Habitat selection by foraging Wrynecks *Jynx torquilla* during the breeding season: identifying the optimal habitat profile

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Capsule Large-scale intensification of agricultural management during the past 50 years has resulted in a reduction of invertebrate abundance and higher and denser ground vegetation. Food availability for insectivorous birds foraging on the ground has been negatively affected, but the interactions between birds and their food availability are complex and often species-specific. Populations of Wrynecks *Jynx torquilla* are declining all over Europe, possibly because of reduced accessibility to their main prey, ground-dwelling ants, due to higher and denser ground vegetation. However, it is not clear which ground vegetation structures are tolerated by foraging Wrynecks and which habitats are preferred.

Aims To identify the optimal ground vegetation structure and the main habitat types in which Wrynecks search for food.

Method We radiotracked seven Wrynecks in high-intensity farmland in Switzerland to study foraging habitat use during the reproduction season. Several habitat variables were mapped at each foraging location and compared with locations selected randomly within individual home ranges.

Results Wrynecks preferentially foraged at places with ≥50% bare ground. Vegetation height was not important. Older fruit tree plantations and fallow land were the preferred foraging habitats.

Conclusion Conservation measures should concentrate on preserving semi-open agricultural landscape matrices with loose ground vegetation cover to provide suitable foraging conditions. This can be achieved even in intensively managed farmland as illustrated in this study.

The populations of many farmland birds are declining due to the intensification of farming (Donald *et al.* 2001, Robinson & Sutherland 2002, Newton 2004). Important effects of the intensification are a homogenization of the landscape due to the removal of trees, hedges and fallow land, a higher and denser vegetation structure of grassland due to fertilizer application and increased cattle densities, and a reduction of invertebrate abundance due to pesticide application. Bird populations can be negatively impacted by these changes basically through loss or reduced availability of nesting places or through reduced food availability (Newton 2004).

Many farmland birds forage on ground-dwelling invertebrates and may therefore be impacted by a change of their availability imposed by a change of the ground veg-

etation structure. Food availability is food abundance that is modified by food accessibility, but each of the two elements – abundance and accessibility – might be differentially impacted by an altered vegetation structure. Invertebrate abundance increases typically with vegetation height (Schaub 1996, Morris 2000, Atkinson *et al.* 2004) and with sward complexity (Vickery *et al.* 2001). This is because a higher amount of plant biomass is available and because the habitat offers more niches if the vegetation is high and diverse. Food accessibility, by contrast, typically declines with increasing vegetation height, density and complexity (Whittingham & Markland 2002, Atkinson *et al.* 2004, Butler & Gillings 2004, Devereux *et al.* 2004). Experimental studies have shown that accessibility of invertebrates is greatly improved when the vegetation height is short (Butler & Gillings 2004, Devereux *et al.* 2004), but the effect of

vegetation density (i.e. the amount of bare ground) is ambiguous. Starlings did not response to altered tiller density (Devereux *et al.* 2006a), while other species preferred foraging areas with bare ground (Perkins *et al.* 2000, Moorcroft *et al.* 2002, Schaub *et al.* 2010). Devereux *et al.* (2006a) hypothesized that species which search for food visually might be more strongly affected by bare ground than species such as Starlings that search for food by probing the soil. Food intake rates of Canaries decrease with increasing complexity of the feeding substrate because of reduced ability to detect food items (Whittingham & Markland 2002). The preference to forage in short vegetation can also result from a need to reduce predation risk (Whittingham & Evans 2004), as potential predators are detected more easily when there are fewer obstructions due to high vegetation (Devereux *et al.* 2006a). Despite these general trends, the interactions between birds and their invertebrate food availability are complex and often species-specific (Atkinson *et al.* 2005). However, understanding these interactions is crucial for developing conservation actions for declining farmland birds.

Foraging behaviour can be studied efficiently by radiotracking. Radiotracking has the advantage over visual observations that birds can always be located, independent of the vegetation structure. Visual observations in dense vegetation are difficult and preference for short vegetation might be wrongly inferred just by the failure to observe birds in high vegetation.

