Food or nesting place? Identifying factors limiting wryneck populations

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submitted by
Valérie Coudrain

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Supervision
Prof. Raphaël Arlettaz
PD Michael Schaub
Institute of Ecology and Evolution
Division of Conservation Biology

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Abstract

1. In the last decades, farmland bird populations have strongly declined as a consequence of agriculture intensification. Birds may have lost breeding sites, food supply or other crucial resources, with the role of multiple factors often remaining unclear. The ant-eating and cavity breeding wryneck *Jynx torquilla* may be limited by the availability of cavities, the amount of ants or their accessibility. By comparing occupied and unoccupied breeding territories, we investigated the relative role of these factors in the decline of wrynecks.

2. We compared the characteristics of known wryneck breeding territories (offer of breeding cavities, food abundance and ground vegetation structure) and randomly selected, fictitious territories (n = 154) in Western Switzerland. We also studied environmental factors that may affect ant nest density.

3. The probability of territory occupancy strongly increased with both nestbox availability and ant abundance. In addition, this probability peaked around 50% of bare ground cover. Habitat types that harbour low ant abundance such as cropland and grassland were avoided. Ant nest density decreased with increasing amount of bare ground, and it was particularly high in vineyards.

4. *Synthesis and application.*
Our results showed that breeding cavities, food availability and its accessibility all limit wryneck distribution. The maintenance and restoration of ant rich grassland, interspersed with patches of bare ground and with hollow trees or dedicated nestboxes in the surroundings are essential to preserve wryneck populations. Such a habitat structure could be achieved even in intensively farmed habitats, such as in vineyards or fruit tree plantations.

1. INTRODUCTION

As a result of the intensification of agriculture, which has considerably modified the structure of most landscapes, many farmland bird populations have collapsed since the mid of the 20th century (Donald et al. 2001, Freemark & Kirk 2001, Wretenberg et al. 2006). The disappearance of unproductive structures such as hedgerows, forest patches and isolated trees, and the decline of arthropod populations caused by systematic ploughing and increased application of fertilizers and pesticides have negatively affected two key ecological factors determining the persistence of farmland birds: the availability of breeding sites and the abundance/accessibility of food resources (Blanco et al. 1998, Benton et al. 2002, McCracken & Tallowin 2004). For most species, yet, it remains unclear which essential resources are the main cause of population collapse (Newton 2004), although their identification is prerequisite to any population conservation/restoration action plan.

Within a breeding territory, essential resources must be available for successful reproduction. Resource availability is resource abundance modified by its accessibility. Availability is often difficult to define and to measure accurately (Hutto 1990, Cornelius et al. 2008), and surrogates are often used. When investigating the realized ecological niche of a species in a given context it is essential to understand the subtle interplay between food abundance and habitat structure because the latter may largely determine food accessibility, i.e. its actual availability. Recognizing these forces directing resource exploitation patterns is crucial for developing corrective measures to conserve and/or restore populations of endangered species.

Here we study the habitat requirements of wrynecks (*Jynx torquilla*)*,* a small migratory woodpecker. The wryneck is a secondary cavity breeder that forages essentially on ground-dwelling ants taken directly from their nests (Cramp 1985, Freitag 1996 and 1998). It inhabits different kinds of semi-open habitats such as orchards, parks, alluvial woods, open pine forests or vineyards, provided that the two main resources, breeding cavities and ground-dwelling ants are available (Weisshaupt 2007, Mermod 2008). Wrynecks have undergone a strong decline in Europe (Tomialojc 1994), with habitat loss or degradation mentioned as the main causes (Hölzinger 1987).

Trees are an important component of wryneck territories. Firstly, they can contain natural cavities, offering breeding opportunities; secondly, they are used for perch hunting, the typical foraging technique of wrynecks (Cramp 1985, Bitz & Rohe, 1993, Freitag 1998, Weisshaupt 2007). With the intensification of agriculture, large trees have been systematically removed and high-stem orchards, a traditional habitat of wrynecks in many areas (Hölzinger 1987, Cramp 1985), have been widely eradicated. The decline of large trees in farmland can therefore be seen as a major factor of decline.

Ground-dwelling ants are the main prey of wrynecks. Their availability to wrynecks is determined by their abundance modified by their accessibility. Availability of ant brood (larvae and pupae) is especially important because it constitutes the main resource for the nestlings (Freitag 1998). As thermophilic organisms that build long-lived sedentary nests, ground-dwelling ants rely generally on warm and stable soil surfaces. They are thus sensitive to any changes and disturbances in the uppermost layer of the soil (Folgarait 1998, Kaspari 2000). Intensive agricultural practices can therefore affect ant colonies directly by mechanical soil disturbance and indirectly by fertilization that increases vegetation density, thus reducing soil surface temperature. Both can result in a considerable decline of ant nest abundance (Folgarait 1998), potentially negatively affecting wryneck populations. However, although

the effect of land management on ant species diversity has raised much interest (Peck et al. 1998, Bromham et al. 1999, Bestelmeyer & Wiens 2001, Underwood & Fischer 2006), its effects on ant abundance have been poorly investigated.

Detection of, and access to food resources is an important issue for many ground-foraging birds in intensive farmland (Wilson et al. 2005). Whilst wrynecks are tolerant to the presence of tall sward, the density of vegetation cover is a major determinant of foraging site selection: wrynecks prefer to feed at places with a vegetation cover lesser than 50% (Kervyn & Xhardez 2006, Weisshaupt 2007). The systematic fertilization of grassland by modern farming practices inexorably leads to a denser sward. Even though a dense ground vegetation cover does not necessarily induce a decrease in ant abundance, ant detectability and accessibility may be seriously affected.

It is largely unknown which factors have caused the large-scale population decline observed in the European wryneck. We investigated in parallel the three main factors mentioned above: decline in the offer of breeding cavities; decline of ant abundance; impeded access and detectability of ant nests. We compared habitat features and ant occurrence in known breeding territories and randomly selected sites currently not occupied by wrynecks, with the aim to identify the relative contribution of the above factors. Additionally, we studied abundance of ants in various habitat types and determined environmental factors affecting their nest density and size. This information will be useful for developing sound conservation action plans for this regionally endangered bird species.

2. MATERIAL AND METHODS

The study was conducted from May to August 2008 in three viticultural regions of Switzerland where wrynecks still occur in reasonable numbers.

The first two regions (Neuchâtel, 47.0 °N, 6.8 °E, 450 m asl and La Côte, 46.5 °N, 6.5 °E, 510 m asl) are situated along the northern banks of the Lakes Neuchâtel and Geneva, respectively. The third region (Geneva, 46.2 °N, 6.0 °E, 370 m asl) is located on the countryside west of the city of Geneva (Fig. 1). All regions, characterised by the proximate presence of a lake, harbour a favourable climate allowing wine production and, especially in La Côte, fruit tree plantations. The study area is therefore intensively managed farmland. Measurements of temperatures (5 cm above ground) were obtained from the 3 nearest meteorological stations (Neuchâtel, Pully, Genève-Cointrin; MeteoSchweiz).

2.1 HABITAT REQUIREMENTS OF WRYNECKS

2.1.1 Sampling design

By comparing currently occupied wryneck territories with randomly selected, non-occupied territories, we aimed to characterize habitat preferences of wrynecks. Based on average home-range sizes as revealed by radio tracking (Weisshaupt 2007), territories were defined as a circle with 111 m radius around a point location (nesting site in case of occupied territories). Actually occupied territories were obtained from nestbox surveys (n = 4 in Neuchâtel, n = 19 in La Côte) and casual observations (n = 4 in Neuchâtel, n = 10 in La Côte, n = 8 in Geneva) from the years 2006-2007, as well as from observations collected during territory mapping in 2008 (see below). To determine unoccupied sites, we generated, for each region, points at random (n = 31 in Neuchâtel, n = 52 in La Côte, n = 36 in Geneva) within the minimal convex polygon defined by all occupied sites in a given region. We excluded forests, lakes and urbanized areas as random locations, because these are unsuitable habitats.

