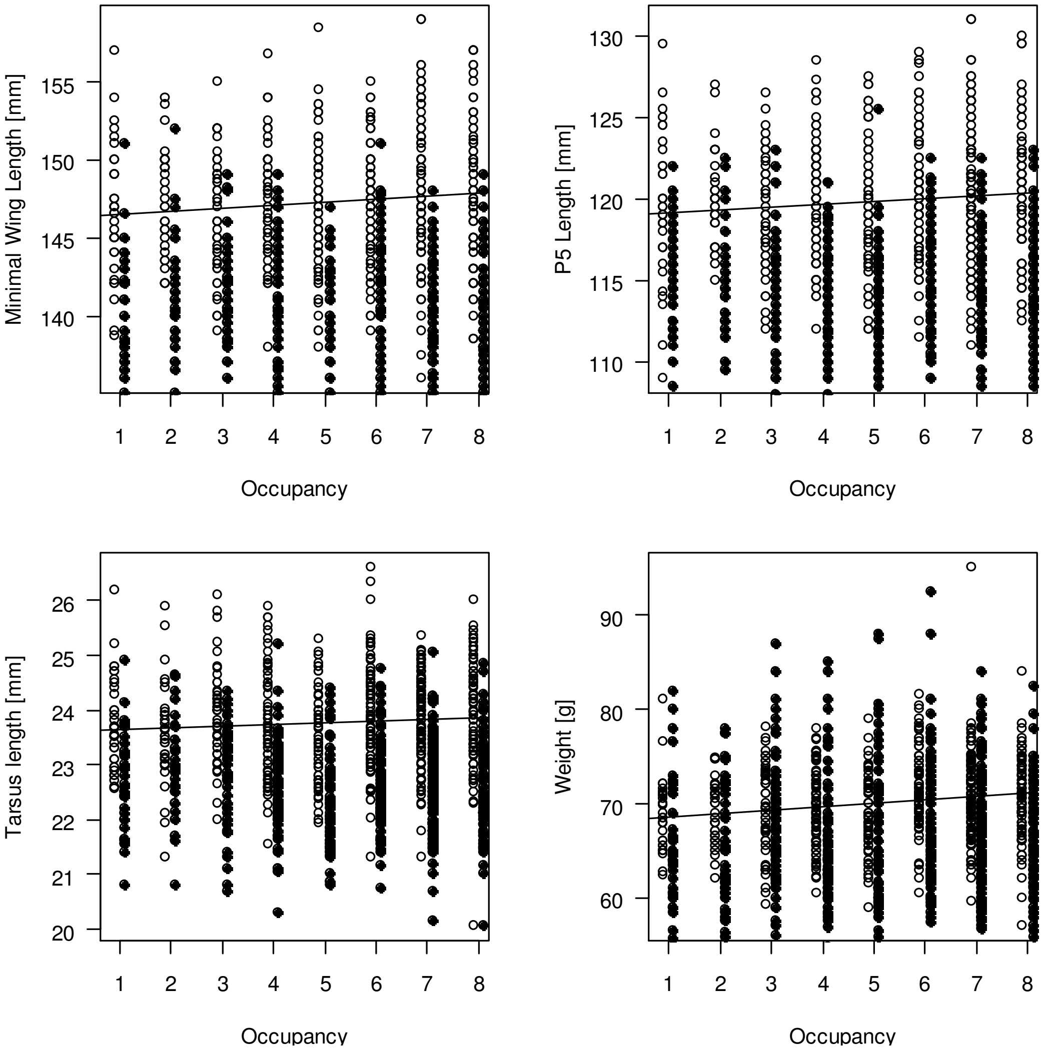
Minimal Wing Length [mm]
140
145
150
155
P5 Length [mm]
110
115
120
125
130
Tarsus length [mm]
20
21
22
23
24
25
26
Weight [g]
60
70
80
90
1
2
3
4
5
6
7
8
Occupancy