Wrynecks *Jynx torquilla* almost exclusively forage on ground-dwelling ants which are exploited directly in the nests (Cramp & Simmons 1980, Freitag 1996). Ant nests are detected visually from perches or the ground. During the past decades Wryneck populations have declined strongly throughout Europe (Tomialojc 1994), and it is likely that the decline is linked with a change in food availability due to an altered ground vegetation structure. Increased farming intensity on grassland usually results in denser swards, but Wrynecks prefer territories with about 30–50% of bare ground (Mermod *et al.* 2009, Coudrain *et al.* 2010). Ant nest density and thus food supply decline with an increase in the amount of bare ground (Coudrain *et al.* 2010), and thus the preference for a large amount of bare ground probably results from better accessibility to food in areas with loose, semi-open ground vegetation structure. Territories of Wrynecks are also characterized by large proportions of ant-rich habitat types such as old pear plantations in the Valais (Switzerland, Mermod *et al.* 2009) or vineyards with sparse ground vegetation in Western Switzerland (Coudrain *et al.* 2010). These

habitat types may actually constitute the main habitats where food is exploited. Habitat use and home range size of Wrynecks have been investigated using radiotracking (Freitag 1998, Poeplau 2005), but without focus on the ground vegetation structure.

Here we study habitat use of Wrynecks by means of radiotracking in an intensively farmed area in Switzerland that is dominated by fruit tree plantations. Our main aims were to identify the optimal vegetation structure and the main habitat types in which Wrynecks search for food. A Bayesian analysis of part of the data focusing on vegetation structure only has revealed that Wrynecks preferred to forage when the amount of bare ground was between 40 and 80% (Schaub *et al.* 2010). The study, however, did not consider in detail the different habitat types, and it is therefore unknown whether this pattern persists even if different habitat types are considered and whether vegetation structure is as important as habitat type for the selection of foraging patches.

METHODS

Study area and data collection

The study was carried out on the plain along the Rhone river between Martigny and Sierre in the Canton of Valais (SW Switzerland, 46°14′N, 7°22′E, 460–520 m a.s.l.). The plain is used intensively for agricultural purposes, especially for cultivation of dwarf fruit trees and vineyards, but pastures, meadows and vegetable gardens are also present. Except along the river, tall trees are scarce and the availability of natural cavities is therefore limited. Between 1997 and 2003 about 700 nest boxes have been installed that serve as nesting opportunities for Wrynecks (Arlettaz *et al.* 2010). From 2002 to 2008, between 34 and 92 (yearly mean: 59 ± 21) broods have been recorded yearly in the area.

Wrynecks were caught either with mist nets mounted in front of the entry to the nest box or with a small hand net that was held in front of the nest hole. The captured birds were measured according to the usual ringing procedure (body mass, HS3, tarsus length) and were equipped with radio-transmitters (Holohil Systems Ltd, Canada, BD-2-P, 0.9–1.3 g, activity sensor, life span 42 days). Wrynecks have a body mass of about 35 g and thus our tags were less than 5% of body mass. The tagged birds were sexed genetically based on blood samples.

The transmitters were fixed with a Rappold harness of two elastic rubber lashes around the legs (Naef-Daenzer

2007). The used lash span was 110 mm, but its size had to be reduced for small individuals. The equipped birds were released immediately after tagging.

Radiotracking of foraging adults started when their chicks were older than 4 days, i.e. when they started to intensify feeding (Geiser *et al.* 2008). Due to the secretive and elusive behaviour of Wrynecks, the homing-in on the animal method (Samuel & Fuller 1996) was used to locate radiotagged birds. Additionally, we attempted to observe foraging individuals to collect more information about their hunting tactic. Tracked individuals were usually approached from two different directions by two observers in order to enhance localization and to collect a maximum of data. Although active foraging could only be confirmed in few cases, we assumed that most localizations refer to search for food given that radiotracking sessions took place during the peak of food provisioning to young. Observations were carried out at different times of day in order to get a good overview of habitat exploitation. We collected 20 locations per individual, which lasted between 1 and 5 days. In order to minimize spatio-temporal autocorrelation a minimum time lapse of 5 minutes between two successive locations was maintained throughout the session if the bird stayed at the same place. Time was set to zero every time a bird flew away, resulting in a mean duration of about 14 minutes between successive locations. The habitat features at actual radiotracking locations ('visited locations') were compared to the same number of randomly chosen locations within an individual's home range. Minimum convex polygons (MCP) were used to delineate home ranges in which random locations were generated with program ARCVIEW (ArcView GIS 3.3, Environmental Systems Research Institute Inc., California, USA). When generating random locations a buffer zone of 20 m was included around visited locations. Habitat type (14 types, see Table 1), proportion of bare ground and ground vegetation height were mapped at each location within a circle of 1 m radius. The proportion of bare ground was estimated visually. The mapping of random locations was always conducted within up to 2 days after completion of the mapping of visited locations.