In each territory initially classified as unoccupied in 2006-2007, we checked for the presence of wrynecks in 2008 by playing back their song twice during one minute. Wrynecks react very strongly to songs of

conspecifics and tape-luring (Reichlin et al. in prep.), rendering this method reliable to assess territory occupancy. The random sites in which the presence of the wryneck was actually assessed were reclassified as "occupied sites" (n = 7 in Neuchâtel, n = 11 in La Côte). In total, the study is based on 154 territories (53 occupied, 101 unoccupied; 39 in Neuchâtel, 71 in La Côte, 44 in Geneva).

2.1.2 Habitat mapping

We mapped habitats within all territories at the scale of parcels (fields with a given culture type that are separated from any other culture types) with the aid of geo-referenced aerial photographs. This ensured accurate mapping. We allocated all parcels to one of seven habitat types (fruit tree plantation, semi-vegetated vineyard, non-vegetated vineyard, cropland, meadowland, pastureland, lawn; see App. 1 for their definition) and recorded the amount of bare ground and vegetation height in each parcel. A territory was thus composed of a number of parcels, each parcel being defined by a habitat type, an estimated vegetation height and an estimated amount of bare ground. In several freshly cut meadowland identification of intensity of management was not possible. As a consequence, categories for meadowland management intensity were only considered for the modelling of ant nest abundance (see 2.2.4). We also noted the number of nestboxes and trees (diameter at breast height > 20 cm) outside forests. Habitat heterogeneity has generally a positive effect on farmland biodiversity (Benton et al. 2003); it also plays a major role in wryneck habitat selection (Mermod 2008). We defined heterogeneity as the number of parcels within a territory. Although wrynecks do not occur in dense forests, they may use trees along forest edges as well as hedges and isolated trees to breed. As hedges and forest edges are often more extensively managed than nearby farmland, they may provide good foraging opportunities (Poeplau 2005). We accounted for this possibility by including the variable "edge length", which combines the total length of both forest border and hedges within a territory. Field

maps were digitalized and the size of the parcels was measured in ArcMap (ArcGIS Version 9.2).

2.1.3 Food resources

Our goal was to get an estimate of the density of ant nests for each territory in order to test whether food supply was a limiting factor. We estimated habitat specific ant densities (see 2.2.3) and extrapolated this information across habitat types for the whole territory.

2.1.4 Statistical analyses

To compare the occupied territories with the random territories we separately analysed two sets of explanatory variables. The first set included structural, continuous variables (amount of bare ground and its square, number of ant nests, edge length, heterogeneity, number of nestboxes and trees). The second set of variables contained the proportion of the 7 different habitat types within the territories. We had to perform two separate analyses due to the different nature of the variables and because of some overlap in the information embedded by the two variable sets (habitat type already contains information about habitat structure).

Using the structural variables, we could test our main hypotheses. First, if food resources limit wryneck distribution we expect an effect of ant nest numbers on occupancy. Second, if access to food limits wryneck distribution we expect a higher amount of bare ground in occupied territories. Likewise, third, if wrynecks are limited by breeding sites, we expect a positive effect of nestboxes or trees on occupancy. Using the habitat types we could additionally test which habitat types are most profitable, which would facilitate strategic choices for habitat management.

The variables as defined above were fixed terms while the region (3 levels) was a random factor. The inclusion of a random effect for region ensured to correct for possible data non-independence. The modelling

procedure was conducted using generalized linear mixed models with a binomial error distribution. We defined 64 candidate models with all possible combinations of the structural variables and 128 candidate models with all possible combinations of habitat types. We did not consider interactions.

2.2 ANT ABUNDANCE MODELLING

2.2.1 Sampling design
We assumed that ant nest density is homogeneous within habitat type but affected by the amount of bare ground (Mermod 2008). We therefore sampled ant nests in the different habitat types in a random subset of occupied and unoccupied wryneck territories. In each considered territory we selected one to several habitat types at random, where ant sampling took place. A total of 135 locations were sampled. The number of sampling locations in the different habitat types is given in Appendix 2.

At each sampling location, we searched for ant nests in five 2 m^2 replicates by scraping the soil with a small rake during 7 minutes. The location of the five replicates was defined by selecting the first location at random, with the four others placed at 10 m distance from that point in each main azimuth direction. We recorded the number of nests, the amount of bare ground, and vegetation height for each replicate. For each nest we noted its diameter (nest size) and presence of breeding activity (winged ants, larvae and pupae). We collected few individuals from each nest for subsequent species determination.

2.2.2 Ant nest detection probability
Because the detection of ant nests is unlikely to be perfect (Mermod 2008), we estimated in a further study ant nest detection probability to correct the raw counts accordingly. We repeatedly sampled 36 2 m^2 plots in semi-vegetated vineyards randomly distributed in the region La Côte. All sampling plots were visited three times with a gap of one week

between visits. We recorded the number of nests, the amount of bare ground, and the vegetation height. Some ants were collected from the detected nests.

The detection histories (a row of three numbers representing the number of recorded ant nest at each of the three visits for each plot) were analysed with a binomial mixture model (Royle & Nichols 2003) using the program PRESENCE (Hines 2006). Before modelling, the three variables used to explain detection – temperature, amount of bare ground, and vegetation height – were standardized. The detection probability (p) of an ant nest at temperature T, amount of bare ground b and vegetation height v was modelled as $\text{logit}(\hat{p}_{T,b,v}) = \beta_o + \beta_1 T + \beta_2 b + \beta_3 v$, where the β are parameters to be estimated.

As wrynecks prey on the most abundant species (Bitz 1993, Freitag 1998), we did not distinguish between the different ant species. We defined 8 candidate models comprising all possible combinations of the factors T, b and v. The density, the other parameter type in the binomial mixture model, was always kept constant. This seems reasonable since we sampled ants only in one homogenous habitat.

The raw counts (C_i) from any replicate i with temperature T, bare ground b and vegetation height v were then corrected by $\hat{N}_i = C_i / \hat{p}_{T,b,v}$.

2.2.3 Predicting ant abundance for each parcel

Our goal was to estimate the abundance of ant nests at the wryneck breeding territory scale by extrapolating the ant nest density to the complete territory surface. We first modelled the corrected ant nest counts ($\hat{N}$) in relation to habitat type, bare ground and its square through a generalized linear mixed model with a Poisson error distribution. Since vegetation height was very variable over short time and was not important for ant nest detection (see results), we did not include vegetation height in the model. The habitat type "cropland" was not included in the analysis because only two ant nests have been found in

this habitat (28 locations sampled), suggesting that ant nest density was very close to 0.

The sampling location (group of five replicates) was treated as random variable to account for possible dependence. We defined eight candidate models comprising all possible combinations of the fixed effect variables and the interaction between amount of bare ground and habitat type to test whether the relationship between bare ground and abundance was the same in each habitat type. The parameter estimates of the best model were used to calculate the ant nest densities in function of identified variables for each parcel. The obtained density (nests/m^2) was multiplied by the size of the corresponding parcel to obtain an estimate of the number of nests.

2.2.4 Variables affecting ant nest density and size
As ant nest density, size and content are assumed to determine food abundance for wrynecks, we identified the main environmental variables affecting them. To determine the variables affecting ant nest density, we applied the same models as described above (2.2.3) to which we added the fixed variable "wryneck presence" that indicates whether the sampling location was within an occupied or unoccupied territory. This allowed testing in addition whether ant nest densities were consistently higher where wrynecks occurred. In total we formulated 19 candidate models comprising all possible combinations of the fixed effect variables and the interaction between bare ground and habitat type, and between wryneck presence and habitat type.

To assess the potential impact of grassland management on ant nest density, we modelled ant nest density in relation to meadow type, where the latter could be accurately determined. As fixed effect variables we included meadow type, amount of bare ground and its square and we treated sampling plots as random factor. We defined six candidate models comprising all possible combinations of the fixed effect variables.

To analyse the relationship between ant nest size and environmental variables, we used generalized linear mixed models with a normal error distribution. As fixed variables we included amount of bare ground, habitat type, temperature and its square. Temperature was included because ants are expected to move deeper into the soil at low or very high temperatures (Freitag 1998), resulting in apparent smaller nests. We considered the same habitat types as for ant nest density modelling but could include also non-vegetated vineyards, because the sample size for this habitat type was large enough. To account for possible data interdependence of nests close from each other, we considered replicates nested in sampling locations as random variables. We defined 14 candidate models comprising all possible combinations of the fixed effect variables.

