The importance of ant-rich habitats for the persistence of the Wryneck *Jynx torquilla* on farmland

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The frequency of territory occupancy is a good indicator of territory quality. We studied territory occupancy in a Swiss population of the Wryneck *Jynx torquilla*, a declining farmland woodpecker, with the aim of identifying key habitat features for conservation management. Both static and dynamic approaches were applied using data on nest-site occupancy of 100 territories from six successive years. The static approach models the probability of territory occupancy; the dynamic approach estimates territory colonization and extinction. Frequently occupied territories were settled earlier in the season, suggesting that they may be of better quality, and birds settling in these territories had higher breeding success. Probability of territory occupancy increased with the area of old pear orchards and decreased with the area of vegetable cultivation. Both the area of old pear orchards and the presence of conspecifics within a territory were positively related to territory colonization, whereas territory extinction was negatively related to habitat heterogeneity. Old pear orchards were characterized by having both the highest density of ant nests and the greatest amount of bare ground. The latter is likely to facilitate access to ant prey. To ensure persistence of Wryneck populations in farmland, heterogeneous habitat matrices with high ant nest density and bare ground should be promoted. Finally, provision of artificial nesting cavities is likely to enhance territory occupancy. Providing that these key resources are present, Wrynecks are likely to persist even in intensively farmed areas.

Keywords: ants, colonization and extinction probabilities, food availability, habitat selection, occupancy model, territory quality.

Individuals preferentially select breeding territories in high-quality habitat patches that provide suitable resources such as food, breeding sites and shelter from predators because reproductive output usually increases with increasing territory quality (Andrén 1990, Tye 1992, Holmes *et al.* 1996, Pärt 2001). Territory selection is therefore crucial to the reproductive fitness of individuals. According to the ideal despotic distribution, the highest quality territories are selected first (Fretwell & Lucas 1969). The occupancy of territories is thus a non-random process, with the best quality territories being monopolized by the strongest individuals

or the first to arrive. If individuals are distributed according to the ideal despotic distribution, the frequency of territory occupancy will be positively correlated with territory quality (Krüger 2002, Sergio & Newton 2003, Sim *et al.* 2007), with low-quality territories only occupied when breeding density is high. Thus, territory variables that are related to the frequency of territory occupancy may be good measures of habitat quality.

This static view of territory occupancy can be extended to a dynamic occupancy approach. Territory occupancy involves two processes: colonization and extinction. These local processes may depend on stochastic, intrinsic or extrinsic factors (Hanski 1998), such as habitat quality or conspecific attraction (Stamps 1988, Muller *et al.*

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1997, Danchin *et al.* 1998). Territory variables that are positively correlated with colonization and negatively with extinction indicate high quality.

A key issue in conservation ecology is the identification of territory quality gradients, to strategically prioritize conservation management. The goal of this study was to identify those habitat features that are the best indicators of habitat quality for Wrynecks *Jynx torquilla*. This species is a secondary cavity breeder that feeds almost exclusively on ground-dwelling ants (Freitag 1998). Wrynecks occur in different kinds of semi-open habitats, such as farmland or open woods, but their populations are declining throughout Europe (Sanderson *et al.* 2006).

We first mapped a number of habitat features in recorded and potential Wryneck breeding territories. We then assessed the abundance of ant nests in territories, as ant broods constitute the staple food provisioned to Wryneck nestlings (Bitz & Rohe 1993, Freitag 1998). Finally, we related habitat type, food availability and the presence of conspecifics to the observed pattern of territory occupancy. Analyses were carried out using both static (variables related to frequency of occupancy) and dynamic occupancy models (variables related to local colonization and extinction processes of a given territory) to identify associations that could lead to the development of conservation management recommendations for farmland Wryneck populations.

METHODS

Study site and study species

The study area was located in the plain of the Rhône valley, between Vernayaz and Sion (south west Switzerland, 46°13′N, 7°22′E; 482 m asl). The area is characterized by intensive farming, consisting mainly of plantations of dwarf fruit trees (hereafter orchards) and vegetable cultivation. The study area covered 62 km^2, within which 351 nest-boxes were installed in 2002 at 195 locations (mostly inside agricultural shacks, most buildings having two boxes each). These nestboxes were spread regularly in apparently suitable semi-open habitats across the study area and their number remained constant during the study period. Natural cavities as well as nestboxes were also present but appeared to be scarce, although their numbers are unknown.

In contrast to most other woodpeckers, Wrynecks are secondary-cavity breeders. They also require foraging grounds offering sparse vegetation cover, facilitating access to ant nests (Hölzinger 1992, Bitz & Rohe 1993, Freitag 1996, N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). In our study area, 90% of the food provisioned to Wryneck nestlings comprised ant larvae and nymphs (Freitag 1998). Telemetry studies in the study area revealed that Wrynecks forage mostly within 100–125 m of their nest-site, having median home-ranges of 3.9 ha (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). Orchards and fallow land are the preferred foraging habitats, and preferred feeding locations have more than 50% cover of bare ground (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data).