Statistical analyses

To evaluate the feeding microhabitat we compared visited with random locations using a hierarchical logistic regression model (Gillies *et al.* 2006). The individual was included as a random effect in this model, allowing

Table 1. Description of the 14 habitat types used in this study. Note that all fruit tree plantations are composed of dwarf trees.

Habitat type	Description
Young apple fruit tree plantation	Tree stem diameter <5 cm
Middle-aged apple fruit tree plantation	Tree stem diameter between 5 and 15 cm
Old apple fruit tree plantation	Tree stem diameter >15 cm
Young pear fruit tree plantation	Tree stem diameter <5 cm
Middle-aged pear fruit tree plantation	Tree stem diameter between 5 and 15 cm
Old pear fruit tree plantation	Tree stem diameter >15 cm
Young other fruit tree plantation	Tree stem diameter <5 cm; apricot, plum or cherry
Middle-aged other fruit tree plantation	Tree stem diameter between 5 and 15 cm; apricot, plum or cherry
Old other fruit tree plantation	Tree stem diameter >15 cm; apricot, plum or cherry
Fallow land	–
Grassland	Meadows and pastures
Vegetables	Vegetable cultures
Vineyard	–
Anthropogenic habitats	Paved streets, buildings, canals, soil with gravel

the combination of the data of all individuals without the problems of pseudo-replication while providing information about habitat selection averaged across individuals. We formulated 16 candidate models that differ in their fixed effects. The considered fixed effects were habitat type, proportion of bare ground and vegetation height. In addition, we considered the square of the proportion of bare ground in order to model a curved relationship between selection and bare ground and to assess whether an optimal proportion of bare ground existed. Moreover, to evaluate whether the proportion of bare ground was only important if the vegetation is tall, we included models with an interaction between proportion of bare ground and vegetation height. The candidate models were composed of different combinations of these effects.

Based on the best model identified in this step, we evaluated whether there was differential preference of the nine types of fruit tree plantations. The variable habitat type had 14 levels, of which nine referred to different types of fruit tree plantations. These are composed of all combinations of three variants of fruit type and three age classes. We compared models where fruit tree plantations did differ only due to age ('young', 'medium-age', 'old'), only due to fruit type ('apple', 'pear', 'other') or were comprised of only one level ('fruit tree plantation').

Models were ranked according to the AIC value and evaluated through their respective AIC weights (probability that the model is the best among all fitted models; Burnham & Anderson 1998). All statistical analyses were performed with program R (R Development Core Team 2004) using function glmmML. Confidence intervals for predictions were obtained by non-parametric bootstrapping (1000 replicates).

RESULTS

Of a total of 12 captured and tagged birds (six males and six females), seven could be successfully tracked (Table 2). Five individuals disappeared after a short time; at least one was predated.

The individual home range sizes of the seven individuals calculated from minimum convex polygon varied between 2.1 and 9.2 ha (mean ± sd = 4.8 ± 2.4 ha). Because it was not certain whether 20 locations sufficed to get an accurate estimate of home range size, we conducted a bootstrap analysis in which the home range sizes were calculated as a function of an increasing number of randomly selected locations among the actual foraging locations (ARCVIEW). It turned out that about 15 locations were enough to get a reasonable estimate of the home range size (Appendix 1).

Model selection for Wryneck habitat use revealed that all top ranked models contained habitat type (Table 3), thus Wrynecks clearly preferred some habitat types for foraging while others were avoided. In addition, the proportion of bare ground was included in all top-ranked models, but there was some uncertainty whether the

Table 3. Model ranking for habitat selection of seven Wrynecks using hierarchical logistic regression models. The model notation shows fixed effects; the random effect individual is included in all models. Notation: ×, interaction; B, proportion of bare ground; B^2, proportion of bare ground^2; H, habitat type; V, vegetation height. Shown are the deviance, the number of estimated parameters (K), ΔAIC (difference in AIC value in regard to best model) and the AIC weight. The models are ranked according to the AIC weight.