As ant brood is an energy rich resource for nestlings, we performed a regression analysis between the presence of ant brood (presence of new queens, larvae, or pupae in the nest) and the size of the nests using generalized linear mixed models with a binomial error distribution. The ant species was included as a random factor.

2.2.4 Ant species determination
The collected ants were inspected with a binocular. The determination was carried out to the species level or to the family level if uncertainty was too high, using the identification keys of Della Santa (1994) and Seifert (1996).

2.3 MODEL SELECTION AND PREDICTIONS
For all modelling procedures described above, the candidate models were ranked according to their AIC (Akaike's Information Criterion) and the models with ΔAIC < 2 were averaged to get parameter estimates, standard errors, and confidence intervals. We used bootstraps (1000 replicates) to calculate predictions and their confidence intervals. All

modelling procedures were conducted in R 2.7.1 with function (lmer) (R Development Core Team, 2008).

3. RESULTS

3.1 ANT ABUNDANCE MODELLING

3.1.1 Ant diversity

We detected 2101 ant nests belonging to eight species. *Lasius niger* was in all regions the most abundant species (38.9 %, n = 818). *Solenopsis fugax* (21 %, n = 442), *Tetramorium caespitum* (18.6 %, n = 391) and *Lasius flavus* (11.1 %, N = 234) were also common and widely distributed. *Myrmica spp.* (6.1 %, n = 128), *Tapinoma erraticum* (2.2 %, n = 47), *Formica spp.* (1.7 %, n = 36), *Aphaenogaster subterraneae* (0.1 %, n = 2), *Lasius alienus* (0.1 %, n = 2) and *Ponera coerctata* (<0.1 %, n = 1) were all relatively rare. The nest density of the more common ant species in the different habitat types is given in Appendix 3.

The 442 nests belonging to *Solenopsis fugax* were excluded from further modelling procedures because this tiny ant is not part of wryneck's diet (Freitag 1998).

3.1.2 Modelling detection probability

Temperature was the main factor influencing ant nest detection probability, followed by the amount of bare ground. Vegetation height had hardly an effect (Tab. 1). Detection probability increased with increasing temperature and amount of bare ground (Fig. 2). Since vegetation height was not important, we estimated detection probability ($\hat{p}_{T,b}$) using only the parameter estimates of temperature and bare ground

($\text{logit}(\hat{p}_{T,b}) = 0.3749 + 0.1605 * T + 0.0771 * b$).

3.1.3 Relationship between ant abundance and environmental variables

According to the AIC ranking, ant nest density was best explained by the model including amount of bare ground, habitat type and presence/absence of wrynecks in the territory (Tab. 2). Uncertainty existed whether or not the interaction of habitat and bare ground should be included. According to the parsimony principle we considered the model without interaction. Moreover, a comparison of model predictions with and without interaction revealed very similar results. Ant nest density decreased with increasing amount of bare ground and was highest in semi-vegetated vineyards, followed by fruit tree plantations, pastures and meadows (Fig. 3). In all habitat types, ant nest density was higher at sites occupied by wrynecks than at unoccupied sites. For ant nest density extrapolation, wryneck presence was not considered in the models. The best model included amount of bare ground and habitat type with similar conclusions as above (Tab. 2).

The modelling of ant nest density in the different meadow types showed that ant nest density was lower in meadows characterized by more intensive management practices (Fig. 4). When bare ground was 40%, ant density in meadows with lowest intensity was 1.25 nests/m^2, while in the meadows with the highest intensity it was only 0.12 nests/m^2 at a same amount of bare ground.

Variations of ant nest sizes were best explained by a quadratic effect of temperature, the amount of bare ground and habitat type (Tab. 3). The recorded ant nest size increased non-linearly with temperature and linearly with amount of bare ground (Fig. 5). The largest nests occurred in semi-vegetated vineyards and the smallest in pastures.

The proportion of nests containing winged breeding ants, worker larvae, sexuate larvae, worker pupae and sexuate pupae increased with increasing nest size (Fig. 6).

3.2 HABITAT REQUIREMENTS OF WRYNECKS

From the modelling of the structural variables, eight models were closely top-ranked (ΔAIC < 2) (Tab. 4). The best models contained all considered variables, suggesting that all were potentially important. The probability that a territory is occupied by a wryneck was much higher when at least one nestbox was present (probability of territory occupancy [mean ± SE]; without nestboxes: 0.203 ± 0.043, with nestboxes: 0.949 ± 0.059). It increased with increasing ant nest density and with increasing number of large trees (Fig. 6). The highest territory occupancy was achieved when the amount of bare ground was about 50%. Territory was only marginally affected by edge length and habitat heterogeneity (Fig. 7).

The modelling of the habitat type variables resulted in five models with ΔAIC < 2 (Tab. 5). These models contained all habitat types, suggesting that all were important for territory occupancy. However, model-averaged effects sizes showed that territory occupancy probability was negatively related with the proportion of cropland, meadowland, pastureland, and lawns (Fig. 8). Fruit tree plantations had a slightly positive effect while both vineyard types hardly had an effect.

4. DISCUSSION

Our study shows clear differences in structural variables and habitat types between occupied and unoccupied wryneck territories. Occupied wryneck territories were characterized by the presence of nestboxes, high number of large trees and high ant nest abundance, as well as by an amount of bare ground around 50%. This suggests that any reduction in nesting sites, food abundance and its access is likely to contribute to the decline of wryneck populations. Both ant abundance and accessibility were influenced by the amount of bare ground, further suggesting that the ground vegetation structure is a key element in the wryneck habitat. This confirms former studies of fine-grained foraging habitat selection in another area of Switzerland (Weisshaupt 2007).

Ant abundance

Our results show that ant nest density decreased while ant nest size only slightly increased with increasing amount of bare ground. Although invertebrate abundance generally increases with vegetation height (Morris 2000), the former observed relationship contradicts this view and our initial hypothesis, that well sun-exposed surfaces such as bare ground are important for ant brood development, which would lead to higher ant occurrence in bare soil areas (Kaspari 2000, Lessard & Buddle 2005, Platner 2006). Actually, the need for vegetation in nest vicinity as a source of food may overrule the thermal needs for colony development. In contrast, ant nest density declined with intensifying grassland management, which gives a more pronounced sward cover. An optimum as regards vegetation cover for ants thus exists, which results from a trade-off between trophic and eco-physiological requirements. A larger ant nest size at high ambient temperature and in the presence of extensive bare ground indicates that ants move deeper into the soil as bad weather or dense sward cool the soil surface (Talbot 1946, Freitag et al. 2001). Finally, the size of an ant nest is an important indication of its energetic value, because the probability of ant brood presence increases with increasing nest size.

The absence of ants in cropland is not surprising because soil disturbance by ploughing hampers ant colonies from establishing (Freitag 1998, Mermod 2008).

Particularly high ant nest densities were recorded in semi-vegetated vineyards. This contrasts with another viticultural region of Switzerland (Valais) where ant nest density was low in vineyards, a habitat type avoided by local wrynecks (Freitag 1998, Mermod 2008, Weisshaupt 2007). We see two reasons for this apparent geographic discrepancy. First, soils are much more mineral (stony) in Valais. Second, vineyards in Valais are still scarcely vegetated (<5% of the total area; Arlettaz et al. in prep.), offering very little room for thriving

ant populations. Vineyards and fruit tree plantations thus represent suitable wryneck habitat only if they are planted in soft substrates and harbour a mix of vegetated and bare strips under the vine rows.

Ant abundance was low in meadows and pastures compared to vineyards. However, ant nest densities differed according to the intensity of grassland management, with highly fertilized meadows containing much lower ant nest densities. Although, the factors affecting ants in intensively managed grassland have been little studied yet, our results indicate that extensification of grassland management would increase ant abundance. Extensification of management practices should consider reduced application of fertilizers and grazing (Folgarait 1998, Underwood & Fisher 2006).