Between 2002 and 2007, all 195 nest-sites were checked fortnightly during the breeding season. Once detected, a brood was monitored every 3–4 days. A brood was defined as any clutch containing at least one egg, irrespective of the outcome, whilst a successful brood yielded at least one fledgling.

Design and habitat variables

A random sample of 100 nest-sites was selected from the 195 available sites in the study area. Around each nest-site we delineated a circle of 111-m radius, to define a 3.9-ha area equivalent to the median foraging home-range size (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). In only three cases was there an overlap between two adjacent estimated home-ranges (maximal overlap of 8.2%). Of the 100 nest-sites, 62 were occupied in at least 1 year. The habitat characteristics of the selected territories were mapped in early summer 2007 (Supporting Information Fig. S1). Variables recorded were habitat type, number of trees and percentage cover of bare ground, these being the features identified as important by N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub (unpubl. data). The percentage of bare ground was estimated visually for each cropping unit (parcel) in the field.

Occupancy models assume that territory quality and food resources remain constant over time and that individuals are able to locate the best quality territories promptly. In our study area, territory quality was assumed to be constant over the 6-year period, as orchards, which covered on average

48.9 ± 0.6% of foraging territories (n = 100), have a slow replacement turnover, and because ant nests are relatively long use (Seifert 1996). In addition, there was an excess of available nest-sites (on average 2.03 ± 0.06 nestboxes per territory), so we assumed that territory selection would operate independently of nest-site availability.

The density of ant nests within a territory was also used as a potential criterion for estimating habitat quality. Perches such as trees, poles, shacks and fences are an important habitat feature for Wrynecks, as perches enhance detectability of ant nests. We thus distinguished between ant nest availability with perches (orchards, vineyards, riverbank and pasture) and without perches (vegetable cultivation, fallow land and meadow). Nests from woodland ant species (*Formica* spp. and *Camponotus* spp.) were not included in the food availability estimates because these species are almost never eaten by Wrynecks (Seifert 1996, Freitag 1998). Ant nest accessibility was accounted for in the modelling, as this depends primarily on the area of bare ground in the vicinity of an ant nest and because Wrynecks capture and eat prey on the ground (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). The quadratic terms of the three discrete variables quantifying bare ground with perches, bare ground without perches and total bare ground were also used to identify optimal proportions of these key habitat components. Finally, an index of potential competition with Hoopoes *Upupa epops*, which use the same nestboxes as Wrynecks, was derived from the number of years between 2002 and 2007 that a Hoopoe pair had occupied one of the two available nestboxes within a territory.

In the dynamic occupancy analysis, we also included a binary variable indicating presence of conspecifics in a given year (scored 1 if there were other breeding Wrynecks within a 500-m radius, twice the maximal foraging distance, of the focal nest-site). Conspecifics may influence site occupancy through patterns of social attraction (Danchin *et al.* 1998).

Spatial data were digitized using ArcGIS 9.1 (ESRI, Redlands, CA, USA). In total, 2589 different cropping units were recorded and their areas calculated from digitized polygons. Multiple units of the same habitat type within a territory were summed and their proportional area was used in the analysis. Total percentage of bare ground within a territory was calculated by summing the percentage of bare ground per unit, weighted by its proportion of the entire territory area.

Food availability: ant nest abundance and accessibility

To estimate overall food availability within a territory, habitat-specific ant nest densities were multiplied by their proportional area of territory and summed. Density of terrestrial ant nests was assessed throughout the study area in 2003 and 2004. Sampling was based on a stratified design (at least 90 randomly selected plots per main habitat type: orchards, vineyards, meadow, riverbank, fallow land and vegetable cultures). From 2005 to 2007, assessments were restricted to orchards (with different fruit types), as these were identified as the most important foraging habitat (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). Sample size varied between habitat types and years, ranging from 10 to 175. Each sampling location was situated in the core of a given crop type to avoid edge effects. Ant nests were surveyed in five 2-m^2, randomly defined replicates, by scraping the topsoil with a rake and counting the nests. Surveys took roughly 5 min per replicate, and 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, vegetation height, and number and relative size of ant nests were recorded. An ant nest was defined by the presence of an aggregation of ≥ 20 imagos, or the presence of eggs or larvae. A few individuals from each nest were sampled for subsequent species identification (Della Santa 1994, Seifert 1996).