Fig. 2

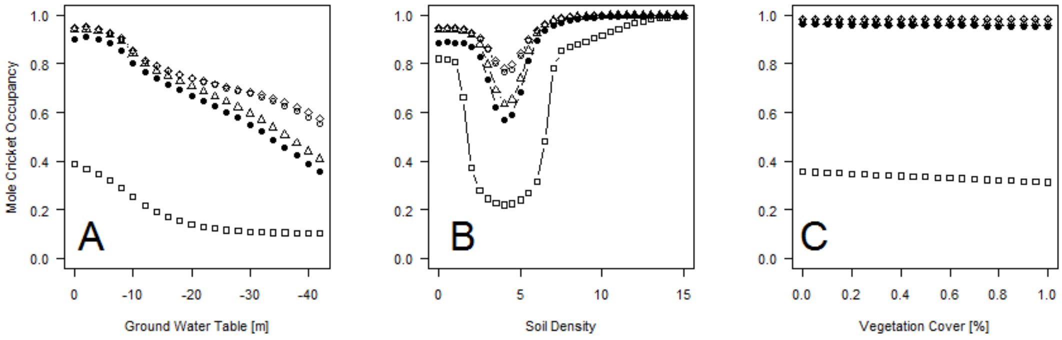
Mole Cricket Occupancy
1.0
0.8
0.6
0.4
0.2
0.0
A
0
-10
-20
-30
-40
Ground Water Table [m]
B
0
5
10
15
Soil Density
C
0.0
0.2
0.4
0.6
0.8
1.0
Vegetation Cover [%]

Fig. 3

APPENDIX

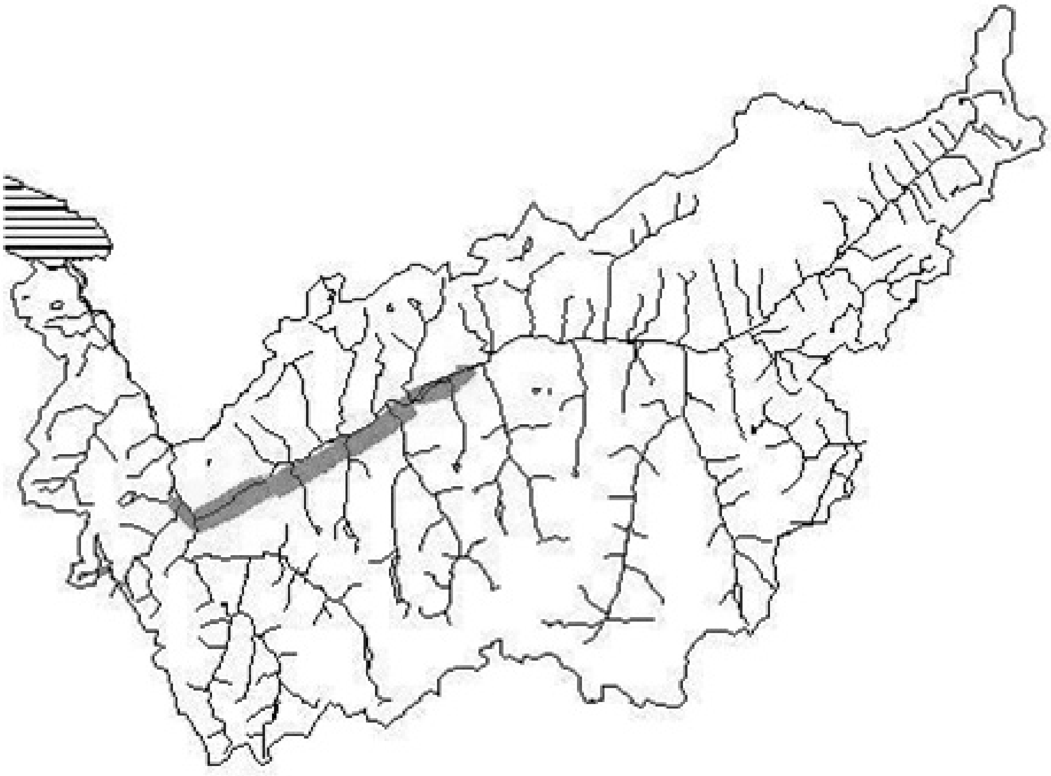

Fig. S1: The canton of Valais (Switzerland) with the study area (grey shaded).

