Key ecological features for the persistence of an endangered migratory woodpecker of farmland, the wryneck (*Jynx torquilla*)

Diplomarbeit

der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

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2008
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ABSTRACT

1. Territory quality is a crucial component of individuals' fitness. Identifying areas with high quality territories is thus essential to ensure the persistence of endangered populations. Territory quality can be estimated using various life history indicators such as arrival date and frequency of site occupancy, or food abundance. We investigated the ecological requirements of an endangered population of the wryneck (*Jynx torquilla*), a declining ant-eating woodpecker species, by using data on nest site occupancy over six successive years (2002–2007) as well as data about ant abundance within territories.

2. Both a static and a dynamic approach were used. We first selected 100 territories at random and mapped habitat features. Food supply within territories was estimated through ant nest density in different habitat types, accounting for imperfect ant nest detection probability. Ecologically relevant variables were selected based on AIC criteria, and model averaging was applied so as to account for model selection uncertainty.

3. Wrynecks selected territories in a non-random way. Frequently occupied territories were systematically settled earlier in the season, suggesting that they may be of higher quality. Breeding success, however, was neither related to territory occupancy nor to territory variables, and appeared therefore not to be site-dependent. The results of the static occupancy approach revealed that the larger the area of old pear orchards and the smaller the area of vegetable culture within a territory, the higher the probability of territory occupancy. The dynamic approach showed that both the proportion of old pear orchards and the presence of conspecifics within a territory were positively related to its territory colonisation rate, whereas territory extinction rate was negatively related to habitat heterogeneity. Finally, ant nest density did not appear to function as a limiting resource.

4. *Synthesis and application.* To ensure the persistence of this endangered wryneck population, pear orchards, especially those consisting of old trees, must be promoted within heterogeneous agricultural matrices offering both a sufficient offer of nest sites (e.g. nest boxes) and suitable foraging grounds (patches of bare ground which enhance food detectability and accessibility; Weisshaupt, 2007). Studies of other wryneck populations are urgently needed to see whether the ecological requirements observed in Switzerland may apply beyond the studied population.

360 words

Key words: territory quality, occupancy model, habitat selection, detection probability, colonisation and extinction probability

1. INTRODUCTION

Territory selection is a crucial life history trait as it has direct consequences on individuals' fitness. Reproductive output is higher in high quality territories (Andrén, 1990; Tye, 1992). An individual should thus optimally settle in a territory offering high quality habitat patches that provide suitable resources, such as food, breeding sites, and protection from predators. According to the ideal despotic distribution (Fretwell & Lucas, 1969), territories are being occupied sequentially according to their quality. The occupancy of territories is thus a non-random process, with the best quality territories being monopolised by the best quality individuals or the first arrived. At the population level, the ideal despotic distribution leads to density-dependent population regulation. At low population size, only the best territories are occupied and the reproductive output peaks. As population size increases, less suitable territories are progressively occupied, resulting in a decrease in mean per capita productivity. This mechanism is called site-dependent population regulation (Pulliam, 1988; Pulliam & Danielson, 1991; Rodenhouse, Sherry & Holmes, 1997).

Territory quality can be assessed directly, measuring territory attributes, for instance the amount of limiting resources, or indirectly, through the performance of the study species – using for example demographic parameters – or by measuring spatial distribution and individual condition (Johnson, 2007). A measure of spatial distribution which is based on the ideal despotic distribution is the frequency of territory occupancy (Andrén, 1990; Sergio & Newton, 2003). If individuals are distributed according to the ideal despotic distribution, the frequency of territory occupancy is positively correlated with territory quality (Krüger, 2002; Sergio & Newton, 2003; Sim et al., 2007). High quality territories tend to be always occupied, whereas low quality ones are only occupied when breeding density is high. Relating the frequency of territory occupancy to territory variables may thus represent a good indicator of habitat quality. Combining these different approaches to assess territory quality may thus lead to an integral and detailed description of the ecological requirements of a focal species, which is essential for its conservation.

This static view of territory occupancy may be extended to a dynamic occupancy approach. Territory occupancy involves two processes: colonisation and extinction. These local processes may depend on stochastic, intrinsic or on extrinsic factors (Hanski, 1998, 1999), such as habitat quality or conspecific attraction (Danchin, Boulinier & Massot, 1998; Muller et al., 1997; Stamps, 1988). Thus territory variables that are positively related with colonisation and negatively with extinction indicate high quality. From a metapopulation dynamics viewpoint it is important to recognise the factors involved in these processes, especially as currently unoccupied territories may still be fundamental for ensuring the long-term persistence of a population. A key issue in conservation ecology is therefore the identification of gradients of territory quality, so as to prioritise conservation and management efforts in a strategic way. The main goal of this study was to identify which habitat features are the best indicators of habitat quality for wrynecks *Jynx torquilla* (Linnaeus 1758) inhabiting farmland so as to make targeted recommendations for conservation management.

One of the basic assumptions of this study is that wrynecks forage mostly within a 111 m radius around their nest (3.9 ha area) which corresponds to the median size of home-ranges of foraging wrynecks previously radio-tracked in the study area (Weisshaupt, 2007). Various habitat features were first mapped in a random subset of 100 out of the 195 breeding territories located at the study site between 2002 and 2007. We then assessed the abundance of ant nests in territories since ant broods constitute the main food of parents provisioning chicks (Bitz & Rohe, 1993). Finally, we related habitat type, food supply, interspecific competition for nest site, as well as conspecific attraction to the pattern of territory occupancy. Analyses were carried out using both a static occupancy model (variables related to frequency of occupancy) and a dynamic occupancy model (variables related to local colonisation and extinction processes of a given territory). Beforehand, we had to test some assumptions inherent to the occupancy models, such as territory selection, settlement order and site-dependent breeding success of different territories. Our main goal was to obtain fine-grained information on patterns of breeding habitat selection to recommend management guidelines which may ensure a long-term stability of that farmland wryneck population. We also hoped to identify key ecological requirements of farmland wrynecks in general, which may be relevant beyond the local context, especially given the precarious status of this species in several parts of its distribution.

2. MATERIAL AND METHODS

2.1. STUDY SITE AND STUDY SPECIES

The study area is located in the plain of the Rhone, between Vernayaz and Sion, in the Canton Valais (SW Switzerland, 46.2 °N, 7.4 °E; 482 m above sea level). It is characterised by a quite homogeneous landscape consisting mostly, outside the villages along the valley, of dwarf fruit plantations and intensive vegetable cultures. The study area harbours 351 nest boxes (hole diameter = 55 mm) which were installed in 2002 at 195 nest sites (mostly inside agricultural shacks, with most buildings having two boxes each).

In contrast to other woodpeckers, the wryneck is a secondary-cavity breeder which depends on the availability of pre-existing holes. Apart from suitable breeding sites, wrynecks require foraging grounds offering a sparse vegetation cover facilitating the access to ant nests, as well as numerous perches from where wrynecks can detect the nests (Bitz & Rohe, 1993; Ehrenbold, 2004; Freitag, 1996; Hölzinger, 1992). In our study area, the food provisioned by wryneck parents to their chicks comprises 90 % larvae and nymphs (Freitag, 1998). Telemetry studies in Valais revealed that wrynecks mostly forage within 100–125 m around their nest site, having home-ranges of 2.1–4.77 ha (Freitag, 1998; Weisshaupt, 2007), with orchards and fallow land being the favourite foraging habitats. Optimal feeding locations typically occur where the proportion of bare ground amounts to 60 % (Weisshaupt, 2007).

Between 2002 and 2007, all 195 nest sites were checked every fortnight during the breeding season. Once detected, a brood was monitored every 3–4 days. We called «brood» any clutch comprising at least one egg, irrespective of the reproductive outcome, whilst a «successful brood» was one yielding at least one fledgling.

2.2. DESIGN AND HABITAT VARIABLES

A random sample of 100 nest sites was selected among the 195 available sites in the study area from 2002 to 2007. Around each nest site we drew a 111 m radius circle in order to delineate a 3.9 ha «foraging territory» (median local foraging home-range size; Weisshaupt, 2007). There was an overlap between two adjacent 3.9 ha territories in only three cases, with a maximal overlap of 8.2 %. The habitat characteristics of the selected territories were mapped in early summer 2007. Variables comprised habitat types, number of trees and percentage of bare ground according to features stressed as important by Weisshaupt (2007; Table 1). An aerial photographic example of a mapped territory is given in Appendix 1.

We distinguished nine types of fruit plantations and orchards with respect to fruit type (apple, pear, apricot) and age of trees (young, medium, and old). The percentage of bare ground was estimated for each culture type (but not for sealed areas such as buildings and paved roads) by walking through the field while visually estimating the percentage of non-covered soil within culture parcels.

The assumptions of occupancy models are that territory quality and food resources remain constant over time and that individuals are able to promptly locate best quality territories. In our study area territory quality was assumed to be constant over the 6 years period since dwarf fruit plantations, which covered on average 48.9 ± 0.6 % of foraging territories (n = 100), have a slow replacement turn-over, and because ant nests are relatively long-lived (Seifert, 1996). In addition, wrynecks had a dense offer of nest sites (on average of 2.03 ± 0.06 boxes per territory) that we assumed that territory selection to operate conforming to individual's fitness maximisation, thus being independent of the variation of nest site availability. Finally, we assumed a despotic distribution of phenotypes between territories, with low quality individuals prevented from settling in high quality territories, and reproductive success reflecting territory quality (site-dependent reproductive success; Donovan et al., 1995; Ens et al., 1992; Pärt, 2001; Tye, 1992; Zajac, Solarz & Bielanski, 2008).

The density of ant nests within a territory was also used as a potential criterion for estimating habitat quality. Lookouts, such as trees, poles, shacks and fences, are an important habitat feature for wrynecks which are perch-hunters, with perches enhancing nest detectability (Freitag, 1998). We thus distinguished between ant nests from areas with look-outs (i.e. from habitat types: orchards, vineyards, riverbank, and pastureland) and those deprived of lookouts (i.e. from habitat types: vegetable cultures, fallow land, and meadowland). Ant nests from woodland were not included in the available food amount estimates because woodland specific ant species are almost never eaten by wrynecks (*Formica sp.* and *Camponotus sp.*, Seifert 1996, Freitag 1998). We also accounted for ant nest accessibility, which depends primarily on the area of bare ground in ant nest vicinity because wrynecks capture and eat prey on the ground (Weisshaupt, 2007). The square terms of the three discrete variables «bare ground with lookouts», «bare ground without lookouts», and «total bare ground» were also used in an attempt to identify optimal proportions of these key habitat components. For each territory, the distance to the next human settlement and to the next road was estimated using GIS (www.esri.com, Environmental Systems Research Institute, California) software based on 25 m resolution maps (Swisstopo, Bundesamt für Landestopographie, Seftigenstrasse 264, CH-3084 Wabern). Finally, an index of potential competition with hoopoes, which use the same nest boxes as wrynecks, was also derived from the number of years between 2002 and 2007 a hoopoe pair had occupied one of the two available nest boxes in the territory. The quadratic term of this index was also used in the analysis.