The ant community was dominated by four species, *Lasius niger*, *L. flavus*, *Tetramorium caespitum*, and *Solenopsis fugax*. These ant species are common prey of wrynecks, with the exception of the tiny *Solenopsis fugax* which was not considered in our analyses (Bitz & Rohe 1993, Freitag 1998, Ehrenbold 2004, Kervyn & Xhardez 2006, Mermod 2008). The habitat associations of these ant species reflected their ecological preferences. *Lasius niger* is a generalist species that occurs abundantly in various habitats (Seifert 1993). *Lasius flavus* is very tolerant towards vegetation cover (Pontin 1963) and was frequently recorded in grassland. *Tetramorium caespitum,* a generalist of dry habitats (Deffernez et al. 1990, Poeplau 2005, Platner 2006), was particularly abundant in vineyards. The habitat which offered good conditions for all species considered was definitely semi-vegetated vineyards. The existence of diverse ant communities may be important for the survival of wrynecks because ant species differing in their breeding phenology (Freitag 1998) may provide long-lasting and abundant food supplies for parents provisioning chicks with eggs and pupae.

Is the number of breeding cavities a limiting factor?

Wrynecks clearly preferred territories containing nestboxes and a high number of large trees, suggesting that a lack or reduction of breeding sites may limit wryneck distribution. This can be understood because woodpeckers typically need more than one cavity per territory (Ligon 1970, Cramp 1985, Bull et al. 1992). The importance of suitable nesting cavities for wrynecks has also recently been confirmed experimentally: in this species, the probability of territory occupancy increases with the number of adequate nestboxes supplied (Zingg 2009).

Hedges and forest borders could be important components of wryneck habitats, as trees in these structures usually provide nesting cavities (Poeplau 2005). In the present study, however, wrynecks did not appear to prefer territories with longer forest borders and hedge rows. This may indicate that availability of suitable cavities close to if not within semi-open foraging patches might be crucial.

Is ant abundance a limiting factor?

The probability that a territory is occupied by wrynecks increased with increasing ant nest density, suggesting that ant abundance has an impact on wryneck populations. Wrynecks also avoided habitat types that had low ant nest densities such as cropland, meadows and pastures. While the avoidance of meadows and pastures might also result from a reduced accessibility (see below), this is unlikely to be true for cropland, where access to ants is not permanently hampered by vegetation.

Meadows and pastures farmed at low intensity in combination with trees (orchards) have historically constituted the favourite habitat of Central European wrynecks (Hölzinger 1987, Cramp 1985). Yet, the traditional management of grassland in orchards has vanished since World War II, being progressively replaced by heavily fertilized meadows and intensively grazed pastures. This may explain why wrynecks are today so rare in what constituted their key habitat in the past. Restoring wryneck populations in grassland dominated landscapes seems thus only possible if the input of fertilizers is reduced massively.

Ant nest densities were consistently higher in territories occupied by wrynecks, regardless of the habitat type. This suggests that wrynecks appraise territory quality by directly estimating ant nest densities.

Could a change in vegetation structure reduce access to or detectability of food resources for wrynecks?

Territories with ca 50% of bare ground were preferred over territories offering less or more bare ground area. This observation is in line with a recent radiotracking study that established that wrynecks forage mainly at locations with more than about 60% of bare ground (Weisshaupt 2007). Theoretically, the accessibility of ant nests should increase linearly with increasing amount of bare ground. However, because ant nest density declines with increasing amount of bare ground, the preference for a medium amount of bare ground appears to be the result of a trade-off between food abundance and food accessibility. Thus, the vegetation structure is important for the accessibility to ants for wrynecks, and the change of the vegetation structure due to increased fertilizer application has probably massively contributed to its decline.

Conclusions and conservation implications

Our results demonstrate that breeding opportunities, ant abundance and accessibility were very important factors limiting the distribution of wrynecks. Wrynecks did not show any clear preferences for particular habitat types, and appear even flexible as regards habitat choice insofar as semi-open landscapes are present. Hence, suitable nesting cavities as well as ant-rich, open ground vegetation structures for foraging are key elements for the persistence of wryneck populations. Nesting cavities can naturally occur at sufficient density where old trees remain numerous; alternatively, nestboxes can be provided (Zingg 2009). In semi-open grassland-dominated matrices, meadows must be managed at low intensity such that the vegetation structure becomes more open, with the intention both to boost ant abundance and to facilitate accessibility to prey

for wrynecks. In vineyards and fruit tree plantations, management practices must promote a mix of bare and vegetated surfaces. These habitat features have been proven essential for many other ground-foraging species (Benton et al. 2003, Aktinson et al. 2004, Butler & Gillings 2004, Arlettaz et al. in prep) and will benefit many other elements of flora and fauna.

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TABLES

Tab. 1: Model selection of ant nest detection probability using the Poisson mixture model from 36 plots with 3 sample occasions. The models refer to the detection probability only, for the abundance always a constant was used. The models are ranked according to

Model	ΔAIC	AIC weights	Deviance	K
T_a	0.000	0.337	1.000	3
T_a + Bare ground	0.790	0.227	0.674	4
T_a + Vegetation height	1.990	0.125	0.370	4
T_a + Vegetation height + Bare ground	2.450	0.099	0.294	5
Constant model	2.570	0.093	0.277	2
Bare ground	3.410	0.061	0.182	3
Vegetation height	4.550	0.035	0.103	3
Vegetation height + Bare ground	5.310	0.024	0.070	4

their AIC weights. K is the number of parameters, T_a = ambient temperature.

Tab. 2: Results of ant nest density modelling with a mixed model fitting a Poisson error distribution and using the counts corrected for detection probability. The models are ranked according to their AIC weights. K is the number of parameters. * The 8 candidate models for ant density extrapolation.

Models	ΔAIC	AIC weights	Deviance	K
Bare ground + Habitat + Wryneck presence	0.000	0.322	1319.244	8
Bare ground + Habitat + Wryneck presence+ Bare ground*Habitat	0.719	0.225	1313.963	11
Bare ground + Bare ground^2 + Habitat + Wryneck presence	1.736	0.135	1318.980	9
Bare ground + Bare ground^2 + Habitat + Wryneck presence + Bare ground*Habitat	2.695	0.084	1313.939	12
*Bare ground + Habitat	2.762	0.081	1324.005	7
*Bare ground + Habitat + Bare ground*Habitat	3.740	0.050	1318.984	10
Bare ground + Habitat + Wryneck presence + Habitat*Wryneck presence	4.344	0.037	1317.587	11
*Bare ground + Bare ground^2 + Habitat	4.748	0.030	1323.992	8
Bare ground + Bare ground^2 + Habitat + Wryneck presence + Habitat*Wryneck presence	5.701	0.019	1318.945	11
*Bare ground + Bare ground^2 + Habitat + Bare ground*Habitat	6.210	0.014	1317.454	12
Habitat + Wryneck presence	8.917	0.004	1330.160	7
*Habitat	12.571	0.001	1335.814	6
Habitat + Wryneck presence + Habitat*Wryneck presence	13.241	0.000	1328.485	10
Wryneck presence	65.687	0.000	1392.931	4
Bare ground + Wryneck presence	67.672	0.000	1392.916	5
Bare ground + Bare ground^2 + Wryneck presence	68.975	0.000	1392.219	6
*Constant model	82.860	0.000	1412.104	3
*Bare ground + Bare ground^2	83.096	0.000	1408.340	5
*Bare ground	83.218	0.000	1410.462	4

Tab. 3: Results of ant nest size modelling using a mixed model with normal error distribution. The models are ranked according to their AIC weights. K is the number of parameters, T_a = ambient temperature.

Modelle	ΔAIC	AIC weights	Deviance	K
Habitat + T_a + T_a^2	0.000	0.409	14209.067	9
Habitat + T_a^2	0.809	0.273	14204.079	8
Bare ground + Habitat + T_a	1.773	0.168	14207.164	9
Bare ground + Habitat+ T_a + T_a^2	2.024	0.149	14214.244	10
Bare ground + Bare ground^2 + Habitat + T_a + T_a^2	11.935	0.001	14199.674	11
Bare ground + Bare ground^2 + Habitat + T_a	13.933	0.000	14204.117	10
Bare ground + Habitat	21.413	0.000	14225.051	8
Habitat	26.589	0.000	14237.647	7
Bare ground + T_a	31.890	0.000	14222.243	5
Bare ground + T_a + T_a^2	33.117	0.000	14228.136	6
Bare ground + Bare ground^2 + Habitat	33.222	0.000	14228.983	9
Bare ground + Bare ground^2 + T_a	41.568	0.000	14245.231	4
T_a + T_a^2	42.625	0.000	14247.414	5
Bare ground + Bare ground^2 + T_a + T_a^2	44.770	0.000	14243.009	6
Bare ground	47.704	0.000	14228.995	4
T_a^2	47.795	0.000	14228.157	7
Bare ground + Bare ground^2	61.286	0.000	14243.010	5
Constant model	64.221	0.000	14266.910	3

Tab. 4: Modelling results of the wryneck territory occupancy probability in relation to structural variables using mixed models with a binomial error distribution. The models that accumulate dAIC weights of 0.9 are represented. The models with ΔAIC < 2 were averaged to make predictions. K = number of parameters.