Ant nests that were small or located deep in the soil could easily be overlooked. Therefore, we estimated detection probability of ant nests in an additional study in 2007, and corrected the ant nest counts accordingly (Supporting Information Appendix S1). We repeatedly searched for ant nests at exactly the same five 2-m^2 plots in 19 randomly selected orchards (95 replicates), using the same technique as for the ant nest density assessment described above. All 95 replicates were recorded over a period of 3–4 days, during three recording sessions in early May, June and July. Data for mean daytime temperature, measured 5 cm above ground, were obtained from MeteoSwiss (on-line database). A few ants were sampled from each nest for subsequent species identification.

The resulting detection histories for each of the 95 replicates were analysed with 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 unbalanced. Vegetation height (range: 0–110 cm), percentage of bare ground (range: 0–100%) and mean hourly temperature (range: 3.3–35.0 °C) were used 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 was always kept constant. Models were ranked according to Akaike's Information Criterion adjusted for small samples (AICc) and the corresponding AICc weights (Burnham & Anderson 1998). Model averaging was performed for the smallest subset of models with accumulated AICc weights summing to 0.95, to account for model selection uncertainty (Burnham & Anderson 1998).

The accessibility of ant nests for Wrynecks is primarily determined by the amount of bare ground (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). As an indication of food accessibility, we therefore used average amount of bare ground for each habitat, estimated with a linear mixed effects model, with territory as a random effect. Estimates and confidence intervals were obtained by bootstrapping, with 1000 repetitions.

Occupancy analyses

Assumptions

According to the ideal despotic distribution hypothesis (Fretwell & Lucas 1969), high-quality territories are settled earlier, and thus more frequently occupied territories should be settled earlier. We used 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 is site-dependent, it should be positively correlated with frequency of territory occupancy. This prediction was tested using linear mixed models with Poisson and binomial error distributions, fitting three components of breeding success of a territory (clutch size, number of fledglings, probability of successfully raising a brood) as dependent variables, territory as a random effect, and frequency of territory as occupancy and year as fixed independent variables. Sample sizes differed between analyses because only complete clutches (defined as a least one egg hatched) for the clutch size analysis and only successful broods for the analysis of the number of fledglings were considered (clutch size: $n = 122$ broods from 53 territories; number of fledglings: $n = 94$ broods from 50 territories; proportion successful: $n = 175$ broods from 62 territories).

Static model

To model the annual probability that a territory was occupied, we used a logistic regression model with a binomial error distribution. The numerator of the response variable was the number of times a territory was occupied, and the denominator was the number of study years ($n = 6$). From all recorded territory variables (Supporting Information Tables S1 and S2), some were excluded from this analysis either due to their irrelevance as foraging habitat (anthropogenic habitat and water), or because they occurred in fewer than 20 territories (riverbank and pasture). The remaining 22 variables were tested for pair-wise correlation, using Spearman's rank correlation test. As a result, the variable relating to ant nests in habitats without perches was excluded, as it was highly correlated ($r_s > |0.7|$) with two other variables. The quadratic terms of the variables relating to total bare ground, bare ground with perches and bare ground without perches were also included, to test for the presence of an optimum, giving 24 explanatory variables. We then fitted univariate models containing each of these explanatory variables and ranked them according to their AICc values. All variables from models with a ΔAIC < 4 when compared with the best model were included into the second modelling step. We built models with all possible combinations of the remaining variables (four variables; 15 models) and ranked them according to their AICc values. Predictions were made using model averaging, including all models within the second step of the analysis that summed to at least 0.95 of the AICc weight.

Dynamic model

To model colonization and extinction probabilities, we used a dynamic occupancy model (MacKenzie

et al. 2003, Royle & Dorazio 2008) fitted with the program MARK (White & Burnham 1999). This model is parameterized with initial occupancy, colonization and extinction probabilities. The same 24 variables were used as for the static occupancy model. In addition, we considered the binary variable relating to the presence of conspecifics. Model selection was performed in multiple steps: first, univariate models were fitted containing each of these 25 variables for extinction and colonization probabilities, with a constant and a time-dependent intercept. All models with a ΔAIC < 4 were selected for inclusion in the extinction and colonization modelling. In the second step, the variables from the selected extinction models were combined with the variables from the selected colonization models. From the selected variables, at most one variable for extinction and one for colonization were combined, using both time-dependent and constant intercepts (36 models). Model averaging was performed for models accounting for 0.95 of the AICc weight. The initial occupancy probability was not modelled against explanatory variables.

Breeding success

To assess whether the important territory variables identified in the static and dynamic approaches were linked to breeding success, we fitted equally structured generalized linear mixed models as used for the relationship between breeding success and frequency of occupancy. The dependent variables were clutch size, number of fledglings from successful broods and proportion of successful broods. Territory identity was entered as a random variable and year as a fixed effect. All possible variable combinations using different territory variables were tested, with models ranked based on ΔAICc.