In the dynamic occupancy analysis we included a variable indicating conspecifics' presence for a given year, i.e. whether there were other breeding wrynecks within a radius of 500 m from the nest site, which is twice the maximal foraging distance from the focus nest site (Freitag, 1998). Conspecifics may actually influence site occupancy through patterns of social attraction, and/or public information about territory quality (Danchin, Boulinier & Massot, 1998; Danchin, Heg & Doligez, 2001; Doligez et al., 2003; Doligez et al., 1999).

Digitisation of the spatial data was done in ArcGIS 9.1. In total, 2589 different culture parcels were recorded and their areas were calculated from the digitalised polygons using XT Tools. The same cultures (e.g. parcels of the same habitat type and age) within a territory were summed up and their proportional area was used in the analysis. Percentage of bare ground within a territory was calculated by summing the percentage of bare ground per parcel weighted by its proportion of the entire territory area.

2.2.1. ESTIMATION OF FOOD SUPPLY: ANT NEST ABUNDANCE

To estimate overall food supply within territories, habitat-specific ant nest densities were multiplied by their proportional area of territory and summed. The density of nests of ground-living ants was assessed throughout the study area in potential wryneck territories in 2003 and 2004, based on a stratified design (with random selection of at least 90 plots per main habitat type among orchards, vineyards, meadowland, river bank, fallow land, and vegetable cultures). From 2005 until 2007 the assessments were limited to orchards (with different fruit types) as it turned out that they were the most important foraging habitat (Weisshaupt, 2007). Sample size varied between habitat types and years, ranging from 10 to 175 according to a given year design. At each sampling location, situated in the core of a given culture type to avoid edge effects (Dauber & Wolters, 2004), five 2 m^2 randomly defined replicates were searched for ant nests by scraping about 5 cm of the upper soil layer with a rake. The assessments were always carried out in the first half of May on 3–9 consecutive days under similar weather conditions. Habitat type (for orchards also age and fruit type), percentage of bare ground, grass vegetation height, number and relative size of ant nests were recorded. An ant nest was defined by the presence of ≥ 20 imagos aggregating together or the presence of eggs or larvae. Few individuals from each nest were sampled and preserved for subsequent species identification (Della Santa, 1994; Seifert, 1996).

To estimate the detection probability of ant nests we conducted a further study in 2007. We repeatedly searched for ant nests at exactly the same five 2 m^2 replicates in 19 randomly selected orchards (= 95 replicates) using the same technique as for the ant nest density assessment described above. The time needed to search for ant nests per replicate was 15–20 minutes. All 95 replicates were recorded within 3–4 days during three recording sessions in early May, June, and July. Mean temperature measured 5 cm above grass at each sampling time were obtained from MeteoSchweiz. A few ants were again taken from each nest for subsequent species identification.

The resulting detection histories for each of the 95 replicates were analysed with the program MARK (White & Burnham, 1999) using occupancy models (MacKenzie et al., 2002). We did not distinguish between detection probabilities of different ant species, as sample sizes of different species were fairly unbalanced. The covariates “height of vegetation” (range: 0–110 cm), “percentage of bare ground” (range: 0–100 %), and “mean hourly temperature” (range: 3.3–35.0 °C) were included to model detection probability. All variable combinations were tested with both a constant and a time dependent intercept, giving a total of 16 models. The occupancy probability ψ_1 was always kept constant. We ranked the models according to the small sample size adjusted Akaike’s Information Criterion (AICc), and the corresponding AICc weights (Burnham & Anderson 2002), and performed model averaging across the smallest subset of models that accumulate AICc weights of 0.95 to account for model selection uncertainty (Burnham & Anderson, 2002).

To obtain an estimate of the number of ant nest ($\hat{N}_i$) for replicate *i*, we divided the ant nest count (C_i) by the replicate specific detection ($\hat{p}_i$)

$$\hat{N}_i = \frac{C_i}{\hat{p}_i} \qquad (1).$$

The replicate specific detection probability is estimated using replicate specific temperature (t_i), vegetation height (v_i), percentage of bare ground (b_i), and the model averaged parameter estimates ($\bar{\hat{\beta}}_x$)

$$\hat{p}_i = \frac{1}{1 + \exp(-\bar{\hat{\beta}}_0 - \bar{\hat{\beta}}_1 t_i - \bar{\hat{\beta}}_2 v_i - \bar{\hat{\beta}}_3 b_i)} \qquad (2).$$

The estimated detection probability from the occupancy model does not match exactly with the detection probability needed to correct the ant nest counts (eq. 1). This is because the occupancy detection probability corresponds to the probability to detect at least one ant nest within a replicate, given that the replicate is occupied by at least one ant nest. To correct the counts, we would need the probability to detect one ant nest. However, because the size of the replicates used to estimate replicate occupancy detection were small, only one ant nest was present in most occupied replicates. Therefore, the two detection probabilities were close.

The counts of ant nests of each replicate were corrected with the corresponding detection probability. The mean ant nest density for each habitat type (fallow land, meadowland, vineyards, vegetable cultures, riverbank, and apple, apricot, and pear orchards) was then estimated by fitting generalised linear mixed models with a Poisson error distribution to *N* for each habitat type separately with program R (Version R 2.5, R Development Core Team 2007). The random effect was “plot per year“, as there were always five replicates in each plot per year, which were not completely independent. For the habitat type “orchard” we did not include the age as the model including “age” showed a higher AICc than the one without “age”. Averaged estimates and standard errors were obtained by using bootstrap with 1000 replicates.

2.3. OCCUPANCY ANALYSES

2.3.1. ASSUMPTIONS

The following analyses were conducted with program R. To test whether wrynecks actively selected their territory or whether they settled randomly, a χ^2 test was performed comparing the observed frequency of territory occupancy (n = 195 and n = 100, respectively) with an expected one drawn from the binomial distribution.

According to the ideal despotic distribution (Fretwell & Lucas, 1969) better territories are settled earlier, and thus, more frequently occupied territories should be settled earlier. We used the laying date of the first egg as an index of territory settlement. To test whether settlement order depended on the year we used linear mixed models and a likelihood ratio test. We then related the median of the laying date of the first egg for each territory to the frequency of its occupancy using linear regression. Only first broods were considered (n = 108).

If breeding success was site-dependent in our studied population, it should be positively correlated with the frequency of territory occupancy. This prediction was tested using linear regression with breeding success of a territory (territory specific average of clutch size, number of hatchlings, and number of fledglings, respectively) as dependent variable and the frequency of territory occupancy as independent variable. Fledgling success (number of fledglings divided by number of hatchlings) was tested as well using general linear regression assuming binomial error distribution. Both, successful first and second broods, were included in this analysis (n = 85).

2.3.2. STATIC MODEL

To model the frequency of occupancy we used a generalised linear model with a binomial error distribution. The nominator of the response variable was the number of times a territory way occupied and the denominator was the number of study years (6). Thus, the parameter that was estimated and modelled was the annual probability that a territory was occupied. From all recorded territory variables some were excluded from this occupancy analysis, either due to their irrelevance as foraging habitat (anthropogenic habitat and water; Table 1), or because they occurred in less than 20 territories (riverbank and pastureland). The remaining 24 variables were pair-wisely correlated and the variable “ant without lookout” was excluded because it was correlated with two other variables ($r_s > |0.7|$). 23 explanatory variables were finally considered. The variables “hoopoe”, “total bare ground”, “bare ground with lookouts”, and “bare ground without lookouts” were additionally considered as square to model potential curvilinear relationships (= 27 variables). We then fitted different models containing each one of these explanatory variables and ranked them according to their AICc weights. All variables from models with a $\Delta AIC < 4$ to the best model were included in a second modelling step. We built models with all possible combinations of the remaining variables (= 3 variables and 8 models) and we compared them using AICc weights. To make predictions, we model averaged across all models within the second modelling step that accumulated at least 0.95 of the AICc weights.

2.3.3. DYNAMIC MODEL

To model colonisation and extinction probabilities, we used a dynamic occupancy model (MacKenzie et al., 2003; Royle & Dorazio, 2008). Let $z_{i,t}$ denote the occupancy status of site *i* at time *t* with z = 0 if the site is unoccupied, and z = 1 if the site is occupied. To model the dynamics of site occupancy a simple formulation in terms of initial (i.e. at time t = 1) occupancy probability (ψ_1), colonisation probability (γ) and extinction probabilities (ε) exists. The initial occupancy state is assumed to be a Bernoulli random variable,

$$z_{i,1} \sim Bern(\psi_1) \qquad (3),$$

whereas in subsequent periods,

$$z_{i,t} \mid z_{i,t\text{-}1} \sim Bern\left(\pi_{i,t}\right) \qquad (4),$$

where

$$\pi_{i,t} = z_{i,t\text{-}1}(1 - \varepsilon_{i\text{-}1}) + (1 - z_{i,t\text{-}1})\gamma_{t\text{-}1} \quad (5).$$

This model was fitted with program MARK (White & Burnham, 1999).

The same 23 variables were considered as described above in the static occupancy model. In addition we considered also the variable “presence of conspecifics”. The variables “total bare ground”, “bare ground with lookouts”, and “bare ground without lookouts” were again used as square terms. In this analysis, the variable “hoopoe” was not used as square term (= 27 variables).

Model selection was performed in multiple steps: first, all 27 variables were tested singly for ε (extinction-models) and for γ (colonisation-models) with a constant and a time dependent intercept whilst the factor without explanatory variable (γ or ε) remained time dependent ((27 variables + null model) * 2 (time dependence or constant intercept) * 2 (γ or ε) = 112 models). All models with a ΔAIC < 4 were selected separately for the extinction- and the colonisation-models. In a second step, the variables from the selected extinction-models were combined with the variables from the selected colonisation-models. From the selected variables, maximally one variable for ε and maximally one for γ were combined using both time-dependent and constant intercepts (= 36 models). A model averaging with models accounting to 0.95 to the AICc weights was performed. The initial occupancy probability (ψ_1) was not modelled with explanatory variables and the detection probability was fixed at one in the complete modelling approach.