Model	Deviance	K	ΔAIC	AIC weight
$B + B^2 + H$	290.184	17	0.000	0.426
$B + H$	293.232	16	1.048	0.252
$B + B^2 + H + V$	290.164	18	1.978	0.158
$B + H + V$	293.205	17	3.020	0.094
$B \times V + H$	293.061	18	4.877	0.037
$B \times V + B^2 \times V + H$	289.335	20	5.150	0.032
$H + V$	316.710	16	24.526	0.000
H	320.321	15	26.137	0.000
$B \times V + B^2 \times V$	359.234	6	49.050	0.000
$B + B^2 + V$	364.536	5	50.352	0.000
$B + B^2$	367.844	4	51.660	0.000
$B + V$	373.858	4	57.674	0.000
B	376.652	3	58.467	0.000
$B \times V$	372.842	4	58.658	0.000
Intercept only	382.603	2	62.418	0.000
V	382.414	3	64.229	0.000

relationship was a straight line or whether it was curved. Vegetation height was included only in lower ranked models suggesting that vegetation height was not important for habitat selection of Wrynecks. Of even less importance was the interaction between proportion of bare ground and vegetation height.

In a next step, we evaluated whether fruit types and age of fruit tree plantations influenced habitat selection (Table 4). The model which differentiated between different age classes of fruit tree plantations performed best. The models which included also fruit type or which did not differentiate between different classes of fruit tree plantations had lower support by the data.

Table 2. Details of the 12 tagged Wrynecks in Central Valais 2006, with the individual ring code, tagging time period home range size (minimum convex polygon), number of recorded foraging locations. The seven individuals that had a large enough sample size and were considered for modelling are indicated with *.

Ring number	Sex	Tagging time period	Home range size (ha)	Number of bearings
Y28720	Female	29–30 June	–	3
Y28561*	Female	14–24 June	2.10	20
Y28565	Male	1–8 June	–	5
Y28705*	Female	20–29 June	9.21	20
Y28706	Male	22–23 June	–	0
Y25361*	Female	12–17 July	5.30	20
Y25509*	Male	8–20 June	3.00	20
Y19376	Male	28 June–3 July	–	4
Y28656*	Male	12–25 June	3.92	20
Y28576	Female	31 May–8 June	–	6
Y28738*	Male	19–20 July	3.37	20
Y28674*	Female	14–24 June	6.46	20

Table 4. Testing which of the nine levels of fruit plantations are important for the habitat selection of seven Wrynecks. The four fitted models differ in the number of levels of fruit tree plantations, but all contain proportion of bare ground and its square as additional fixed effects as well as the other five habitat types. Note that the model denoted 'Interaction age × fruit type' is the same as model '$B + B^2 + H$' from Table 3. The models are ranked according to the AIC weight.