All statistical analyses were performed using the program R version 2.5 (R Development Core Team 2004), unless stated otherwise.

RESULTS

Food supply: ant nest abundance and accessibility

During the three visits to orchards carried out in 2007, 242 ant nests were located belonging to four species: *Lasius niger* (75.6%) was by far the most frequently recorded species; *L. flavus* (14.9%), *Tetramorium caespitum* (7.4%) and *Solenopsis fugax* (2.1%) were less common.
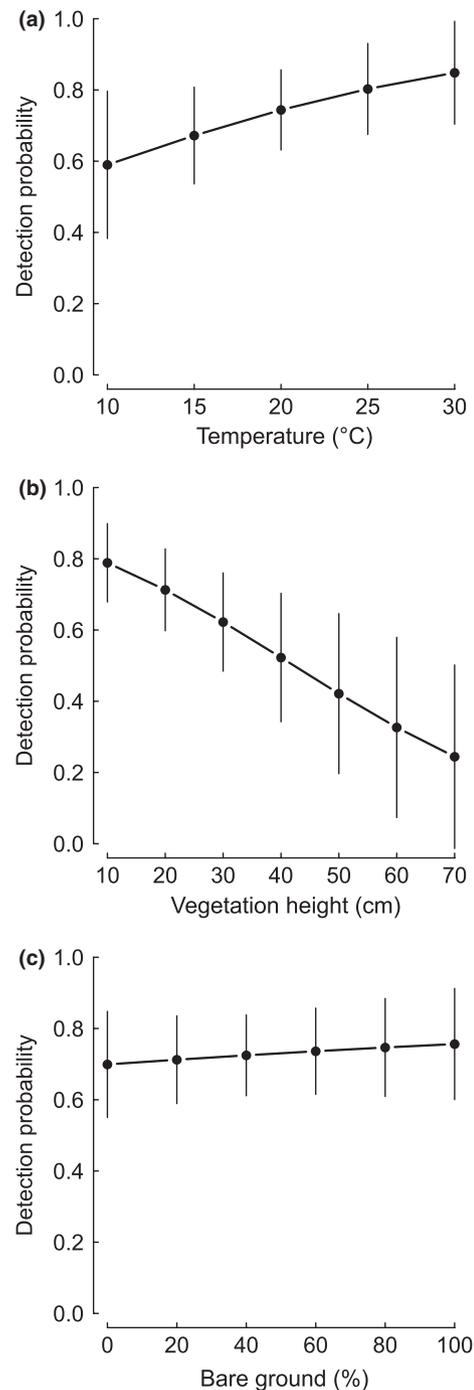
Figure 1. Relationship between detection probability of ant nests and temperature (a), vegetation height (b) and amount of bare ground (c). Shown are model-averaged predictions (based on results in Supporting Information Table S3) with 95% confidence intervals.
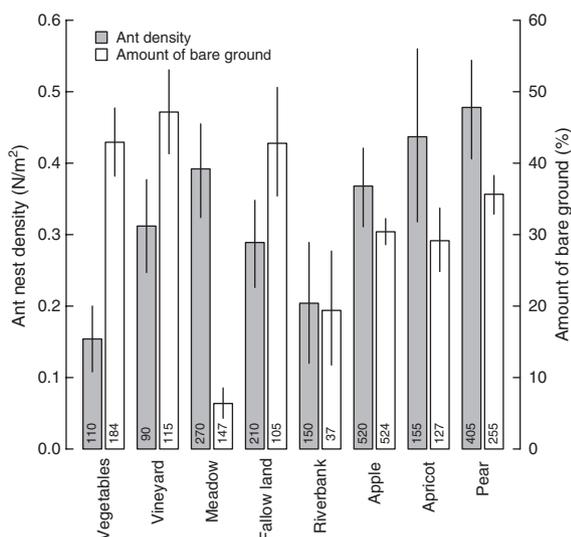
Figure 2. Estimated ant nest densities and amount of bare ground per habitat type obtained by fitting linear mixed models. Shown are the estimates for each habitat type with 95% confidence intervals. Ant densities are corrected for imperfect detection probability. The number of samples for each habitat type is given at the bottom of each bar.

Detection probability increased with temperature, decreased with vegetation height, increased slightly with amount of bare ground (Fig. 1) and declined with season (mean ± se; May: 0.723 ± 0.058; June: 0.588 ± 0.061; July: 0.438 ± 0.059) (see Supporting Information Table S3).

To estimate the detection probability of ant nests for each replicate, we used the model averaged parameter estimates from May and the replicate-specific variables. Ant nest densities corrected for detection probability were lowest in vegetable cultures and highest in orchards, especially in pear orchards (Fig. 2).