2.4. BREEDING SUCCESS

To test whether the important territory variables identified in the static and in the dynamic approaches were linked to breeding success, we fitted generalised linear mixed models with Poisson error distribution. The dependent variable was the “number of fledglings” from successful broods (n = 50). The random effect was “territory identity” and the fixed effects were those explanatory variables that affected occupancy, colonisation or extinction rate. All possible variable combinations were tested (= 53 models) and we used the ΔAICc to rank these models. Only the successful first and second broods from the 100 selected territories were included in the analysis (n = 50).

3. RESULTS

3.1. ESTIMATION OF FOOD SUPPLY: ANT NEST ABUNDANCE

During the three visits to orchards carried out in 2007 we could locate 242 ant nests belonging to four species: *Lasius niger* (75.6 %, n = 183) was by far the most abundant species, *Lasius flavus* (14.9 %, n = 36), *Tetramorium caespitum* (7.4 %, n = 18), and *Solenopsis fugax* (2.1 %, n = 5) were less common.

Model selection revealed that ant nest detection probability was strongly dependent on temperature, vegetation height, and that it varied across time (Table 2). The amount of bare ground also affected detection probability, but there was more uncertainty compared to the other variables (Table 3). Mean model averaged detection probabilities decreased in the course of the season (May: 0.723 (SE: 0.058), June: 0.588 (SE: 0.061), July: 0.438 (SE: 0.059)). Detection probability increased with temperature (Fig. 1a), decreased with vegetation height (Fig. 1b), and increased slightly with amount of bare ground (Fig. 1c). The averaged occupancy probability was 0.837 (SE: 0.046). The false absence rate obtained for three visits was $p = (1-p_1)*(1-p_2)*(1-p_3) = 0.064$.

To calculate the detection probability of ant nests for each replicate, we used the model averaged parameter estimates (Table 3) and the replicate specific variables. Since the large survey was conducted in May, we used the detection probability of this month. Thus, the equation used to calculate replicate specific ant nest detection probabilities was: $p = 1/(1+\exp(-0.63206012 - 0.06966036 * \text{temperature [°C]} - 0.00300383 * \text{bare ground [\%]} + 0.04090232 * \text{vegetation height [cm]}))$.

The habitat specific ant nest density estimates were calculated by fitting generalised linear mixed models for each habitat type and using bootstrap method. Vegetable cultures had the lowest ant nest density among the sampled habitat types. Vineyards, fallow land, meadowland, and riverbank showed medium ant nest densities. The highest densities were found in orchards, especially in pear orchards (Table 4).

3.2. OCCUPANCY ANALYSES

3.2.1. ASSUMPTIONS

The frequency distribution of the territory occupancy deviated significantly from a randomly generated frequency distribution ($\chi^2 = 42.22$, df = 6, $p < 0.000$; Fig. 2) indicating that wrynecks did not settle randomly but that they chose their territories. This was true also when considering only the sampled 100 territories ($\chi^2 = 20.77$, df = 6, p = 0.002).

More frequently occupied territories were settled earlier in the season (estimate = -3.298, SE: 0.894, $p < 0.000$, Fig. 3). Settlement order was independent of the year (Likelihood ratio test, $\chi^2 = 1.726$, df = 1, p = 0.189).

Breeding success was not significantly correlated with frequency of territory occupancy. Clutch size (estimate = 0.110, SE: 0.120, p = 0.363), number of hatchlings (estimate = 0.259, SE: 0.178, p = 0.148), and number of fledglings (estimate = 0.245, SE: 0.194, p = 0.209) showed a positive trend (linear regression), whereas fledgling success showed a negative trend (estimate = 0.016, SE: 0.128, p = 0.903; general linear regression).

3.2.2. STATIC MODEL

In the first modelling step, we tested each of the 27 explanatory variables singly. The strongest impact on occupancy had "old pear orchard", while the other variables were clearly worse (Table 5). The second and third best variables, "vegetable cultures" and "ant nests from area with lookouts", were still within 4 ΔAICc units and were also considered for the second modelling step.

The second modelling step showed that the combination of "old pear orchard" and "vegetable cultures" resulted in the best model (Table 6). The averaged estimate for the intercept was -1.271 (SE: 0.249, CI: -1.759, -0.782), for old pear orchards 0.032 (SE: 0.012, CI: 0.009, 0.056), for vegetable cultures -0.013 (SE: 0.010; CI: -0.033, 0.006), and for ant nests from area with lookouts 0.00001 (SE: 0.00002, CI: -0.00003, 0.00005). Model averaged predictions showed that the probability of occupancy was positively related with the proportion of old pear orchards within a territory and negatively with the proportion of vegetable cultures (Fig. 4).

3.2.3. DYNAMIC MODEL

In the first modelling step, we tested the impact of each of the 27 variables on colonisation and extinction rate (Appendix 2 and 3). The best models (defined as ΔAICc < 4) included “number of parcels” and proportion of “young apple orchards” affecting the extinction rate, and the proportion of “old pear orchards” and ”presence of conspecifics” affecting the colonisation rate. In addition, colonisation rate differed across study years, while the extinction rate did not.

In the second modelling step, the identified potentially important variables were combined (Table 7). The best model included “number of parcels” affecting extinction probability and the proportion of “old pear orchards” affecting colonisation probability. For the colonisation probability there was also some support for “presence of conspecifics”, while the proportion of “young apple orchards” had almost no support.

Model averaging was performed with the 13 best models which accounted for 0.95 of the AICc weights (Table 7). Extinction rate (ε) was negatively affected by the number of parcels (averaged parameter estimate on logit scale: estimate = -0.038, SE: 0.027, CI: -0.092, 0.016) and weakly positively affected by the percentage area of young apple orchards within a territory (estimate = 0.002, SE: 0.004, CI: -0.006, 0.010). Colonisation rate (γ) was positively affected by the percentage area of “old pear orchards” within a territory (estimate = 0.044, SE: 0.029, CI: -0.013, 0.101) and by the “presence of conspecifics” (estimate = 0.241, SE: 0.375, CI: -0.494, 0.976). These estimates were back transformed from logit scale in order to calculate the averaged predictions, which were based on the year 2004 (arbitrary chosen reference year) if the model was time-dependent.

Model averaged predictions showed that the extinction rate negatively depended on the “number of parcels” and only very weakly on the proportion of young apple orchards within a territory (Fig. 5a, b). The colonisation rate strongly increased with increasing proportion of old pear orchards within the territory (Fig. 5c). It was also slightly enhanced when conspecifics were present compared to when no conspecifics were present (Fig. 5d).

3.3. BREEDING SUCCESS

The breeding success did not depend on the as important identified explanatory variables (old pear orchards, number of parcels, presence of conspecifics, vegetable cultures, and young apple orchards). The model in which breeding success was constant was better supported by the data than any combination of these explanatory variables (Appendix 4).

4. DISCUSSION

Wrynecks selected territories not randomly and the best territories were settled earlier in the season. The probability that territories were occupied and the probability that territories were newly colonised were positively related with the proportion of old pear orchards within the territories, while the probability that territories got extinct was negatively related with the number of parcels within the territories. In addition, territories with presence of conspecifics in the vicinity were slightly more likely to be colonised than territories without them. However, the reproductive success was not related to these territory variables.

Territory selection and territory quality

The proportion of old pear orchard within a territory appears to be an important factor affecting territory colonisation and occupancy. Old and medium orchards, but not necessarily old pear orchards, were preferred foraging habitats of wrynecks in the study area as evidenced by telemetry studies (Freitag, 1998; Weisshaupt, 2007). Indeed, orchards generally had higher ant nest densities than other habitat types, and pear orchards harboured higher densities than apple or apricot orchards (Table 4). The preference of pear orchards may be due to higher food density and to better access and higher detection probability, as old pear orchards have higher percentage of bare ground than old apple or old apricot orchards (average percentage of bare ground in old pear orchards: 38.7 ± 22.9 %, in old apple orchards: 32.4 ± 18.5 %, in old apricot orchards: 22.3 ± 19.8 %; ANOVA $F = 6.714$, $df = 6$, $p < 0.001$). Overall, trees in old orchards had a denser foliage than the younger trees of orchards, often leading both to denser aphid populations and sparse ground vegetation (bare ground), two factors that are likely to increase the abundance of food for the ants and thus their abundance and accessibility for the wrynecks. The negative impact of the area devoted to vegetable cultivation is in line with findings of Freitag (1998) and Weisshaupt (2007), who observed an avoidance of radio-tracked foraging wrynecks for vegetable cultures and gardens, urban areas and riparian forests. Although areas with vegetable cultures were usually sparsely vegetated and therefore would allow a good access to ant nests, they had a low ant nest density and were mostly free of look-out points. Thus, these areas were not suitable foraging habitats and therefore negatively affected territory occupancy.

The results of the dynamic occupancy analysis suggest that wrynecks may select their territories based, firstly, on directly observable habitat features (presence of pear orchards, habitat heterogeneity), secondly, on indirect criteria (presence of conspecifics). Territory extinction probability was negatively affected by the number of parcels, i.e. with the heterogeneity of the agricultural landscape matrix. According to Dauber & Wolters (2004), most ant species, including *Lasius niger* (the staple food of the Valais wrynecks; Freitag, 1996, 1998) can experience an edge effect, which would lead to differences in abundance between the centre and the edge of a culture parcel. This may provide a functional explanation, different from the traditional view that habitat complementarity itself is the main reason for favouring heterogeneity, in habitat selection decisions (Benton, Vickery & Wilson, 2003; Boecklen, 1986; Roth, 1976). Moreover, territories with many different culture parcels are likely to be more buffered against disturbance (removal of single orchards, different pest application) and thus provide constant availability of food. This may be especially important in areas with intensively managed agriculture.

Territory colonisation probabilities differed between years, whereas the extinction probability remained constant. This indicates that colonisation also depends on time-dependent factors (e.g. weather-induced variation in food resource availability and/or foraging habitat accessibility; Geiser, Arlettaz & Schaub, in press) or it may indicate also a considerable amount of stochasticity.