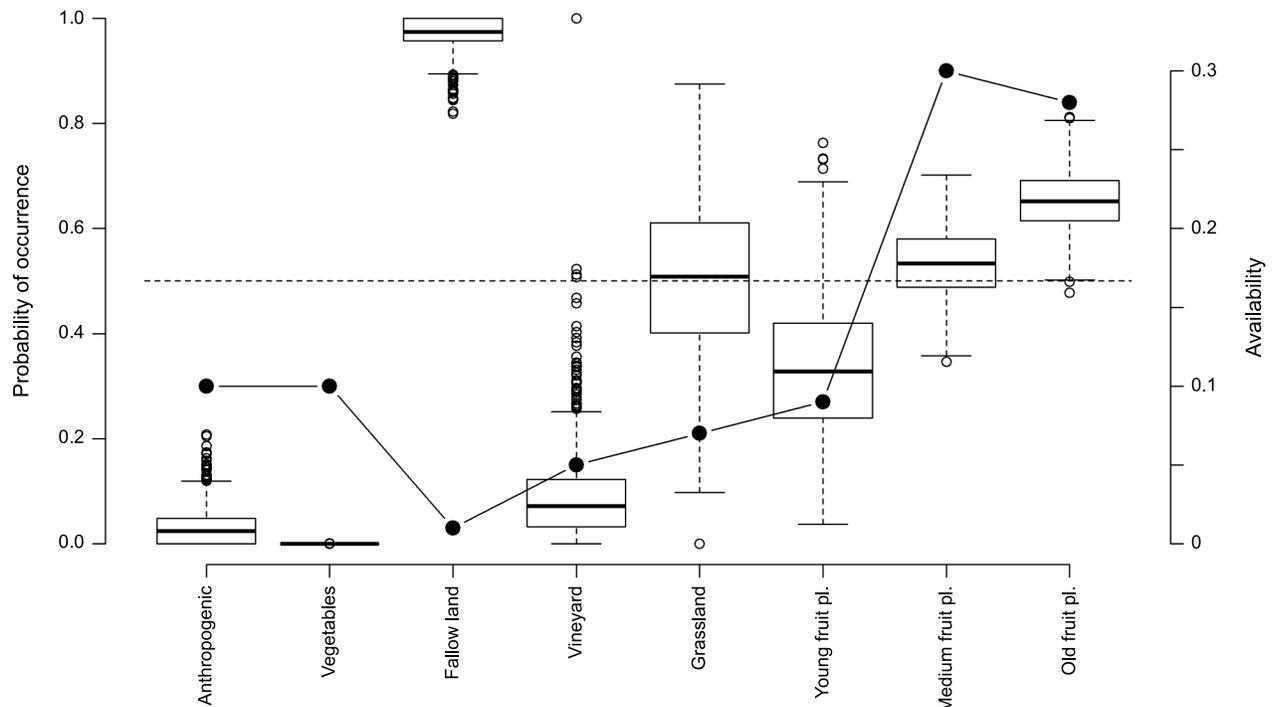| Fruit plantation levels	Deviance	K	ΔAIC	AIC weight
Age only	294.309	11	0.000	0.695
No differentiation between age and fruit type	300.411	9	2.101	0.243
Fruit type only	299.621	11	5.312	0.049
Interaction age × fruit type	290.184	17	7.875	0.014

Figure 1. Box plot of the probability of occurrence of foraging Wrynecks in different habitat types as estimated by the best model (Table 4), and proportional availability of these habitat types in the Wryneck territories (closed dots). Occurrence probabilities lower than 0.5 (broken line) indicate avoidance, probabilities larger than 0.5 indicate preference.

We used the best model (Table 4) to visualize the effects. The preferred habitat types for foraging were old fruit tree plantations and fallow land, while anthropogenic habitats, vegetables cultures and vineyards were avoided (Fig. 1). No clear selection was found for grassland as well as for young and medium-aged fruit tree plantations. The dominant habitat types were old and medium-aged fruit tree plantations, while the highly preferred fallow land was only a marginal habitat type in our study (Fig. 1).

The probability of foraging increased strongly with increasing proportion of bare ground up to about 60% bare ground (Fig. 2). If the proportion of bare ground increased further, occurrence probability remained almost stable.

DISCUSSION

The structure of ground vegetation was important for the selection of sites where Wrynecks foraged. The preference for foraging sites increased with increasing proportion of bare ground up to about 0.6 of bare ground and remained more or less stable thereafter. By contrast, the height of the ground vegetation was unimportant for the selection of foraging sites. Fallow land and old fruit tree plantations were the preferred habitat types for foraging, while vineyards, vegetable plantations and anthropogenic habitats were avoided.