The amount of bare ground differed significantly between habitat types (Fig. 2). Bare ground cover was moderate in orchards, with pear orchards having more than other orchards. The combination of both high ant density and a large amount of bare ground (i.e. high accessibility) was highest in orchards, vineyards and fallow land.

Occupancy analyses

Assumptions
The most frequently occupied nest-sites were settled earlier in the season (estimate = −3.298 ± 0.894, $P < 0.001$), and settlement order was

independent of year (likelihood-ratio test, $\chi^2_1 = 1.726$, $P = 0.189$). Clutch size (estimate = 0.011 ± 0.127, $P = 0.921$) and number of fledglings (estimate = 0.011 ± 0.149, $P = 0.907$) were not associated with the frequency of territory occupancy, but the probability that a brood was successful increased significantly with the frequency of occupancy (estimate = 0.057 ± 0.029, $P = 0.047$).

Static model
In univariate models, cover of old pear orchards showed the strongest impact on occupancy (Supporting Information Table S4). The next best variables, bare ground with perches squared, vegetable cultures and ant nests from area with perches, were still within 4 ΔAICc units, so they were included in the second step.

Table 1. Summary results of the static occupancy modelling of Wryneck territories, when the three explanatory variables selected in the first step (Supporting Information Table S4) are used together. Given are the ΔAICc, AICc weights (w_i), number of parameters (K) and residual deviance. The models are ranked according to their AICc weight.

Model	ΔAICc	w_i	K	Deviance
Old pear orchard + vegetable cultures	0.00	0.304	3	218.52
Old pear orchard + vegetable cultures + bare ground with perches^2	1.61	0.136	5	216.12
Old pear orchard + bare ground with perches^2	1.64	0.134	4	218.16
Old pear orchard + vegetable cultures + ant with perches	1.99	0.112	4	218.51
Old pear orchard + vegetable cultures + ant with perches + bare ground with perches^2	2.55	0.085	6	215.06
Old pear orchard	3.17	0.062	2	223.69
Old pear orchard + ant with perches + bare ground with perches^2	3.40	0.055	5	217.92
Old pear orchard + ant with perches	3.42	0.055	3	221.93
Vegetable cultures + bare ground with perches^2	6.28	0.013	4	222.79
Bare ground with perches^2	6.48	0.012	3	225.00
Vegetable cultures	6.81	0.010	2	227.33
Ant with perches	6.91	0.010	2	227.43
Ant with perches + bare ground with perches^2	8.04	0.005	4	224.56
Vegetable cultures + ant with perches + bare ground with perches^2	8.23	0.005	5	222.75
Constant model	12.43	0.001	1	234.94
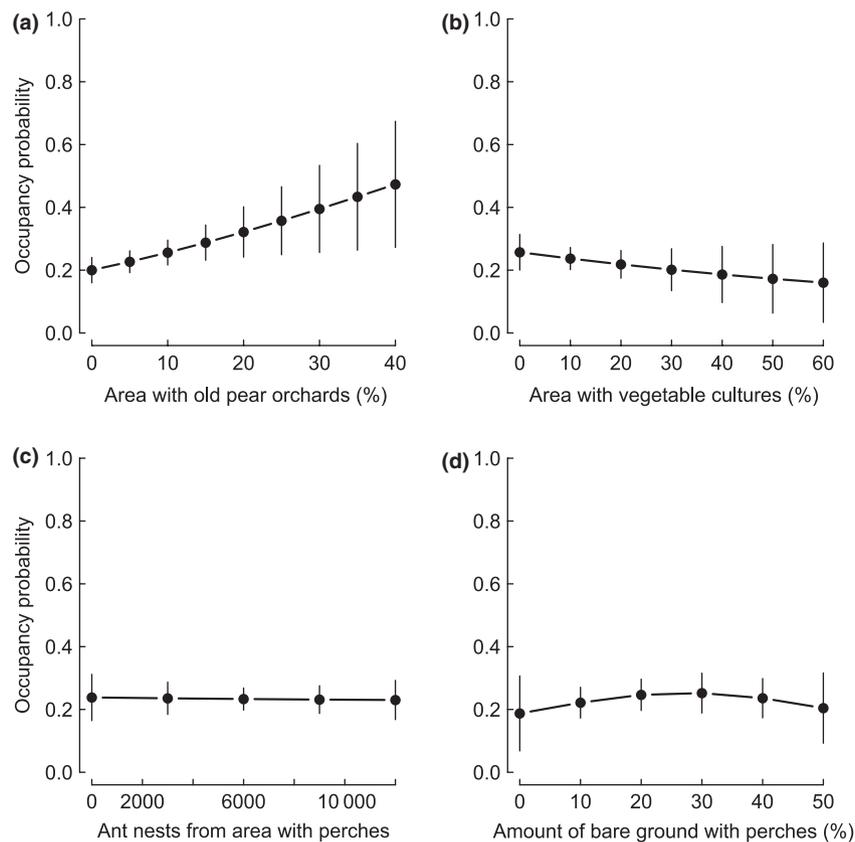
Figure 3. Predicted model-averaged probability of Wryneck territory occupancy, calculated from the best models accounting for 0.95 of the AICc weight (Table 1), in relation to the proportion of old pear orchards (a), vegetable cultures (b), ant nests from area with perches (c) and amount of bare ground with perches (d). The figures show averaged estimates with 95% confidence intervals.