The presence of conspecifics affected the colonisation probability positively, which is in accordance to many dispersal studies (Muller et al., 1997; Stamps, 1988). In colonial or open nesting birds the reproductive success, which is predictive for new recruits, can easily be assessed as public information (Brown, Brown & Danchin, 2000; Danchin, Boulinier & Massot, 1998). The quality of a territory is therefore reflected as patch reproductive success (PRS; Boulinier & Danchin, 1997). However, in non-colonial, hole-nesting birds, such as the wryneck, PRS may be difficult and/or more costly to assess (Doligez et al., 1999). While experienced birds rely more on individual reproductive success (IRS), which eventually leads to site fidelity (Martínez, Pagán & Calvo, 2006; Switzer, 1997), juveniles and unsuccessful breeders preferentially rely on PRS (Doligez et al., 1999) or on the presence of conspecifics to evaluate territory quality (Muller et al., 1997). Our results show that wrynecks preferred to colonise territories in the presence of conspecifics within a 500 m radius. Since wrynecks' breeding success was not related to territory quality, settlement decisions were probably less influenced by public information (such as PRS) than by an assessment of obvious territory features (presence of old pear trees, vegetable cultures, habitat heterogeneity) and/or by the presence of conspecifics. This conclusion seems supported by the high individuals' turn-over observed in the studied population: 78.8 ± 5.3 % of the wrynecks captured during breeding season from 2003–2007 were new to the study area (n = 248 capture events out of 311). If most of these newcomers were juveniles (age is extremely difficult to determine in wrynecks) or unsuccessful breeders, two classes more likely to disperse (Switzer, 1997), then the hypothesis of territory evaluation through the mere presence of conspecifics would be supported.

The outcome of the static model was mostly congruent with the outcome of the dynamic model, although slight discrepancies appeared. The advantage of the dynamic approach is that territory selection can be modelled for each year, getting rid of the constraint that territory variables must remain constant across time (for example the hoopoe population, i.e. the suspected interspecific competition pressure, increased from 2002 till 2007). This dynamic approach is therefore a promising way of analysing habitat selection patterns even in the context of a changing environment.

In contrast to our expectations based on a previous study of the same wryneck population (Weisshaupt, 2007), the proportion of bare ground within a territory was neither important for territory occupancy, nor for extinction nor for colonisation, despite that wrynecks chose to forage at places that had about 60 % of bare ground (radio-track study of micro-habitat selection; Weisshaupt 2007). This discrepancy is most probably due to a scale effect (George & Zack, 2001; Orians & Wittenberger, 1991): while at the micro-habitat scale the proportion of bare ground is important, it might be not that crucial at a larger spatial scale. Still, at larger spatial scale some proportion of bare ground is certainly necessary, but the limiting amount may be far less than 60 % and presumably this necessary amount was already reached in most territories in our study area.

It may be argued that the actual factors driving patterns of habitat selection in our wrynecks could have been masked, firstly, by an ecological trap effect potentially generated by nest boxes' availability and their spatial location (Mänd et al., 2005; Robertson & Hutto, 2006; Schlaepfer, Runge & Sherman, 2002). We believe, however, that the wide offer of artificial breeding sites in the study area renders this hypothesis very unlikely. Secondly, factors dictating habitat selection would also be difficult to identify if the agricultural landscape matrix would be too homogeneous; in this case, territory occupancy would be governed solely by metapopulation dynamic processes. Although we think this does not apply to the whole study area, where agricultural parcel size remains relatively small (less than ca 0.5 ha on average), the absence of link between reproductive success and territory quality among our subsample might have been confused by a sort of homogenisation effect, with, in this scenario, all good territories with high reproductive output being more or less ecologically equivalent. This problem would be more acute if the population would be well below its carrying capacity. Then, breeding success itself, as measured here, may not be the most important fitness component for wrynecks; instead, post-fledging survival, lifetime reproductive success or individual quality may play a more crucial role. Finally, actual territory quality may be lowered by nest predation or interspecific nest site competition, although the latter is dismissed by the non-inclusion of the variable "hoopoe", one of the most likely competitors locally as regards nest sites, in the best models.

Are ants as main food resource a limiting factor?

The ant nest density estimates which were not corrected for imperfect detection probability and the low ant species richness in orchards, with predominance of *Lasius niger,* corroborate former findings by Freitag (1996; 1998). After correcting for detection probability, the highest ant nest densities were observed in orchards, followed by riverbank and meadowland, whilst the lowest density was found in parcels with vegetable cultures. The latter habitat is characterized by frequent disturbance (ploughing, fertilisation, pesticides application, culture rotation), which is detrimental to the installation of most ant species (Freitag, 1998). Although Freitag's (1996) estimates of ant nest density were higher than ours (0.45 nests/m^2 in orchards, 0.33 nests/m^2 in riverbank, and 0.274–0.390 nests/m^2 in orchards, 0.205 nests/m^2 in riverbank in this study, respectively), the relative densities in different habitat types were similar: vineyards and vegetable cultures were sparsely populated, whilst orchards and meadowlands harboured higher densities. In their long-term study, Dauber & Wolters (2005) showed that there was no drastic change in ant species composition and richness over time in grassland. We also observed no change in ant nest abundance during our five years of study in any habitat type. It seems therefore that food supply is not a limiting factor for the Valais wryneck population, at least at its current density.

Detection probability of ant nests strongly depended on vegetation height and ambient temperature, and less on the percentage of bare ground. The strong dependence on ambient temperature is not surprising for poikilothermal insects such as ants (Mellanby, 1939). Ants displace their brood deeper into the soil in response to both temperature increase and heavy rainfall (Seifert, 1996). The vegetation height affected the visibility of ant nests which were mostly not mounds.

Species belonging to a homogeneous taxon (e.g. order or family) can have different detection probabilities according to their spatial and temporal abundance, their conspicuousness and lifestyle (Kéry & Schmid, 2004). In our analysis, we did not estimate a separate detection probability for each of the four ant species for three reasons. First, the sample sizes of the species were far from even; second, the different ant species were found in the same plots, which would have led to pseudo-replication; third, an overall estimate of detection probability is more convenient than a species-specific one for extrapolations to other habitat types, especially when guild arrangements are habitat specific (Seifert, 1996).

The four detected ant species in this study are very much alike as regards habitus and behaviour; they all enter the diet of wrynecks which feed opportunistically on the available ant species (Freitag, 1996, 1998). *Lasius sp.* are typical prey, due to their high abundance, relatively large nests excavated in open areas, and densely populated colonies facilitating detection. *Tetramorium sp.* is less profitable due to its much smaller body size. By contrast, *Solenopsis*, which is also found in orchards, is small, rather rare and builds only small colonies (Freitag, 1998), which renders it less profitable. Altogether, the differences in ant nest abundance observed between habitat types may be to some extent due to agricultural practices varying between culture types, such as mowing regime or application of pesticides, which may reduce the abundance of food for ants (e.g. treatment against aphids).

Implications for conservation

The persistence of a wryneck population in the plain of the Rhone in Valais seems to depend primarily on the presence of orchards, especially on the availability of old pear trees. A richly-structured mosaic agricultural matrix appears also beneficial as wrynecks tend remain longer in territories offering higher local habitat heterogeneity (number of parcels and/or culture types) than average, possibly due to edge effects favouring ant abundance and/or the detectability and accessibility of their nests. Although the study area consisted mainly of intensively managed orchards, the abundance of food resources (ants) did not seem to be a limiting factor, at least at the current wryneck density. However, previous fine-grained radio-tracking investigations of foraging habitat selection in the wryneck suggest that the detectability and the accessibility of ant food is a crucial parameter (Weisshaupt 2007). In particular, the presence of patches of bare ground at the micro-scale (circle of 1 m radius), with an optimum around 60 %, seems to be decisive for optimal foraging behaviour (Weissaupt 2007). It is thus essential that these various habitat features are maintained simultaneously in the habitat matrix. Finally, the availability of a high offer of nest sites could also favour conspecific attraction, which seems to impact on the capacity to colonise a given habitat patch. In the quasi absence of natural tree cavities, nest boxes are the best solution here. The European wryneck currently declines almost throughout its European range (Ryttman, 2003; Tomialorc, 1994). This study constitutes the first evidence-based contribution to a better understanding of species' ecological requirements, and as such may orientate the focus of conservation research on other populations whose status is critical.

5. ACKNOWLEDGMENTS

I am grateful to PD Michael Schaub for his excellent supervision and support during fieldwork and statistical analyses and also to Prof. Raphaël Arlettaz for his supervision and giving me the opportunity to work in the very fascinating field of conservation biology. I thank Thomas Reichlin, who introduced me to the fieldwork and assisted very patiently, and Laura Dafond and Myles Menz for the good collaboration during fieldwork. Thanks go also to Natalina Signorell who helped with GIS program, to Fitsum Abadi Gebreselassie who supported me in statistics, and to Valérie Coudrain for her help with ant species identification. I thank all CB members for their encouragement and their helpful discussions and I specially thank my boyfriend, Thomas Riebli, for his great support during my diploma work.

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TABLES

Table 1. Variables retained for habitat characterisation for each of the 100 territories with a total area of 390 ha. The habitat types, “bare ground proportion” and “other variables” were recorded in 2007. The “food resources” were computed based on a separate survey and the “disturbance” variables were taken from GIS-maps. Given are also some summary statistics about the variables: for habitat types the total area (ha), mean size of a culture (ha), total number of parcels, and number of territories in which the culture occurred; for the other variables the minimum (zero values excluded), maximum, and average per territory, and the number of territories where the variable occurred are shown.