Models	ΔAIC	AIC weights	Deviance	K
Nestbox + Trees + Edge + Ants + Bare ground + Bare ground^2	0.000	0.137	126.591	8
Nestbox + Trees + Ants + Bare ground + Bare ground^2	0.158	0.127	128.750	7
Nestbox + Edge + Ants + Bare ground + Bare ground^2	1.607	0.062	130.199	7
Nestbox + Trees + Edge + Ants	1.612	0.061	132.204	6
Nestbox + Ants + Bare ground + Bare ground^2	1.766	0.057	132.358	6
Nestbox + Trees + Edge + Ants + Bare ground + Bare ground^2 + Heterogeneity	1.787	0.056	126.379	9
Nestbox + Trees + Ants + Bare ground + Bare ground^2 + Heterogeneity	1.818	0.055	128.409	8
Nestbox + Ants + Bare ground + Bare ground^2 + Heterogeneity	2.109	0.048	130.700	7
Nestbox + Edge + Ants	2.199	0.046	134.791	5
Nestbox + Edge + Ants + Bare ground + Bare ground^2 + Heterogeneity	2.212	0.045	128.804	8
Nestbox + Edge + Ants + Heterogeneity	2.868	0.033	133.459	6
Nestbox + Bare ground + Bare ground^2 + Heterogeneity	3.026	0.030	133.617	6
Nestbox + Edge + Bare ground + Bare ground^2 + Heterogeneity	3.081	0.029	131.673	7
Nestbox + Trees + Edge + Ants + Heterogeneity	3.212	0.028	131.804	7
Nestbox + Ants	3.622	0.022	138.213	4
Nestbox + Edge + Bare ground + Bare ground^2 + Heterogeneity	3.825	0.020	130.416	8
Nestbox + Trees + Bare ground + Bare ground^2 + Heterogeneity	3.855	0.020	132.446	7
Nestbox + Trees + Ants	3.911	0.019	136.502	5
Nestbox + Ants + Heterogeneity	3.962	0.019	136.553	5

Tab. 5: Modelling results of the wryneck territory occupancy probability in relation to habitat type variables using a mixed model with binomial error distribution. The models that accumulate ΔAIC weights of 0.9 are represented. The models with ΔAIC < 2 were averaged. K is the number of parameters.

Models	ΔAIC	AIC weights	Deviance	K
Meadow + Pasture + Lawn + Cropland	0.000	0.200	172.586	6
Meadow + Pasture + Lawn + Fruit tree plantations + Cropland	0.999	0.121	171.586	7
Cropland + Meadow + Lawn	1.630	0.088	176.216	5
Meadow + Pasture + Lawn + Non-vegetated vineyard + Cropland	1.709	0.085	172.295	7
Meadow + Pasture + Lawn + Semi-vegetated vineyard + Cropland	1.788	0.082	172.374	7
Meadow + Pasture + Lawn + Fruit tree plantations + Non-vegetated vineyard + Cropland	2.802	0.049	171.388	8
Meadow + Pasture + Lawn + Fruit tree plantations + Semi-vegetated vineyard + Cropland	2.994	0.045	171.580	8
Meadow + Pasture + Lawn + Non-vegetated vineyard + Semi-vegetated vineyard + Cropland	3.463	0.035	172.049	8
Cropland + Meadow + Pasture	3.369	0.037	177.955	5
Cropland + Meadow + Fruit tree plantations	4.019	0.027	178.605	5
Low-stem orchard + Semi-vegetated vineyard	4.162	0.025	180.749	4
Cropland + Meadow	4.239	0.024	180.826	4
Cropland + Fruit tree plantations + Semi-vegetated vineyard	4.524	0.021	179.110	5
Meadow + Pasture + Lawn + Fruit tree plantations + Non-vegetated vineyard + Semi-vegetated vineyard + Cropland	4.786	0.018	171.372	9
Meadow + Fruit tree plantations + Semi-vegetated vineyard	5.015	0.016	179.602	5
Cropland + Meadow + Semi-vegetated vineyard	5.204	0.015	179.791	5
Cropland + Low-stem orchard + Lawn + Semi-vegetated vineyard	5.537	0.013	178.123	6
Meadow + Lawn + Fruit tree plantations + Non-vegetated vineyard + Semi-vegetated vineyard + Cropland	5.578	0.012	174.164	8
Low-stem orchard + Lawn + Semi-vegetated vineyard	5.793	0.011	180.379	5
Pasture + Fruit tree plantations + Semi-vegetated vineyard	5.897	0.010	180.483	5
Cropland + Pasture + Fruit tree plantations + Semi-vegetated vineyard	5.933	0.010	178.520	6
Meadow + Fruit tree plantations + Non-vegetated vineyard + Semi-vegetated vineyard + Cropland	5.980	0.010	176.566	7
Fruit tree plantations + Semi-vegetated vineyard + Non-vegetated vineyard	6.068	0.010	180.655	5
Cropland + Meadow + Non-vegetated vineyard	6.193	0.009	180.779	5
Cropland + Fruit tree plantations + Semi-vegetated vineyard + Non-vegetated vineyard	6.519	0.008	179.105	6
Cropland + Pasture + Fruit tree plantations + Lawn + Semi-vegetated vineyard	6.605	0.007	177.191	7
Meadow + Pasture + Fruit tree plantations + Non-vegetated vineyard + Semi-vegetated vineyard + Cropland	6.690	0.007	175.276	8
Cropland + Pasture + Fruit tree plantations + Lawn	7.179	0.006	179.765	6

FIGURE CAPTIONS

Figure 1: Location of the three study regions. NE: Neuchâtel; VD: La Côte; GE: Genève.

Figure 2: Model-averaged relationship between ant nest detection probability and a) temperature, b) amount of bare ground, and c) vegetation height estimated from the binomial mixture model (Table 1).

Figure 3: Model-averaged ant nest density in relation to proportion of bare ground in different habitat types that are occupied and unoccupied by wrynecks. Vertical lines indicate standard errors. S-v: semi-vegetated.

Figure 4: Model-averaged ant nest density in relation to proportion of bare ground for meadows managed at different intensities. The categories of meadow management are described in Appendix 1.

Figure 5: Model-averaged ant nest diameter in relation to a) temperatures and b) amounts of bare ground for different habitat types. Vertical lines indicate standard errors. S-v: semi-vegetated. N-v: non-vegetated.

Figure 6: Proportion of ant nests containing a brood in relation to ant nest size. Dotted lines indicate standard errors.

Figure 7: Model-averaged probability that a territory is occupied by a wryneck in relation to a) ant nest density, b) forest edge and hedge length, c) number of large trees, d) habitat heterogeneity and e) proportion of bare ground for territories without nestboxes (broken lines) and with nestboxes (solid lines). The dotted lines indicate standard errors.