The preference for foraging sites that are characterized by a large proportion of bare ground is probably related primarily to accessibility to ant nests. To have access to an ant nest requires that the nest can be detected and approached. In fact, ant nest accessibility increases with increasing proportion of bare ground and should be best if there is no ground vegetation at all. However, the abundance of ant nests declines with increasing proportion of bare ground (Coudrain *et al.* 2010), probably because ant food abundance is positively linked with vegetation. The quadratic function of preference for proportion of bare ground can thus be seen as a trade-off between food abundance and food accessibility. The optimal vegetation structure of a Wryneck foraging site seems therefore to be a small-scaled mosaic incorporating vegetated patches where food is developed (ants) and bare patches where unrestricted accessibility to food is ensured. A behavioural reaction to the risk of being predated may also contribute
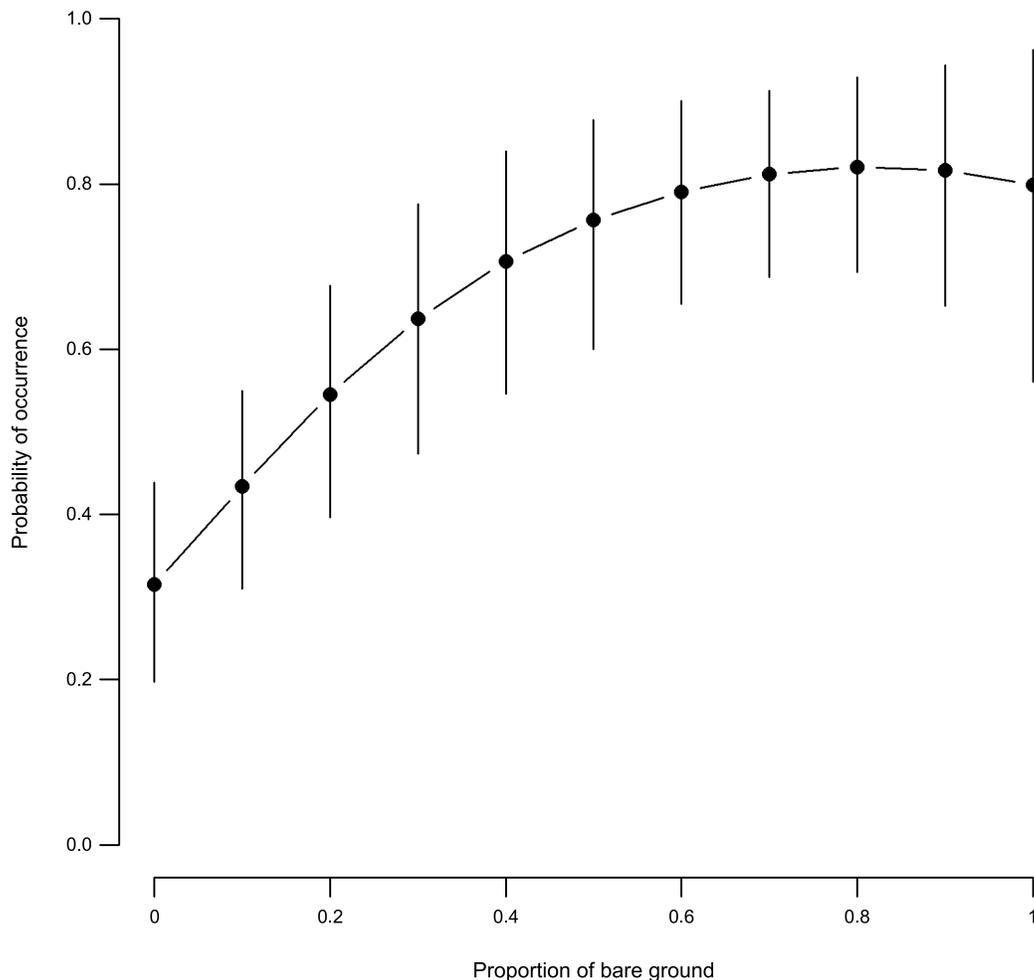
Figure 2. Predicted occurrence probabilities of Wrynecks in relation to the proportion of bare ground based on the best model (Table 4). The predictions are averaged across habitat types. Vertical lines show the 95% confidence intervals.

to the preference for foraging sites with bare ground (Cresswell 2008). Predators are detected faster when the site is not obstructed by vegetation (Devereux *et al.* 2006b). Avoidance of predation risk and increased accessibility to food appear to be the main reasons for the preference of foraging patches with bare ground, and the two reasons are not mutually exclusive. At the level of the territory the proportion of bare ground was slightly lower (Mermod *et al.* 2009, Coudrain *et al.* 2010) than at the level of the foraging patch (Schaub *et al.* 2010, this study). This is to be expected, because an optimal territory must contain a sufficient number of potential foraging sites, but interspersed areas that are not suited as foraging locations are also tolerated. It begs the questions about how many foraging patches an optimal Wryneck territory must contain and how they are best distributed spatially. Similar preferences for

bare ground have been found in other farmland bird species that search their food on the ground such as Hoopoe and Wood Lark (Schaub *et al.* 2010), Ortolan Bunting (Menz *et al.* 2009), Common Redstart (Martinez *et al.* 2010) and Yellowhammer (Douglas *et al.* 2009).