Habitat type	Description	total area (ha)	mean size of culture (ha)	total number of parcels	number of territories
Anthropogenic	road, building	35.930	0.359	590	100
Water	canal, Rhone river, ponds	13.573	0.247	82	55
Vegetable cultures	vegetable cultures, garden	46.209	0.624	183	74
Fallow land	fallow land, vegetated canalbanks	27.917	0.317	309	88
Woodland		12.520	0.358	65	35
Pastureland		9.519	0.501	34	19
Meadowland		33.052	0.466	149	71
Riverbank		6.465	0.497	21	13
Vineyards		18.751	0.750	114	25
Old orchards	recorded separately for apple, apricot, pear. Stem diameter > 15 cm	55.877	0.170	328	86
Medium orchards	recorded separately for apple, apricot, pear. Stem diameter 5–15 cm	70.788	0.206	343	89
Young orchards	recorded separately for apple, apricot, pear. Stem diameter < 5cm	62.666	0.232	270	83

Food resources		**min [No of nests]**	**max [No of nests]**	**mean [No of nests]**	**number of territories**
Ant nests in habitats with lookouts	habitat types: orchards, riverbank, pastureland, vineyards	182.012	12511.826	6695.996	98
Ant nests in habitats without lookouts	habitat types: vegetable cultures, fallow land, meadowland	4.034	4522.718	1303.169	90
Bare ground proportion (%)		**min [%]**	**max [%]**	**mean [%]**	
Bare ground in habitats with look-outs	habitat types: orchards, riverbank, pastureland, vineyards	0.471	50.622	19.419	98
Bare ground in habitats without lookouts	habitat types: vegetable cultures, fallow land, meadowland	0.086	50.010	7.468	92
Total bare ground within territory		5.938	57.658	25.901	100
Other variables		**min**	**max**	**mean**	
Tall trees	n° of trees higher than 4 m	1	118	20.714	49
Number of parcels	per territory	6	37	19.030	100
Number of years a hoopoe occupied same territory	over all six study years	1	6	3.069	58
Breeding conspecifics within < 500 m	binomial for each year; only for dynamic occupancy analysis	NA	NA	NA	NA
Disturbance		**min [m]**	**max [m]**	**mean [m]**	
Distance to next road	25 m resolution map	25	111.803	41.768	37
Distance to next human settlement	25 m resolution map	25	903.120	384.049	98

Table 2: Model selection summary of detection probability of ant nests as function of season (time), temperature, percentage of bare ground, and vegetation height evaluated by occupancy models. Also given are the ΔAICc, AICc weights ($w_i = \exp(-0.5*\Delta AICc_i)/\Sigma\exp(-0.5*\Delta AICc)$), number of parameters (*K*) and the residual deviance. The occupancy probability (Ψ_1) was constant in all models. The models are ranked according to their ΔAICc. T_a = ambient temperature.

Model	ΔAICc	w_i	*K*	Deviance
Time + T_a + vegetation height	0.000	0.527	6	358.017
Time + T_a + bare ground + vegetation height	1.160	0.295	7	356.844
Time + vegetation height	3.577	0.088	5	363.875
Time + bare ground + vegetation height	4.393	0.059	6	362.410
Time + T_a + bare ground	6.936	0.016	6	364.953
Time + bare ground	8.610	0.007	5	368.908
Time + T_a	10.153	0.003	5	370.451
T_a + vegetation height	11.514	0.002	4	374.041
Time	11.682	0.002	4	374.209
Vegetation height	13.309	0.001	3	378.017
T_a + bare ground + vegetation height	13.497	0.001	5	373.794
Bare ground + vegetation height	15.053	0.000	4	377.580
T_a + bare ground	17.566	0.000	4	380.093
T_a	17.911	0.000	3	382.618
Bare ground	18.139	0.000	3	382.847
Constant model	18.753	0.000	2	385.594

Table 3: Model averaged parameter estimates, standard errors and confidence intervals (95 % CI) of the parameters that influence ant nest detection probability.

Parameters	Estimate	Standard Error	Lower CI	Upper CI
Intercept	0.632	0.878	-1.089	2.353
T_a	0.070	0.042	-0.012	0.151
Bare ground	0.003	0.005	0.013	-0.007
Vegetation height	-0.041	0.014	-0.068	-0.014

Table 4: The estimated ant nest densities obtained by fitting generalised linear mixed models and using bootstrap method. Shown are the naïve estimates (i.e. not corrected for imperfect detection probability), and the estimates which were corrected for imperfect detection probability with their standard errors and sample size.

Habitat type	Estimated density per m^2 (naïve estimates)	Estimated density per m^2 (corrected for detection probability)	Standard error	Sample size
Vegetable cultures	0.011	0.079	0.005	110
Vineyards	0.100	0.133	0.016	90
Meadowland	0.112	0.187	0.014	270
Fallow land	0.114	0.154	0.014	210
Riverbank	0.191	0.205	0.021	150
Apple orchards	0.240	0.274	0.016	520
Apricot orchards	0.233	0.305	0.030	155
Pear orchards	0.314	0.390	0.024	405

Table 5. Summary results of the static occupancy modelling when all 27 explanatory variables were used as single variable (note that the squared variables also contained the main effect). Given are the ΔAICc, the AICc weights ($w_i = \exp(-0.5*\Delta AICc_i)/\Sigma\exp(-0.5*\Delta AICc)$), the number of parameters (*K*) and the residual deviance. The models are ranked according to their ΔAICc. The first three models are within ΔAIC < 4 and were thus selected for the second analysis step.

Model	ΔAICc	w_i	*K*	Deviance
Old pear orchard	0.00	0.612	2	223.69
Vegetable cultures	3.64	0.099	2	227.33
Ant with lookouts	3.74	0.094	2	227.43
Number of parcels	5.36	0.042	2	229.05
Bare ground with lookouts	6.86	0.020	2	230.55
Hoopoe	7.38	0.015	2	231.07
Medium apple orchard	7.52	0.014	2	231.21
Medium apricot orchard	7.59	0.014	2	231.28
Old apricot orchard	8.37	0.009	2	232.06
Total bare ground	9.00	0.007	2	232.69
Total bare ground^2	9.11	0.006	3	232.80
Constant model	9.26	0.006	1	234.94
Number of tall trees	9.28	0.006	2	232.97
Young pear orchard	9.36	0.006	2	233.05
Bare ground with lookouts^2	9.47	0.005	3	233.16
Young apricot orchard	9.72	0.005	2	233.41
Hoopoe^2	10.19	0.004	3	233.88
Distance to next road	10.48	0.003	2	234.17
Woodland	10.49	0.003	2	234.18
Vinyards	10.59	0.003	2	234.28
Bare ground without lookouts	10.64	0.003	2	234.33
Fallow land	10.79	0.003	2	234.48
Distance to next human settlement	10.86	0.003	2	234.55
Young apple orchard	11.13	0.002	2	234.82
Old apple orchard	11.23	0.002	2	234.92
Bare ground without lookouts^2	11.23	0.002	3	234.92
Medium pear orchard	11.25	0.002	2	234.94
Meadowland	11.26	0.002	2	234.94

Table 6: Summary results of the static occupancy modelling when the three explanatory variables selected in the first step (Table 5) are used jointly. Given are the ΔAICc, the AICc weights ($w_i = \exp(-0.5*\Delta AICc_i)/\Sigma\exp(-0.5*\Delta AICc)$), the number of parameters (*K*) and the residual deviance. The models are ranked according to their AICc weight.

Model	ΔAICc	w_i	*K*	Deviance
Old pear orchards + vegetable cultures	0.00	0.538	3	218.52
Old pear orchards + vegetable cultures + ant with lookouts	1.99	0.199	4	218.44
Old pear orchards	3.17	0.110	2	223.69
Old pear orchards + ant with lookouts	3.41	0.098	3	222.80
Ant with lookouts + vegetable cultures	6.66	0.019	3	226.64
Vegetable cultures	6.81	0.018	2	227.33
Ant with lookouts	6.91	0.017	2	230.27
Constant model	12.43	0.001	1	234.94

Table 7. Model selection summary of extinction (ε) and colonisation (γ) rates of wryneck territories. Shown are the 13 best models (from originally 36 fitted models). Given are the ΔAICc, the AICc weights (w_i = exp(-0.5*ΔAICc$_i$)/Σexp(-0.5*ΔAICc)), the number of parameters (*K*) and the residual deviance. A constant intercept is indicated with (.), a time dependent one with "year". The initial occupancy probability (Ψ_1) is set constant in every model (average estimate: 0.290 (SE: 0.045)).

Model	ΔAICc	w_i	*K*	Deviance
ε(number of parcels) γ(year + old pear orchards)	0.000	0.439	9	595.385
ε(number of parcels) γ(year + presence of conspecifics)	2.923	0.102	9	598.308
ε(year + number of parcels) γ(year + old pear orchards)	2.958	0.100	13	590.027
ε(.) γ(year + old pear orchards)	3.703	0.069	8	601.149
ε(number of parcels) γ(presence of conspecifics)	3.839	0.064	5	607.428
ε(young apple orchards) γ(year + old pear orchards)	3.966	0.060	9	599.351
ε(number of parcels) γ(old pear orchards)	5.881	0.023	13	592.950
ε(year number of parcels) γ(year + presence of conspecifics)	6.626	0.016	8	604.072
ε(.) γ(year + presence of conspecifics)	6.685	0.016	9	602.070
ε(year + number of parcels) γ(presence of conspecifics)	6.889	0.014	9	602.274
ε(young apple orchards) γ(year + presence of conspecifics)	7.264	0.012	12	596.422
ε(year) γ(year + old pear orchards)	7.307	0.011	13	594.375
ε(year + young apple orchards) γ(year + old pear orchards)	2.923	0.102	9	598.308

FIGURE CAPTIONS

Figure 1. Relationship between detection probability of ant nests and temperature (a), vegetation height (b), and amount of bare ground (c). Shown are model averaged predictions (based on results in Table 2) with standard errors.

Figure 2. Expected and observed frequencies of territory occupancy over the six study years. Expected frequencies are calculated using the binomial distribution. The observed frequency of territory occupancy significantly deviates from the expected one.

Figure 3. Relationship between territory quality and the date of settlement. Shown is the linear regression between territory occupancy and the median of the date of egg laying of a territory.

Figure 4. Predicted model averaged probability of territory occupancy, calculated from the best models accounting to 0.95 of the AICc weight (Table 6) in relation to proportion of old pear orchards (a), of vegetable cultures (b), and of ant nests from area with lookout (c) within the territory. The figures show averaged estimates with standard errors.

Figure 5. Predicted model averaged probabilities of local territory extinction and colonisation from the best models accounting to 0.95 of the AICc weight (Table 7). Shown are the number of parcels (a), and proportion of young apple orchards within the territory (b) in relation to extinction rate, and the proportion of old pear orchards within a territory (c), and the presence of conspecifics within a radius of 500 m to the nest site (d) in relation to colonisation rate. In time-dependent models the predictions are shown for the year 2004. The figures show averaged estimates with standard errors.