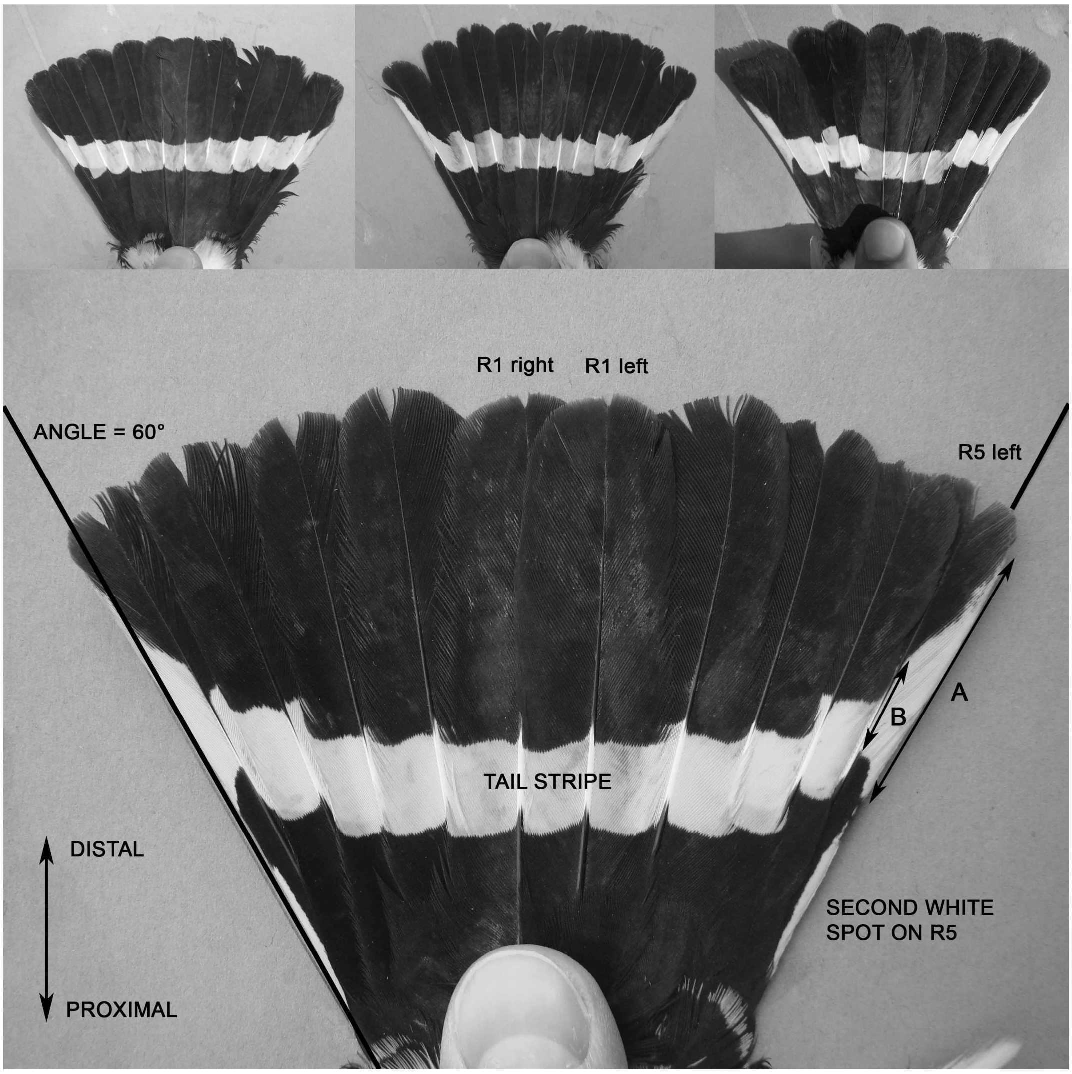

Fig. S2: Hoopoe tail morphology and measurements. The tail was spread within an gradient of 60° and pictures taken from above. The large picture shows the different parameters that were measured. The small pictures show the three different regularity classes: homogenous, medium and heterogeneous (from left to right).

Table S1: Model selection summary for the molecricket occupancy- (Ψ) and detection probability (p) in response to different covariates. Shown are the differences between the best and the current model (ΔAICc), the AIC weight of the current model (w_i), the number of estimated parameters (K) and the deviance.