For many bird species that forage on the ground, vegetation height is an important element of vegetation structure: short vegetation is often clearly preferred (Schaub 1996, Atkinson *et al.* 2004, Butler & Gillings 2004, Devereux *et al.* 2004). Again, this preference is mostly due to a better accessibility to food, as the invertebrate abundance usually decreases with declining vegetation height (Schaub 1996, Morris 2000, Atkinson *et al.* 2004) and due to the need to reduce predation risk. For Wrynecks, vegetation height appeared to be unimportant for the selection of foraging sites. Likewise,

the interaction between vegetation height and proportion of bare ground was unimportant, indicating that the tolerance of high vegetation did not change with proportion of bare ground. We offer two explanations for this rather unexpected result. First, Wrynecks mainly try to detect ant nests from perches (Freitag 1998) and they usually only walk short distances on the ground in contrast to other terrestrially foraging insectivorous birds of farmland such as Hoopoes. Therefore, the impeded manoeuvrability in high vegetation would not pose a big problem for Wrynecks. Second, ants seem to construct especially conspicuous hill nests in high vegetation to improve the thermal demands (Seifert 1996), i.e. ant nests may be easier to detect and to exploit there.

The most preferred habitat types for foraging were old fruit tree plantations and fallow land, while vineyards, vegetable cultures and anthropogenic habitats were avoided and meadows were neither preferred nor avoided. Due to their high availability, old fruit tree plantations were likely much more important foraging areas than the rare fallow land. At the scale of the territory, there was a preference for old pear plantations, most likely because ant nest density is higher in pear than in other fruit plantations (Mermod *et al.* 2009). This does not match exactly with the selection of foraging patches where a preference for old, but not necessarily pear fruit tree plantations has been found. This discrepancy might be explained by a small sample size bias in the current study or by scale effects. The differential habitat use is probably the result of differential food abundance, food accessibility and availability of perches. We will illustrate this for the following habitat types; fruit tree plantation, vineyard, vegetable cultures and meadows. Food abundance differed between habitat types within the study area, with fruit tree plantations having the highest (~0.45 nests m^{-2}), meadows and vineyards having average (~0.35 nests m^{-2}) and vegetables cultures the lowest densities (~0.15 nests m^{-2}; Mermod *et al.* 2009). The proportion of bare ground was high in vineyards (>0.5) and vegetable cultures (~0.5), lowest in fruit tree plantations (0.1–0.3) and very low in meadows (0.05). Perches were usually absent in vegetable cultures, while they were numerous in fruit tree plantations, vineyards and meadows. Thus, vegetable cultures were avoided because they had low food abundance and no perches, despite a large proportion of bare ground and thus good food accessibility. Fruit tree plantations were preferred because they offered high food abundance and numerous perches. Yet, they were not used uniformly; sites with a large proportion of bare ground were more likely to be selected. Meadows were not preferred, because they offered low proportion of bare ground despite relatively high ant nest abundance. The avoidance of vineyards in our study area is more difficult to explain. In fact, ant abundance is only slightly lower in vineyards than in fruit tree plantations, there are many perches and based on the proportion of bare ground accessibility must be excellent. Yet, the ground in vineyards is mostly very mineral in our study area (almost completely covered with small stones, gravels and pebbles) and it may be difficult for Wrynecks to move stones to access ant broods in their nests. Thus in vineyards food accessibility was obviously far worse than suggested by the proportion of bare ground. In other areas, where vineyards occur on soft ground, they are a preferred habitat type for Wrynecks (Cramp & Simmons 1980, Coudrain *et al.* 2010).

In our opinion, the slight preference for old over medium-aged and young fruit tree plantations can only be explained by a higher density of ant nests, since ground vegetation cover and availability of perches do not fundamentally differ with respect to age. What differs substantially, however, is the mass of foliage, which would support denser aphid populations in older fruit tree plantations. Dense aphid populations may result in high ant nest densities, as aphids are a main food resource for ants (Seifert 1996).