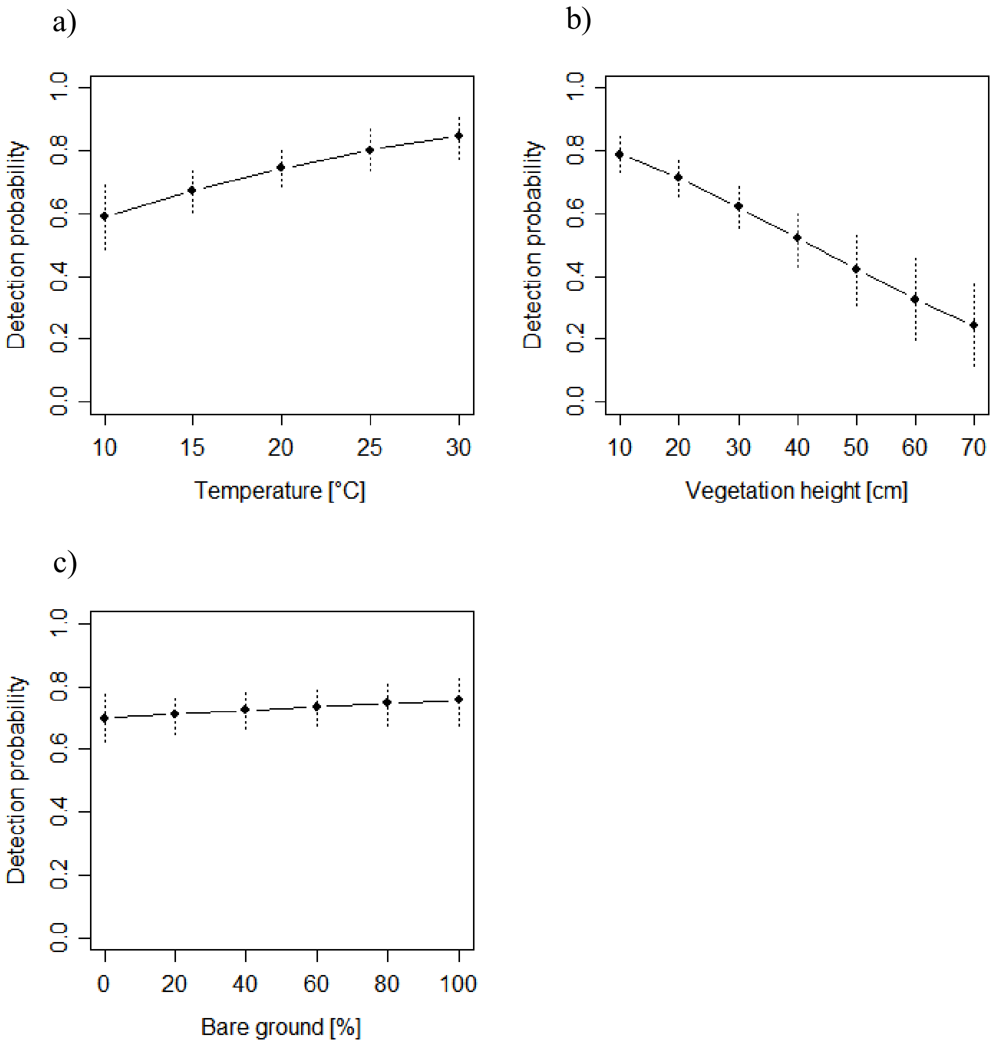
a)
b)
c)
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
10
15
20
25
30
Temperature [°C]
10
20
30
40
50
60
70
Vegetation height [cm]
0
20
40
60
80
100
Bare ground [%]

Figure 1

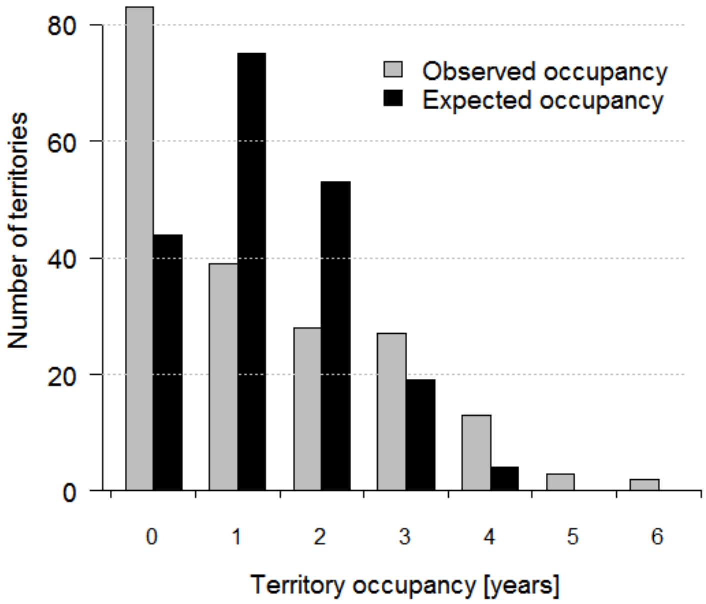
80
60
40
20
0
Number of territories
Observed occupancy
Expected occupancy
0
1
2
3
4
5
6
Territory occupancy [years]

Figure 2

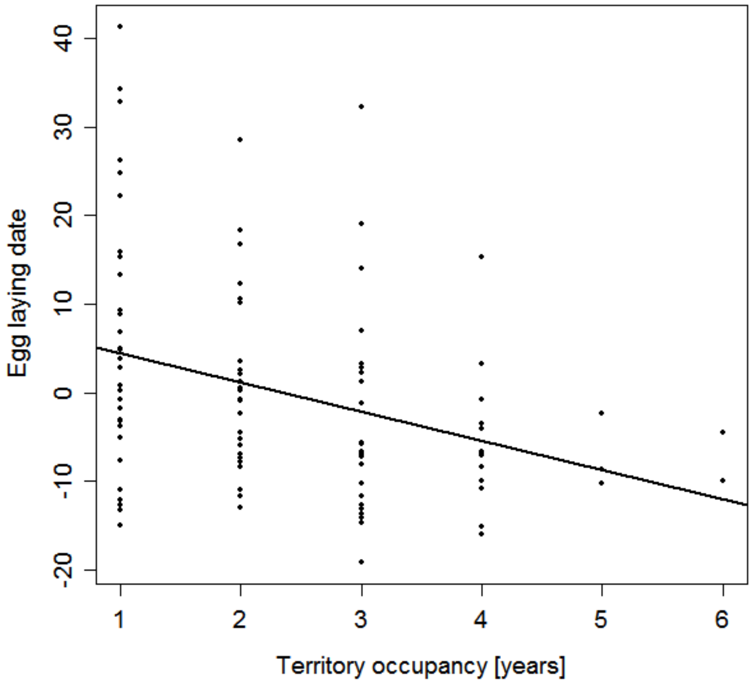
Egg laying date
40
30
20
10
0
-10
-20
1
2
3
4
5
6
Territory occupancy [years]

Figure 3

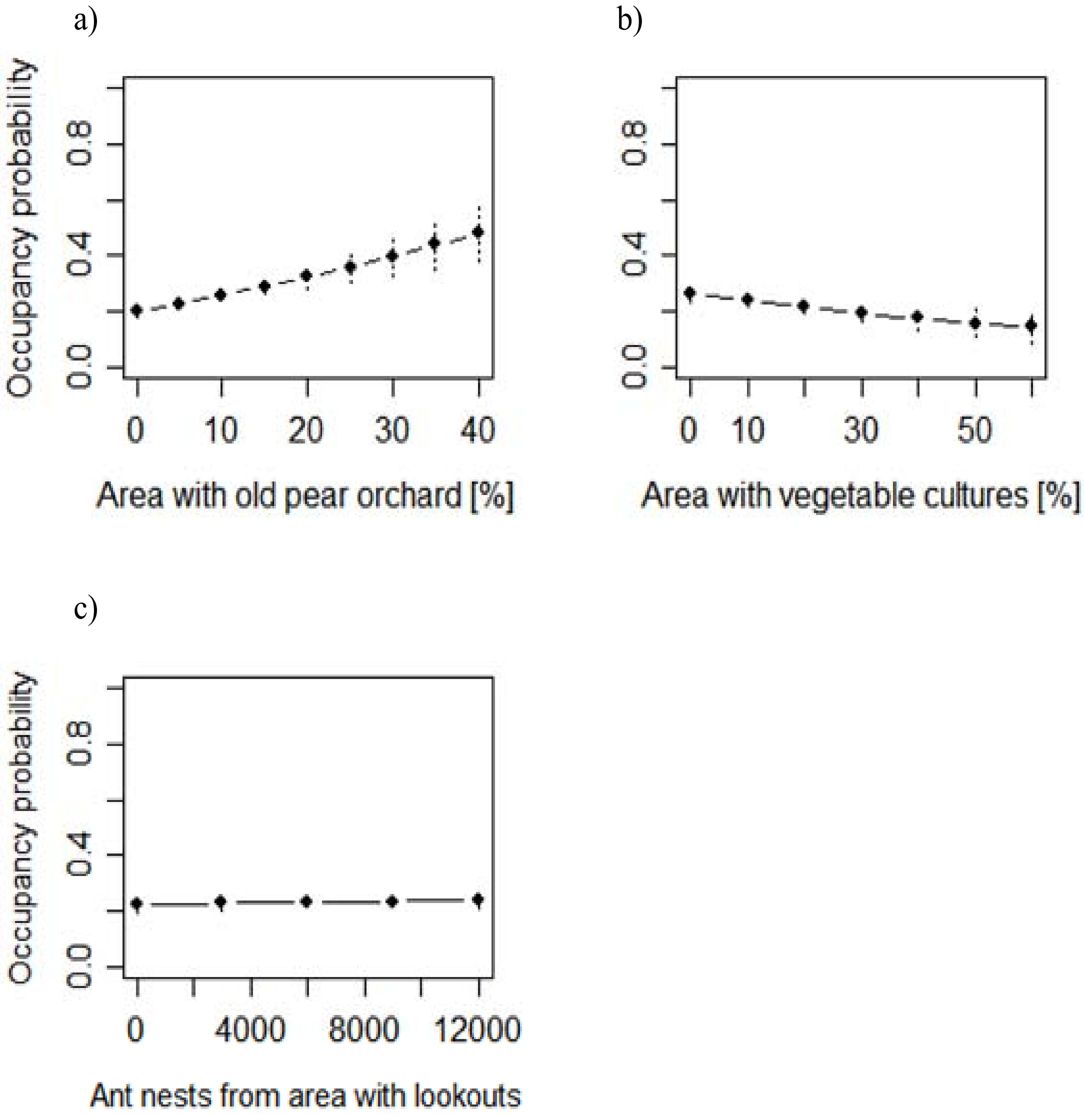
a)
Occupancy probability
0.0
0.4
0.8
0
10
20
30
40
Area with old pear orchard [%]
b)
0.0
0.4
0.8
0
10
30
50
Area with vegetable cultures [%]
c)
Occupancy probability
0.0
0.4
0.8
0
4000
8000
12000
Ant nests from area with lookouts