Figure 8: Model-averaged probability that a territory is occupied by a wryneck in relation to different habitat types. Vertical lines indicate standard errors. S-v: semi-vegetated. N-v: non-vegetated.
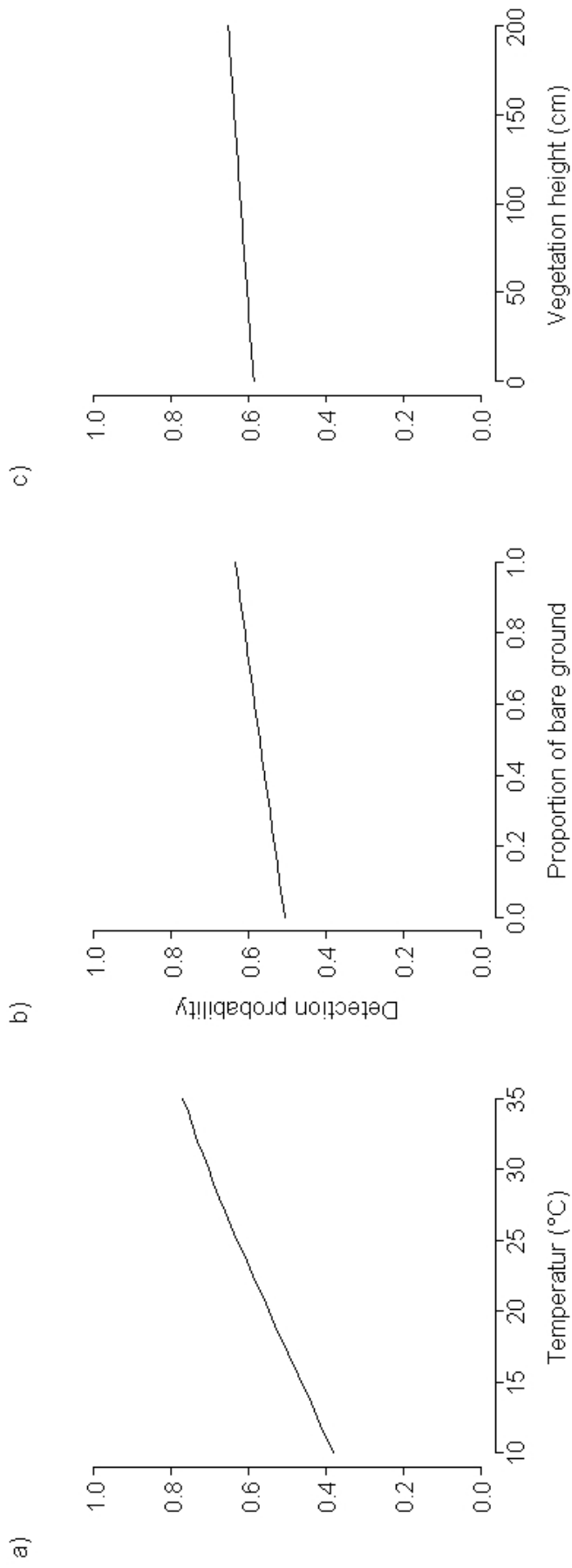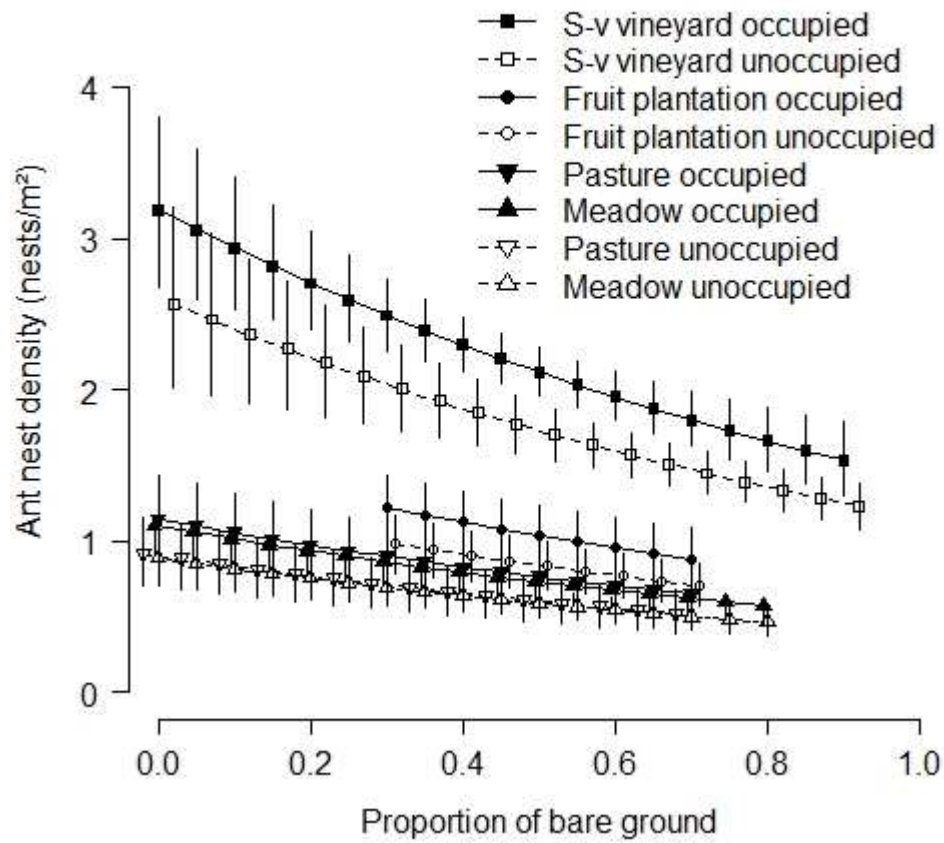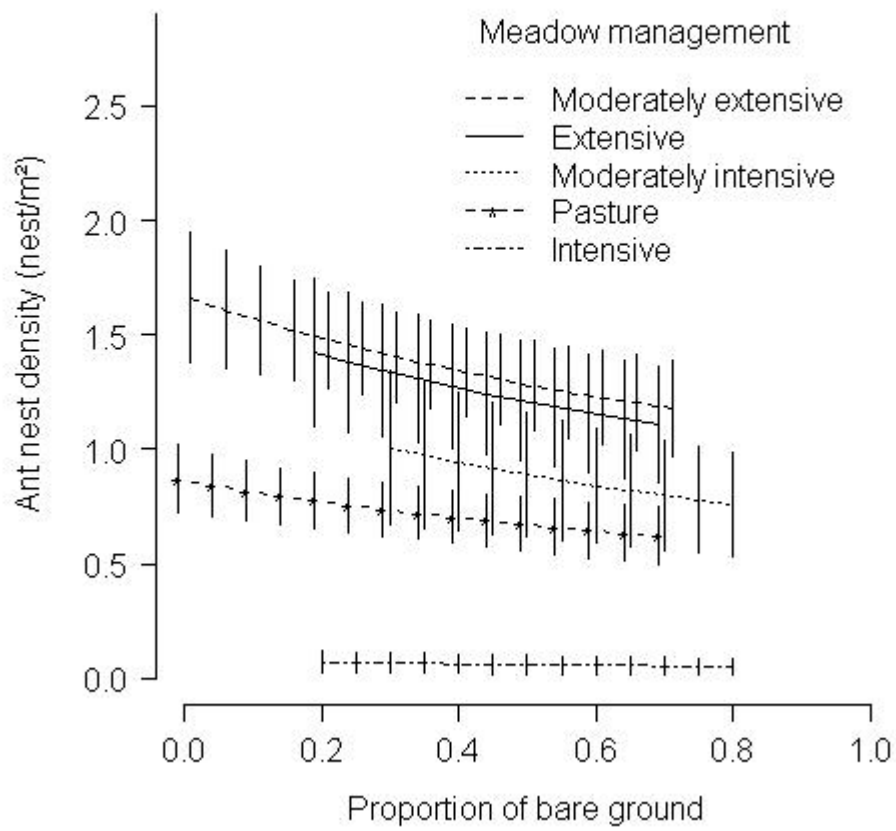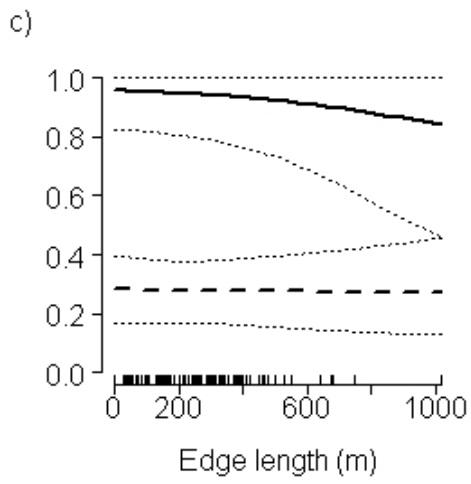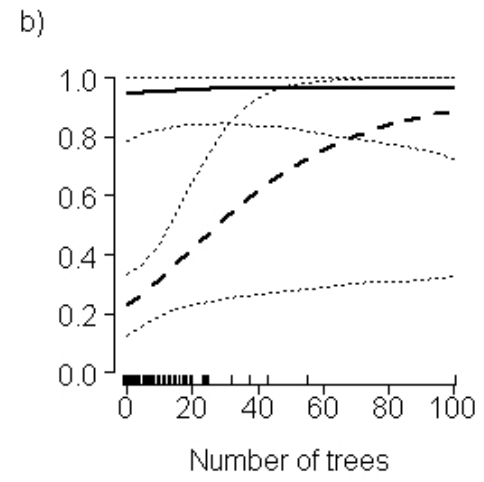
Fig. 1