The second step showed that the combination of old pear orchards and vegetable cultures resulted in the most parsimonious model (Table 1). Model-averaged occupancy probabilities increased with the proportion of old pear orchards and decreased with the proportion of vegetables (Fig. 3). Occupancy was highest when the cover of bare ground was around 30%, but remained almost constant with increasing number of ant nests.

Dynamic model
The most parsimonious set of univariate models (ΔAICc < 4) affecting extinction probability included number of cropping units and cover of young apple orchards (Supporting Information Table S5). The most parsimonious set of models affecting colonization probability included cover of old pear orchards and presence of conspecifics (Supporting Information Table S6). In addition,

colonization probability differed across study years, whereas extinction probability did not.

Multivariate models of extinction probability retained only number of cropping units, whereas the most parsimonious multivariate model of colonization retained only cover of old pear orchards (Table 2). In addition, there was some support for an effect of the presence of conspecifics on colonization probability but almost none for the cover of young apple orchards on extinction probability.

Model-averaged probabilities of territory extinction decreased with increasing number of cropping units and increased slightly with the proportion of young apple orchards within a territory (Fig. 4a,b). Territory colonization probability strongly increased with increasing proportion of old pear orchards within the territory (Fig. 4c). It was also slightly enhanced when conspecifics were present (Fig. 4d). There was no significant relationship

Table 2. Summary results of extinction (ε) and colonization (γ) modelling for Wryneck territories. Shown are the 12 best models from originally 36 fitted models. Given are the ΔAICc, AICc weights (w_i), number of parameters (K) and residual deviance. A constant intercept is indicated with (.) and a time-dependent intercept with 'year'. The initial occupancy probability (Ψ) is constant for every model. See Supporting Information Tables S5 and S6 for the first modelling steps.

Model	ΔAICc	w_i	K	Deviance
ε (number of parcels) γ (year + old pear orchard)	0.00	0.439	9	595.39
ε (number of parcels) γ (year + presence of conspecifics)	2.92	0.102	9	598.31
ε (year + number of parcels) γ (year + old pear orchard)	2.96	0.100	13	590.03
ε (.) γ (year + old pear orchard)	3.70	0.069	8	601.15
ε (number of parcels) γ (presence of conspecifics)	3.84	0.064	5	607.43
ε (young apple orchard) γ (year + old pear orchard)	3.97	0.060	9	599.35
ε (number of parcels) γ (old pear orchard)	5.88	0.023	13	592.95
ε (year number of parcels) γ (year + presence of conspecifics)	6.63	0.016	8	604.07
ε (.) γ (year + presence of conspecifics)	6.69	0.016	9	602.07
ε (year + number of parcels) γ (presence of conspecifics)	6.89	0.014	9	602.27
ε (young apple orchard) γ (year + presence of conspecifics)	7.26	0.012	12	596.42
ε (year) γ (year + old pear orchard)	7.31	0.011	13	594.38

between any measure of breeding success and the cover of old orchards or the number of cropping units (Table 3).

DISCUSSION

The most frequently occupied Wryneck territories were settled earlier in the season and the probability that a territory was occupied or newly colonized was positively related to the proportion of old pear orchards within the territory. The probability that a territory was abandoned was negatively related to the number of cropping units within the territory (i.e. a structure mosaic effect). Pear orchards had the highest density of ant nests, thus offered the highest density of food resources, and were sparsely vegetated, which enhanced ant detection/accessibility. Finally, territories where conspecifics were present in the vicinity were slightly more likely to be colonized. Breeding success, however, was not related to any of these variables.

Territory selection and territory quality

Territory occupancy can be regarded as the result of two selection processes. The first selection separates locations in which essential resources are lacking from locations in which all essential resources are available. The second selection follows the gradient of habitat quality. In our analysis we did not differentiate between these two processes because we regarded all studied areas as potentially suitable for Wrynecks, assuming that no essential resource was lacking. Nestboxes were installed only in areas that were considered to be suitable, semi-open habitat. Furthermore, nesting cavities are a key resource for Wrynecks (Coudrain 2009), and all our territories harboured at least two nesting cavities.