Figure 4

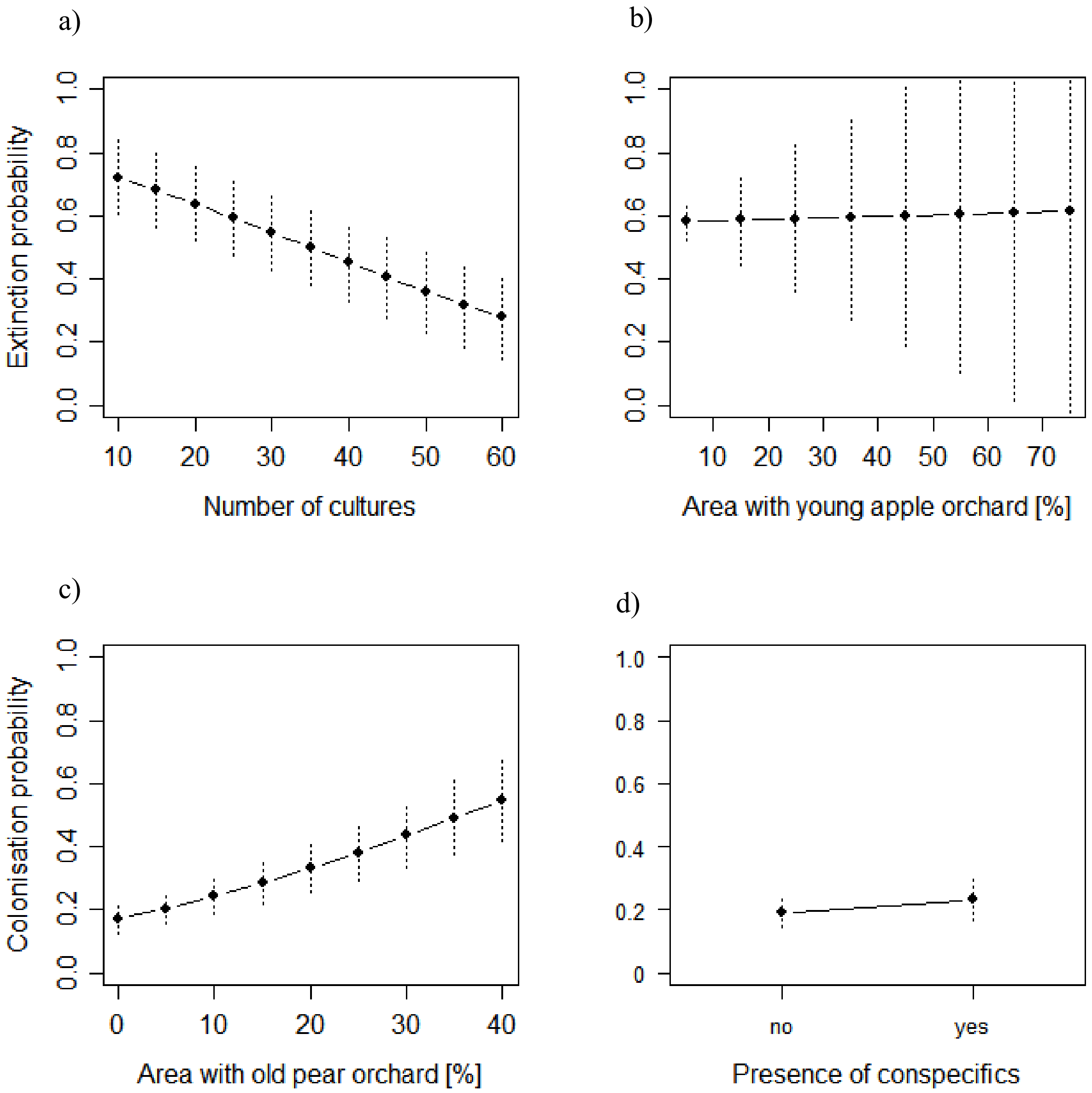
a)
Extinction probability
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
50
60
Number of cultures
b)
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
50
60
70
Area with young apple orchard [%]
c)
Colonisation probability
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
Area with old pear orchard [%]
d)
1.0
0.8
0.6
0.4
0.2
0
no
yes
Presence of conspecifics

Figure 5

APPENDIX

Appendix 1. An example of a mapped, digitalised territory. The borders of each parcel were drawn directly on the Orthophoto in the field and were digitalised in GIS afterwards. As the Orthophotos were made in 2004/2005, some cultures have been changed until 2007 (e.g. on this map the parcel below the centre was recorded as building in 2007 instead of a vegetable culture as displayed).

Appendix 2. Summary results of the dynamic occupancy modelling for the colonisation rate (γ) when all 27 explanatory variables were used as single variable (note that the squared variables also contained the main effect). The extinction rate (ε) remained time-dependent in all models. Given are the ΔAICc, the AICc weights ($w_i = \exp(-0.5*\Delta AICc_i)/\Sigma\exp(-0.5*\Delta AICc)$), the number of parameters (K) and the residual deviance. The models are ranked according to their ΔAICc. The first three models are within ΔAIC < 4 and their variables are selected for the second analysis step.

Model	ΔAICc	w_i	K	Deviance
ε(year) γ(year + old pear orchard)	0.000	0.598	12	596.422
ε(year) γ(year + presence of conspecifics)	2.923	0.139	12	599.345
ε(year) γ(presence of conspecifics)	3.756	0.091	8	608.465
ε(year) γ(old pear orchard)	5.621	0.036	8	610.331
ε(year) γ(year + ant with lookout)	7.300	0.016	12	603.722
ε(year) γ(year + total bare ground)	7.481	0.014	12	603.903
ε(year) γ(year + vegetable cultures)	7.544	0.014	12	603.966
ε(year) γ(year + bare ground with lookout)	8.714	0.008	12	605.136
ε(year) γ(year + total bare ground^2)	8.992	0.007	13	603.324
ε(year) γ(year + distance to next human settlement)	9.121	0.006	12	605.542
ε(year) γ(year + old apricot orchard)	9.181	0.006	12	605.603
ε(year) γ(year + bare ground with lookout^2)	9.458	0.005	13	603.790
ε(year) γ(year)	9.459	0.005	11	607.963
ε(year) γ(year + medium apple orchard)	9.964	0.004	12	606.386
ε(year) γ(year + old apple orchard)	10.147	0.004	12	606.569
ε(year) γ(year + bare ground without lookout^2)	10.386	0.003	13	604.718
ε(year) γ(year + distance to next road)	10.511	0.003	12	606.933
ε(year) γ(year + young apple orchard)	10.602	0.003	12	607.024
ε(year) γ(year + young apricot orchard)	10.616	0.003	12	607.037
ε(year) γ(year + meadowland)	10.896	0.003	12	607.318
ε(year) γ(year + medium pear orchard)	11.149	0.002	12	607.571
ε(year) γ(year + tall trees)	11.201	0.002	12	607.623

ε (year) γ(year + vineyard)	11.262	0.002	12	607.684
ε (year) γ(year + fallow land)	11.412	0.002	12	607.834
ε (year) γ(year + medium apricot orchard)	11.445	0.002	12	607.867
ε (year) γ(year + bare ground without lookout)	11.475	0.002	12	607.897
ε (year) γ(year + hoopoe)	11.485	0.002	12	607.907
ε (year) γ(year + young pear orchard)	11.515	0.002	12	607.937
ε (year) γ(year + woodland)	11.523	0.002	12	607.945
ε (year) γ(year + number of parcels)	11.541	0.002	12	607.963
ε (year) γ(total bare ground)	11.869	0.002	8	616.579
ε (year) γ(ant with lookout)	12.267	0.001	8	616.973
ε (year) γ(vegetable cultures)	12.627	0.001	8	617.337
ε (year) γ(total bare ground^2)	13.228	0.001	9	615.876
ε (year) γ(distance to next human settlement)	13.260	0.001	8	617.970
ε (year) γ(bare ground with lookout)	13.471	0.001	8	618.180
ε (year) γ(old apricot orchard)	13.749	0.001	8	618.459
ε (year) γ(.)	14.064	0.001	7	620.828
ε (year) γ(bare ground with lookout^2)	14.328	0.000	9	616.976
ε (year) γ(old apple orchard)	14.702	0.000	8	619.412
ε (year) γ(medium apple orchard)	14.887	0.000	8	619.597
ε (year) γ(young apple orchard)	14.917	0.000	8	619.627
ε (year) γ(young apricot orchard)	14.981	0.000	8	619.691
ε (year) γ(bare ground without lookout^2)	15.028	0.000	9	617.676
ε (year) γ(distance to next road)	15.252	0.000	8	619.961
ε (year) γ(meadowland)	15.517	0.000	8	620.227
ε (year) γ(vineyard)	15.694	0.000	8	620.404
ε (year) γ(hoopoe)	15.708	0.000	8	620.418
ε (year) γ(medium pear orchard)	15.786	0.000	8	620.496
ε (year) γ(tall trees)	15.793	0.000	8	620.503
ε (year) γ(bare ground without lookout)	15.990	0.000	8	620.700
ε (year) γ(fallow land)	15.996	0.000	8	620.706
ε (year) γ(young pear orchard)	16.013	0.000	8	620.722
ε (year) γ(woodland)	16.054	0.000	8	620.764
ε (year) γ(medium apricot orchard)	16.077	0.000	8	620.787
ε (year) γ(number of parcels)	16.111	0.000	8	620.821

Appendix 3. Summary results of the dynamic occupancy modelling for the extinction rate (ε) when all 27 explanatory variables were used as single variable (note that the squared variables also contained the main effect). The colonisation rate (γ) remained time-dependent in all models. Given are the ΔAICc, the AICc weights (w_i = exp(-0.5*ΔAICc$_i$)/Σexp(-0.5*ΔAICc)), the number of parameters (*K*) and the residual deviance. The models are ranked according to their ΔAICc. The first four models are within ΔAIC < 4 and their variables are selected for the second analysis step.