Fig. 2

Fig. 3

Fig. 4

a)

b)
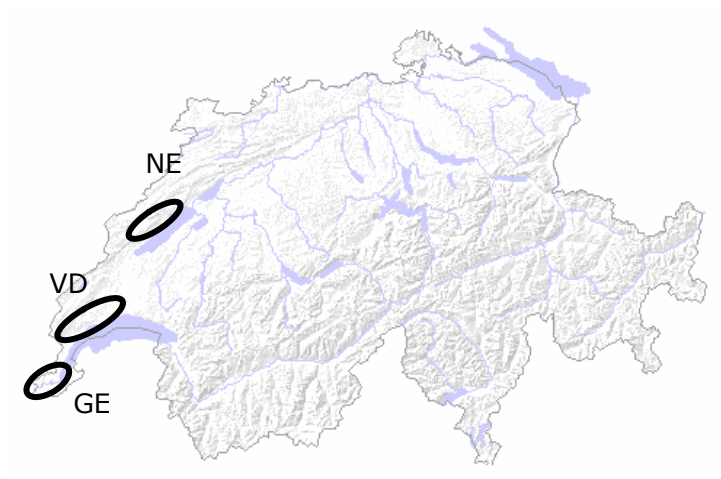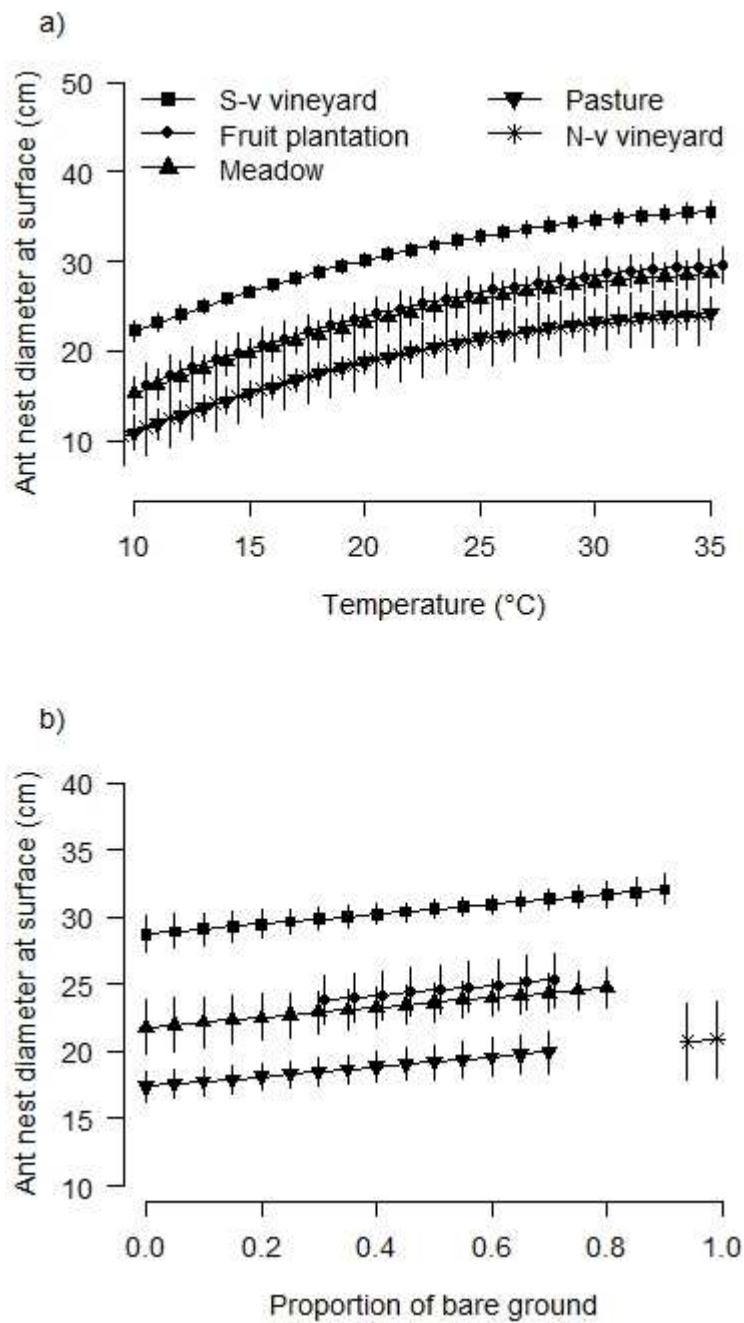
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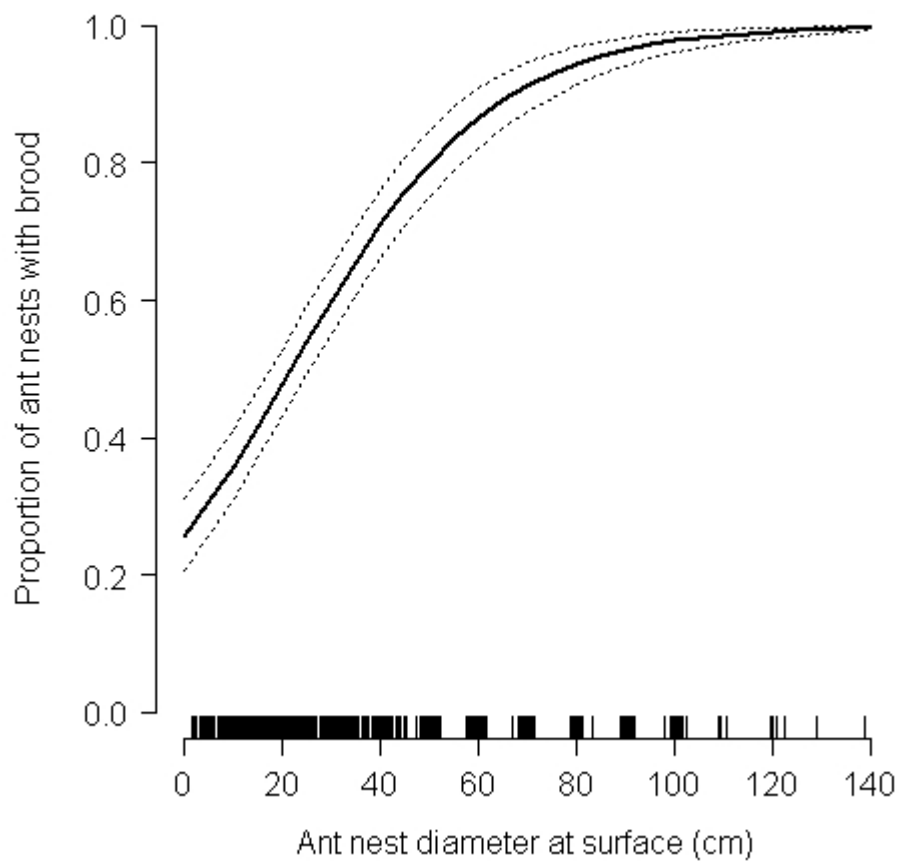
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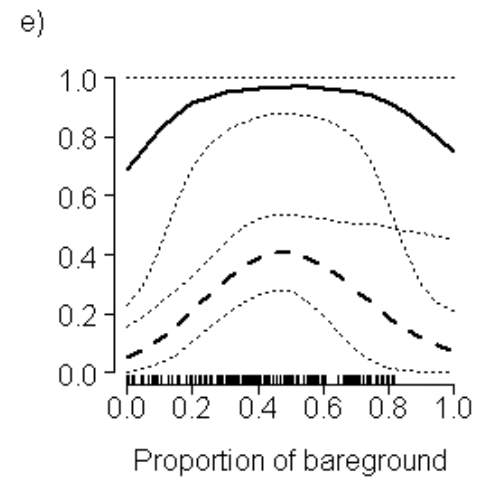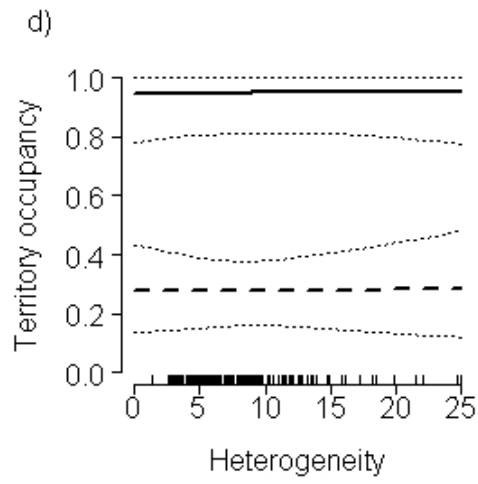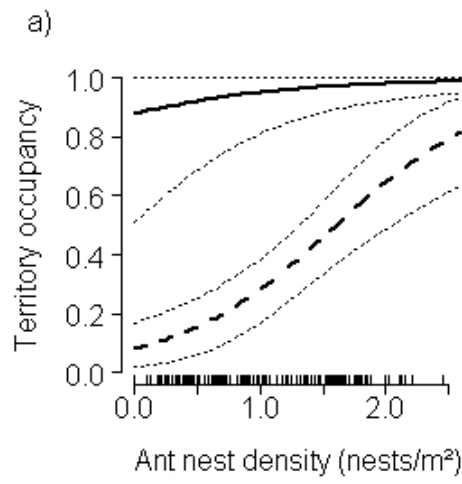
Fig. 7
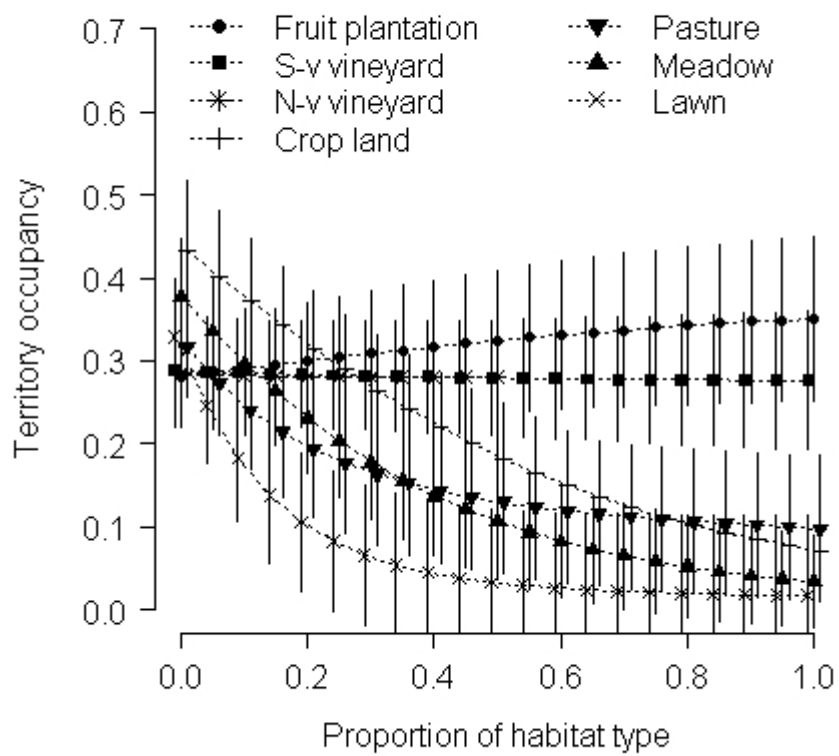
Fig. 8