The proportion of old pear orchards within a territory appears here to be an important factor affecting territory colonization and occupancy. In a previous study of the same population, old fruit orchards, but not necessarily old pear orchards, had been determined to be preferred foraging habitats of Wrynecks (Freitag 1998, N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). In general, fruit tree orchards had higher densities of ant nests than other habitat types, with pear orchards harbouring higher nest densities than apple or apricot orchards. Pear orchards also had a higher proportion of bare ground than apple and apricot orchards, and old pear orchards had a slightly higher proportion of bare ground (39%) than middle-aged (32%) and young pear orchards (34%). Thus, pear orchards are a favoured habitat type due to high food density and good prey accessibility. The negative impact of the proportion of vegetable cultivation is in line with the findings of Freitag (1998) and N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub (unpubl. data), who observed an avoidance of vegetable cultivation by foraging Wrynecks. Although areas of vegetable production were sparsely vegetated, which would allow easy access to ant nests, they had a low ant nest density and were mostly devoid of perches. Thus, these areas were not suitable foraging habitats and negatively affected territory occupancy.

Territory extinction probability was negatively affected by the number of cropping units, which indicates a positive effect of habitat heterogeneity in the agricultural matrix. According to Dauber and Wolters (2004), most ant species can experience
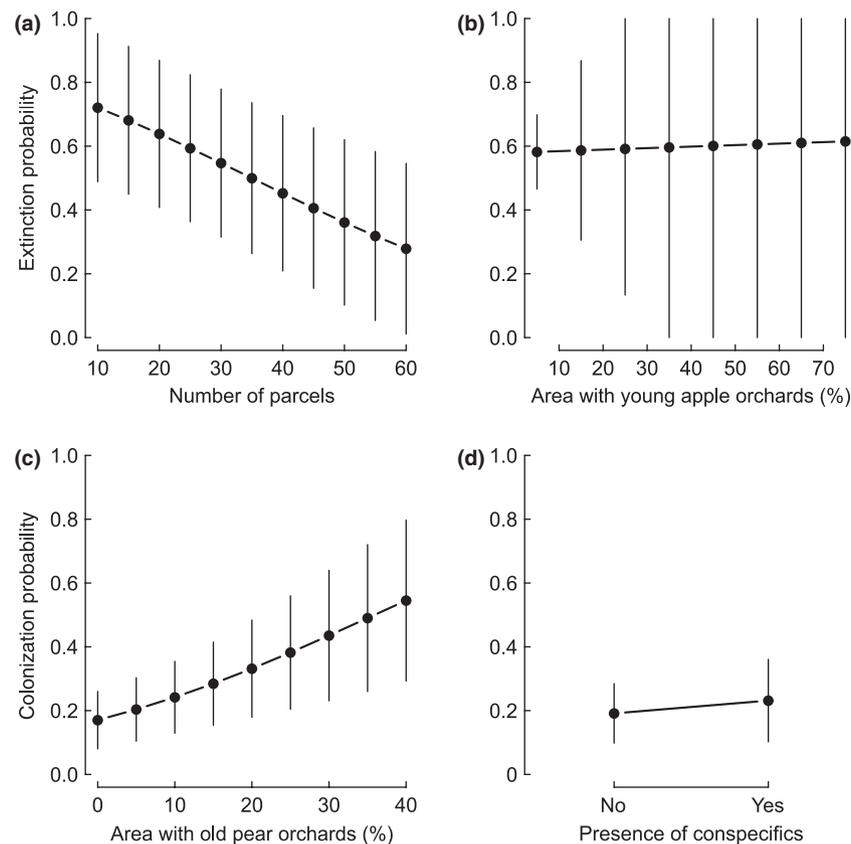
Figure 4. Predicted model-averaged probabilities of Wryneck territory extinction and colonization from the best models accounting for 0.95 of the AICc weight (Table 2). Shown are the number of parcels (a) and proportion of young apple orchards within the territory (b) in relation to extinction probability, 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 colonization probability. For time-dependent models, the predictions shown are for the year 2004. The figures show averaged estimates with 95% confidence intervals.

a positive edge effect, which would lead to differences in abundance between the centre and the edge of a culture parcel. This may provide a functional, trophic explanation for why Wrynecks select heterogeneous habitats (Roth 1976, Benton *et al.* 2003). Moreover, territories within highly structured farmland matrices are less likely to be affected by all sorts of habitat disturbance occurring at single cropping units (e.g. removal of fruit tree orchards, pesticide application) and may thus provide more stable food resources. This may be especially important in areas with intensively managed agriculture.