Model	ΔAICc	w_i	*K*	Deviance
ε (number of parcels) γ(year)	0.000	0.299	8	606.926
ε (year + number of parcels) γ(year)	2.930	0.069	12	601.568
ε (.)γ(year)	3.710	0.047	7	612.690
ε (young apple orchard) γ(year)	3.966	0.041	8	610.892
ε (hoopoe) γ(year)	4.575	0.030	8	611.501
ε (medium apricot orchard) γ(year)	4.906	0.026	8	611.832
ε (young pear orchard) γ(year)	5113	0.023	8	612.039
ε (old apple orchard) γ(year)	5.176	0.022	8	612.102
ε (tall trees) γ(year)	5.207	0.022	8	612.133
ε (young apricot orchard) γ(year)	5.259	0.022	8	612.185
ε (presence of conspecifics) γ(year)	5.298	0.021	8	612.223
ε (distance to next road) γ(year)	5.367	0.020	8	612.293
ε (woodland) γ(year)	5.386	0.020	8	612.311
ε (old apricot orchard) γ(year)	5.512	0.019	8	612.437
ε (ant with lookout) γ(year)	5.585	0.018	8	612.510
ε (old pear orchard) γ(year)	5.669	0.018	8	612.594
ε (bare ground with lookout) γ(year)	5.678	0.018	8	612.604
ε (vineyard) γ(year)	5.682	0.017	8	612.608
ε (bare ground without lookout) γ(year)	5.696	0.017	8	612.622
ε (fallow land) γ(year)	5.726	0.017	8	612.652
ε (meadowland) γ(year)	5.736	0.017	8	612.661
ε (vegetable cultures) γ(year)	5.742	0.017	8	612.668
ε (distance to next human settlement) γ(year)	5.748	0.017	8	612.673
ε (medium apple orchard) γ(year)	5.757	0.017	8	612.683
ε (medium pear orchard) γ(year)	5.758	0.017	8	612.684
ε (total bare ground) γ(year)	5.761	0.017	8	612.687
ε (year) γ(year)	7.243	0.008	11	607.963

ε(year + young apple orchard) γ(year)	7.279	0.008	12	605.916
ε(bare ground with lookout^2) γ(year)	7.548	0.007	9	612.412
ε(bare ground without lookout^2) γ(year)	7.711	0.006	9	612.576
ε(total bare ground^2) γ(year)	7.819	0.006	9	612.683
ε(year + presence of conspecifics) γ(year)	8.373	0.005	12	607.011
ε(year + tall trees) γ(year)	8.574	0.004	12	607.212
ε(year + hoopoe) γ(year)	8.641	0.004	12	607.279
ε(year + young apricot orchard) γ(year)	8.712	0.004	12	607.350
ε(year + old apple orchard) γ(year)	8.746	0.004	12	607.384
ε(year + distance to next road) γ(year)	8.854	0.004	12	607.492
ε(year + medium apricot orchard) γ(year)	8.919	0.003	12	607.557
ε(year + young pear orchard) γ(year)	8.982	0.003	12	607.620
ε(year + bare ground without lookout) γ(year)	9.020	0.003	12	607.658
ε(year + old apricot orchard) γ(year)	9.087	0.003	12	607.724
ε(year + vegetable cultures) γ(year)	9.095	0.003	12	607.733
ε(year + bare ground with lookout) γ(year)	9.100	0.003	12	607.738
ε(year + woodland) γ(year)	9.156	0.003	12	607.793
ε(year + old pear orchard) γ(year)	9.226	0.003	12	607.864
ε(year + ant with lookout) γ(year)	9.229	0.003	12	607.866
ε(year + meadowland) γ(year)	9.289	0.003	12	607.926
ε(year + medium apple orchard) γ(year)	9.302	0.003	12	607.940
ε(year + fallow land) γ(year)	9.310	0.003	12	607.948
ε(year + vineyard) γ(year)	9.324	0.003	12	607.961
ε(year + distance to next human settlement) γ(year)	9.324	0.003	12	607.961
ε(year + total bare ground) γ(year)	9.325	0.003	12	607.962
ε(year + medium pear orchard) γ(year)	9.325	0.003	12	607.962
ε(year + bare ground without lookout^2) γ(year)	11.093	0.001	13	607.642
ε(year + bare ground with lookout^2) γ(year)	11.110	0.001	13	607.659
ε(year + total bare ground^2) γ(year)	11.399	0.001	13	607.947

Appendix 4: Summary results of generalised linear mixed models with breeding success (number of fledglings) as dependent variable and "year" and the six territory variables from the static as well as from the dynamic occupancy analyses as fixed effects. Territory identity was included as random effect (n = 50). Given are the ΔAICc, the AICc weights ($w_i = \exp(-0.5*\Delta AICc_i)/\Sigma \exp(-0.5*\Delta AICc)$), the number of parameters (*K*) and the restricted maximum residual deviance.

Model	ΔAICc	w_i	*K*	Deviance
Constant model	0.000	0.570	2	434.3
Presence of conspecifics	1.766	0.236	3	433.8
Ant with lookout	4.366	0.064	3	436.4
Number of parcels	5.966	0.029	3	438
Ant with lookout + presence of conspecifics	6.234	0.025	4	435.9
Old pear orchard	7.166	0.016	3	439.2
Number of parcels + presence of conspecifics	7.834	0.011	4	437.5
Young apple orchard	8.066	0.010	3	440.1
Vegetable cultures	8.266	0.009	3	440.3
Old pear orchard + presence of conspecifics	8.934	0.007	4	438.6
Young apple orchard + presence of conspecifics	9.834	0.004	4	439.5
Vegetable cultures + presence of conspecifics	10.134	0.004	4	439.8
Number of parcels + ant with lookout	10.234	0.003	4	439.9
Vegetable cultures + ant with lookout	11.434	0.002	4	441.1
Old pear orchard + ant with lookout	11.934	0.001	4	441.6
Young apple orchard + ant with lookout	11.934	0.001	4	441.6
Number of parcels + presence of conspecifics + ant with lookout	12.108	0.001	5	439.3
Old pear orchard + number of parcels	13.234	0.001	4	442.9
Vegetable cultures + presence of conspecifics + ant with lookout	13.408	0.001	5	440.6
Old pear orchard + presence of conspecifics + ant with lookout	13.908	0.001	5	441.1
Young apple orchard+ presence of conspecifics + ant with lookout	13.908	0.001	5	441.1
Young apple orchard + number of parcels	14.134	0.000	4	443.8
Vegetable cultures + number of parcels	14.434	0.000	4	444.1
Old pear orchard + presence of conspecifics + number of parcels	15.108	0.000	5	442.3

Old pear orchard + young apple orchard	15.234	0.000	4	444.9
Old pear orchard + vegetable cultures	15.534	0.000	4	445.2
Young apple orchard + number of parcels + presence of conspecifics	16.008	0.000	5	443.2
Vegetable cultures + presence of conspecifics + number of parcels	16.308	0.000	5	443.5
Vegetable cultures + young apple orchard	16.334	0.000	4	446
Old pear orchard + presence of conspecifics + young apple orchard	17.208	0.000	5	444.4
Old pear orchard + vegetable cultures + presence of conspecifics	17.408	0.000	5	444.6
Vegetable cultures + number of parcels + ant with lookout	17.608	0.000	5	444.8
Young apple orchard + number of parcels + ant with lookout	17.808	0.000	5	445
Old pear orchard + number parcels + ant with lookout	18.008	0.000	5	445.2
Vegetable cultures +presence of conspecifics+young apple orchard	18.208	0.000	5	445.4
Old pear orchard + vegetable cultures + ant with lookout	19.108	0.000	5	446.3
Vegetable cultures + young apple orchard + ant with lookout	19.308	0.000	5	446.5
Old pear orchard + young apple orchard + ant with lookout	19.508	0.000	5	444.7
Vegetable cultures + number of parcels + presence of conspecifics + ant with lookout	19.598	0.000	6	446.2
Young apple orchard + number of parcels + presence of conspecifics + ant with lookout	19.798	0.000	6	444.4
Old pear orchard + number of parcels + presence of conspecifics+ ant with lookout	19.998	0.000	6	444.6
Old pear orchard + vegetable cultures + presence of conspecifics + ant with lookout	21.198	0.000	6	445.8
Vegetable cultures + young apple orchard + presence of conspecifics + ant with lookout	21.398	0.000	6	446
Old pear orchard + young apple orchard + number of parcels	21.408	0.000	5	448.6

Old pear orchard + young apple orchard + presence of conspecifics + ant with lookout	21.598	0.000	6	446.2
Old pear orchard + vegetable cultures + number of parcels	21.708	0.000	5	448.9
Vegetable cultures + young apple orchard + number of parcels	22.508	0.000	5	449.7
Old pear orchard + young apple orchard + presence of conspecifics + number of parcels	23.498	0.000	6	448.1
Old pear orchard + vegetable cultures + young apple orchard	23.608	0.000	5	450.8
Old pear orchard + vegetable cultures + presence of conspecifics + number of parcels	23.698	0.000	6	448.3
Vegetable cultures + young apple orchard + number of parcels + presence of conspecifics	24.498	0.000	6	449.1
Old pear orchard + vegetable cultures + ant with lookout+number of parcels	25.498	0.000	6	450.5
Vegetable cultures + young apple orchard + number of parcels + ant with lookout	25.498	0.000	6	450.1
Old pear orchard +vegetable cultures + young apple orchard + presence of conspecifics	25.598	0.000	6	450.2
Old pear orchard + young apple orchard + ant with lookout + number of parcels	25.598	0.000	6	450.2
Old pear orchard + vegetable cultures + young apple orchard + ant with lookout	26.898	0.000	6	451.5
Old pear orchard + vegetable cultures + number of parcels + presence of conspecifics + ant with lookout	27.511	0.000	7	449.4
Vegetable cultures + young apple orchard + number of parcels + presence of conspecifics + ant with lookout	27.611	0.000	7	449.5
Old pear orchard + young apple orchard + number of parcels + presence of conspecifics + ant with lookout	27.811	0.000	7	449.7
Old pear orchard + vegetable cultures + young apple orchard + presence of conspecifics + ant with lookout	29.011	0.000	7	450.9
Old pear orchard + vegetable cultures + young apple orchard + number of parcels	29.898	0.000	6	454.5

Old pear orchard + vegetable cultures + young apple orchard + number of parcels + presence of conspecifics	32.011	0.000	7	453.9
Old pear orchard + vegetable cultures + young apple orchard + number of parcels + ant with lookout	33.311	0.000	7	455.2
Old pear orchard + vegetable cultures + young apple orchard + number of parcels + presence of conspecifics + ant with lookout	35.457	0.000	8	454.5