APPENDIX

App. 1: Variables considered in the occupancy model
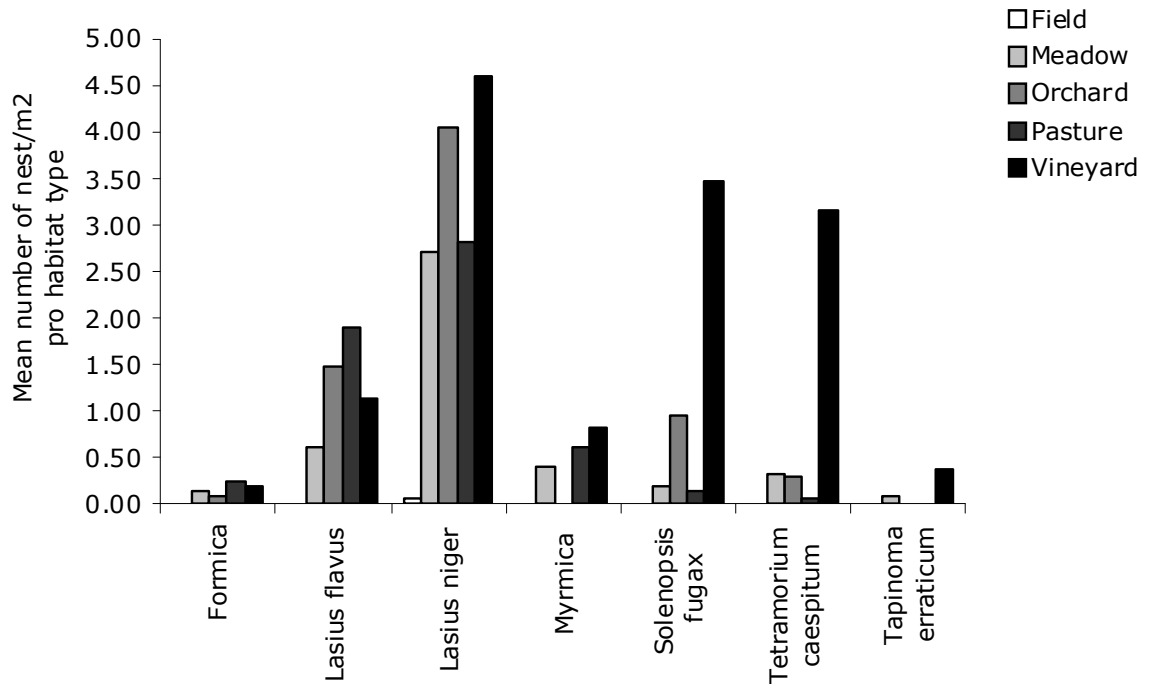
Category	Variables	Description
Habitat types	Fruit plantation	Intensively cultivated small fruit trees in lines
	Non-vegetated vineyard	Vineyard with < 5 % vegetation on the ground
	Semi-vegetated vineyard	Vineyard with 5 - 90 % vegetation cover on the ground
	Meadow	4 categories of management (I1 – I4, see below)
	Lawn	
	Pasture	
	Cropland	Crop, maize, rape, vegetables
Structural variables	Edge	Total length of hedges and forest border
	Bare ground	Proportion of visible bare ground when looking vertically from above
	Large trees	Number of trees with a diameter larger than 15 cm
	Nestboxes	Presence of at least one nest box within the site
	Heterogeneity	Number of parcels within a territory

Types of meadow management:

- I1: Extensive meadows with one or two cuts pro year.
- I2: Extensive meadows with two to three cuts per year. The vegetation is dominated by *Arrhenatherum elatius*.

- I3: Moderately intensive meadows with several cuts per years. The vegetation is dominated by *Dactylis glomerata*.
- I4: Intensively fertilised meadows with several cuts per years. The vegetation is dominated by *Lolium perenne*.

App. 2: Number of habitat type parcels where ant nests were sampled.

Region	Habitat type	Occupied	Unoccupied	Total
Neuchâtel	Cropland	2	8	10
	Meadow	9	12	21
	Low-stem orchard	0	0	0
	Pasture	7	7	14
	Non-vegetated vineyard	2	0	2
	Semi-vegetated vineyard	32	0	32
	Total Neuchâtel	52	27	79
La Côte	Cropland	1	6	7
	Meadow	0	9	9
	Low-stem orchard	11	12	23
	Pasture	2	4	6
	Non-vegetated vineyard	1	0	1
	Semi-vegetated vineyard	24	20	44
	Total La Côte	39	51	90
Geneva	Cropland	3	8	11
	Meadow	5	11	16
	Low-stem orchard	0	0	0
	Pasture	0	1	1
	Non-vegetated vineyard	0	0	0
	Semi-vegetated vineyard	6	32	38
	Total Geneva	14	52	66
Total		105	130	135

App. 3: Nest density of the more common ant species in the different habitat types.