In contrast to our expectations based on a previous study of the same population (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data), the proportion of bare ground within a territory had only a marginal effect on territory occupancy, and none for

extinction or colonization, despite the fact that Wrynecks preferentially forage in areas with more than 50% bare ground (N. Weisshaupt, R. Arlettaz, T.S. Reichlin, A. Tagmann-loset, M. Schaub, unpubl. data). This discrepancy is most probably due to a scale effect (Orians & Wittenberger 1991, George & Zack 2001). At the micro-habitat scale, the proportion of bare ground appears to be important, whereas at a larger spatial scale, it might not be that crucial.

The presence of conspecifics positively affected colonization probability, which is in accordance with many dispersal studies (e.g. Stamps 1988, Muller *et al.* 1997). Whereas experienced birds often rely on their own reproductive success to assess territory quality, which eventually leads to site fidelity (Schaub & von Hirschheydt 2009), juveniles and unsuccessful breeders may rely either on reproductive success

Table 3. Model selection results for clutch size (complete clutches of n = 122 broods from 53 territories), the number of fledglings from successful broods (n = 94 from 50 territories) and the proportion of successful broods (n = 175 broods from 62 territories) in relation to the amount of old pear orchards and the number of parcels within the territories, evaluated with a generalized liner mixed model with Poisson or binomial error distributions. Year is included as a fixed effect in all models, and territory as a random effect. Given are the ΔAIC, AIC weights (w_i), number of estimated parameters (K) and the deviance.

Model	ΔAIC	w_i	K	Deviance
Clutch size				
Intercept	0.00	0.404	7	449.00
Old pear orchard	1.94	0.153	8	448.95
Number of parcels	0.46	0.321	8	447.46
Old pear orchard + number of parcels	2.39	0.122	9	447.40
Number of fledglings				
Intercept	0.00	0.401	7	427.70
Old pear orchard	1.56	0.184	8	427.26
Number of parcels	0.66	0.288	8	426.37
Old pear orchard + number of parcels	2.28	0.128	9	425.99
Proportion of successful broods				
Intercept	0.00	0.498	7	248.89
Old pear orchard	1.94	0.189	8	248.83
Number of parcels	1.58	0.226	8	248.46
Old pear orchard + number of parcels	3.50	0.087	9	248.38

of other individuals (Doligez *et al.* 1999) or on the presence of conspecifics to evaluate it (Muller *et al.* 1997).

High-quality territories should provide a fitness benefit for the territory holder, most likely in terms of increased breeding success (Andrén 1990, Holmes *et al.* 1996, Pärt 2001). In the present study, breeding success of Wrynecks was not related to habitat variables identified as important and only marginally to the frequency of territory occupancy, pointing towards a possible mismatch between habitat preference and fitness (Arlt & Pärt 2007). One likely reason for this result is that the breeding success of Wrynecks has a stochastic component because it is affected by the prevailing weather (Geiser *et al.* 2008). This might blur any relationship with habitat variables. A further explanation is that the considered components of breeding success are not the relevant fitness components. Other components such as nestling growth, and post-fledging and adult survival may be more strongly affected by territory quality.

Implications for conservation

Throughout its range, the Wryneck occurs in various savannah-like landscapes such as light woodland, traditional orchards, parks and vineyards (Glutz von Blotzheim & Bauer 1980). In our study area, intensively farmed pear orchards seem to offer the best foraging conditions for Wrynecks, offering a high density of ant nests and optimal prey detectability/accessibility. The reduction of food availability due to increasing density of ground vegetation cover affecting accessibility to ants or due to the reduction of ant abundance, both as a result of intensive farming, has undoubtedly strongly contributed to the large-scale decline of Wryneck populations. Farming practices that maintain or create sparsely vegetated patches (e.g. through stopping fertilizer application, mechanical or chemical destruction of ground vegetation, removal of topsoil) within savannah-like landscapes are likely to enhance Wryneck populations. Although the Wryneck is often viewed as a species that can only survive in traditional, low-intensity farmed areas (Hölzinger 1987), our study suggests that the persistence of Wrynecks is possible in areas with intensive agriculture, as long as the essential resources (access to ground-dwelling ants and breeding cavities) are present.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description how to obtain habitat-specific ant nest densities corrected for imperfect detection.

Table S1. Description and summary statistics of recorded habitat types for each of the 100 territories.

Table S2. Description and summary statistics of territory variables for each of the 100 territories.

Table S3. Model selection summary for detection probability of ant nests.

Table S4. Model selection results for univariate static occupancy models of Wryneck territories.

Table S5. Model selection results for univariate extinction probability models.

Table S6. Model selection results for univariate colonization probability models.

Figure S1. Example of a mapped, digitized territory.

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