Overall, Wrynecks do not appear to be very specific to particular habitat types. While in the Valais they preferred old fruit tree plantations and fallow land (Freitag 1998, Mermod *et al.* 2009, this study), Wrynecks preferred vineyards with sparse ground vegetation in Western Switzerland (Coudrain *et al.* 2010), open pine forests in Hesse (Germany; Poeplau 2005), extensively grazed sheep and cattle pastures in Central Germany (Hübner *et al.* 2004, Becker & Tolkmitt 2008), and traditional high-stem orchards in Rhineland-Palatine (Germany; Bitz 1992). A common feature of these habitat types appears to be that they have a high density of ant nests, that the ground vegetation is not too dense and that there are perches in the vicinity of the main foraging patches.

Conservation implications

The intensification of agricultural practices implies an increasing use of fertilizers, which results in denser ground vegetation cover. Wrynecks forage preferentially on bare ground patches, a microhabitat which has become rare in the agricultural landscape matrix in

central Europe. Unless new practices develop which lead to an extensification of grassland, there is not great hope for the survival of bird species in grassland-dominated intensive farmland. The elimination of hedges and trees in homogenized matrices represents another serious obstacle as the availability of hunting perches and nesting cavities is considerably reduced. However, Wryneck populations may sustain in intensively farmed cultures such as fruit tree plantations or vineyards. It requires that the ground vegetation is heterogeneous with bare and vegetated patches and that nesting cavities are available (Coudrain *et al.* 2010, Zingg *et al.* 2010). Conservation strategies for farmland birds should therefore also try to optimize habitat structures and management in intensive farmland, which may offer good conditions for some endangered species such as the Wryneck, instead of unilaterally requesting a reduction of farming intensity which is in many cases out of scope due to a growing demand on commodities.

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APPENDIX 1.
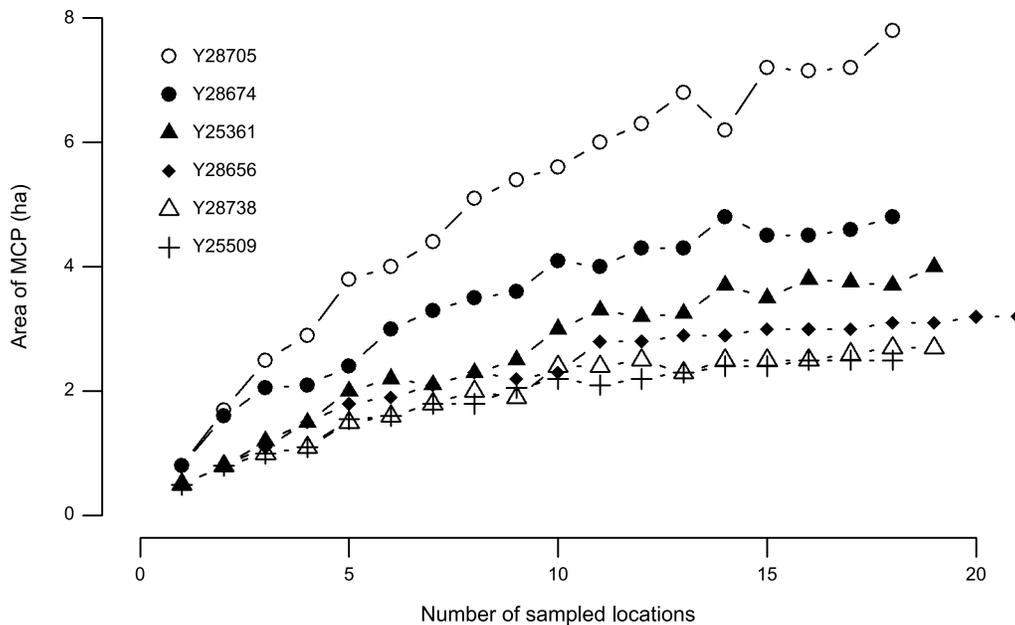
Simulation of the minimum locations needed to calculate the home range size (minimum convex polygon, MCP) for six tagged Wrynecks. The graph shows the increase of the estimated home range size as a function of the number of locations.