Model	ΔAICc	w_i	K	Deviance
Ψ (soilt+dens+gw+dens^2) p (veg+sun)	0.00	0.46	11	401.15
Ψ (dens+gw+dens^2) p (t+veg+sun)	3.35	0.09	10	407.05
Ψ (dens+dens^2) p (t+veg+sun)	4.51	0.05	9	410.72
Ψ (soilt+dens+dens^2) p (t+veg+sun)	4.79	0.04	13	400.62
Ψ (soilt+dens+veg+dens^2) p (t+veg+sun)	5.01	0.04	14	398.09
Ψ (dens-veg+gw+dens^2) p (t+veg+sun)	5.06	0.04	11	406.21
Ψ (dens+gw+dens^2+gw^2) p (t+veg+sun)	5.11	0.04	11	406.26
Ψ (dens+gw+dens^2) p (veg+sun)	5.51	0.03	7	416.55
Ψ (dens+veg+dens^2) p (t+veg+sun)	5.86	0.02	10	409.57
Ψ (soilt+dens+dens^2) p (veg+sun)	6.31	0.02	10	410.02
Ψ (soilt+dens+veg+dens^2) p (veg+sun)	6.45	0.02	11	407.60
Ψ (soilt+dens+gw+dens^2+gw^2) p (t+veg+sun)	6.46	0.02	15	396.71
Ψ (soilt+dens+veg+gw+dens^2+gw^2) p (t+veg+sun)	6.66	0.02	16	394.01
Ψ (soilt+dens+gw+dens^2) p (t+veg+sun)	6.72	0.02	14	399.80
Ψ (dens+dens^2) p (veg+sun)	6.75	0.02	6	420.12
Ψ (dens+veg+gw+dens^2+gw^2) p (t+veg+sun)	6.82	0.02	12	405.34
Ψ (dens+veg+gw+dens^2) p (veg+sun)	7.07	0.01	8	415.73
Ψ (dens+gw+dens^2+gw^2) p (veg+sun)	7.08	0.01	8	415.74
Ψ (soilt+dens+veg+gw+dens^2) p (t+veg+sun)	7.22	0.01	15	397.47
Ψ (soilt+dens+gw+dens^2+gw^2) p (veg+sun)	7.56	0.01	12	406.08
Ψ (soilt+dens+veg+gw+dens^2+gw^2) p (veg+sun)	7.67	0.01	13	403.51
Ψ (dens+veg+dens^2) p (veg+sun)	8.00	0.01	7	419.04
Ψ (soilt+dens+veg+gw+dens^2) p (veg+sun)	8.47	0.01	12	406.99
Ψ (dens+veg+gw+dens^2+gw^2) p (veg+sun)	8.64	0.01	9	414.85

Covariates: dens = soil density, gw = height of ground water table, soilt = soil type, sun = daily sunshine duration, t = sampling occasion, veg = vegetation cover, dens^2 = quadratic term of soil density, gw^2 = quadratic term of ground water table.

Table S2: Model selection summary for the effects of habitat variables on frequency of territory occupancy (in fruit tree plantations only) for a radius of 300 m (n = 1182) and 200 m (n = 634). Shown are the differences between the best and the current model (ΔAIC), the AIC weight of the current model (w_i), the number of estimated parameters (K) and the deviance.

	radius = 300m				radius = 200m			
Model	ΔAIC	w_i	K	Deviance	ΔAIC	w_i	K	Deviance
intercept	0.00	0.34	2	469.83	0.00	0.34	2	395.44
mow	1.94	0.13	3	469.77	1.89	0.13	3	395.33
gw	1.97	0.13	3	469.80	1.98	0.13	3	395.42
veg	1.98	0.13	3	469.81	2.00	0.13	3	395.44
mcrickets	1.99	0.13	3	469.83	2.00	0.13	3	395.44
dens	2.00	0.13	3	469.83	2.00	0.13	3	395.44
manag	5.90	0.02	5	469.73	5.60	0.02	5	395.04
soilt	9.96	0.00	7	469.79	9.87	0.00	7	395.31
dens+gw+veg+mcrickets+soilt+manag+mow	26.66	0.00	15	469.50	25.34	0.00	15	394.77

Covariates: dens = soil density, gw = ground water table, veg = vegetation cover, manag = ground management, mow = mowing, mcrickets = molecricket occurrence probability, soilt = soil type