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A matter of pipes: Wryneck *Jynx torquilla* habitat selection and breeding performance in an intensive agroecosystem

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Abstract - In intensive permanent crops, the declining Wryneck had been reported to be favoured by nest-boxes contrasting the lack of suitable breeding sites; however, it occurs in very intensive vineyard, apparently deprived of suitable nesting sites.Considering the wryneck concerning conservation status and the increasing vineyard share and intensification over Europe, investigating habitat selection and use of nesting sites in intensive vineyards is urgently required.

With this aim, we investigated for the first time territory-scale habitat selection in a Wryneck population inhabiting a vineyard-dominated landscape (in NE Italy) without conservation measures addressed to the species and provided a preliminary assessment of its breeding biology.

We investigated the effect of land-cover, management, and nest-site availability on Wryneck occurrence considering 44 territories and an equal number of control plots. In the subsequent year, Wryneck nests were surveyed in a subset of simple landscapes (<20% of semi-natural habitats). All nest boxes and holes provided by pipe beams supporting traditional *pergola* vineyards were checked twice during the breeding season.

According to the territory model, Wrynecks did not select particular habitat types, but set territories in sunny areas in which *pergola* vineyards were more abundant than *spalliera* ones and had a higher availability of pipe holes and in simpler landscapes.

Breeding attempts in pipes were few and all failed during egg deposition; conversely, 39% of the few available nest boxes were occupied with an overall breeding success of 57%. 36% of the eggs laid resulted in fledged juveniles.

Although pipes provide potential nesting sites and positively affect territory settlement, they finally resulted in breeding failure, potentially even exacerbating the impact of intensive agricultural management on the species (i.e. a pattern recalling an ecological trap). Nest boxes may supply safer breeding sites for Wrynecks; however, a wider assessment of the reproductive outcomes following nest-box supplementation should be planned.

Keywords – bare ground; cavity breeder; habitat selection; nest boxes; territory; vineyards.

1. Introduction

In Europe, agricultural systems harbour nearly 120 species of birds, which adapted to this habitat during the course of the millenarian development of agriculture (Tucker and Heath 1994; Krebs et al. 1999).

The European wild bird indicator shows that farmland bird populations have halved across the continent since 1980, while the populations of other bird species were generally stable or increasing (Fuller et al. 1995; Gregory et al. 2005; http://www.ebcc.info/). Agricultural intensification, which is likely the primary cause of direct negative effects on farmland bird populations (Newton 2004; Donald et al. 2006), impacts birds and biodiversity at two distinct but interconnected spatial scales: the landscape and the local scales. At the landscape scale, it causes the removal of marginal habitats, homogenization, and fragmentation through the conversion of grassland-like habitats into crops, increases in field size, and ultimately resulting in highly simplified landscapes. At the field scale, intensification mainly means increasing the intensity of farming practices (e.g. greater fertilizer/pesticide inputs, deep ploughing, massive use of machinery, large scale irrigation) (Tscharntke et al. 2005; Fahrig et al. 2011). Attempts to reverse the negative trend of farmland birds in Europe mostly failed. A recent assessment showed that avian abundance and biomass are both still declining with most of this decline attributed to common avian species, in particular farmland species (Inger et al. 2014). In the years to come, farming will likely represent the single greatest source of threat to birds in Europe and worldwide (Green et al. 2005; BirdLife International 2015).

The Wryneck *Jynx torquilla* is one the farmland species that underwent the largest decline throughout Europe in the last decades (Birdlife International 2004; Sanderson et al. 2006), with an estimated decline rate of -57% in the period from 1980-2013 (http://www.ebcc.info/trends2015.html). Although its population remained nearly stable in the last decade (2004-2013; http://www.ebcc.info/trends2015.html), the species has continued to decline in several countries, including Italy (Rete Rurale Nazionale and LIPU 2015). Wryneck breeds in sunny and dry semi-open environments, in particular in extensively managed farmland; however, it is not a farmland specialist, as it exploits a variety of other habitats including open woodland, forest margins, copses, parks, and gardens, provided that two basic resources occur: cavities for breeding, since the species is a secondary cavity breeder, and ground-dwelling ants (Formicidae), as it feeds almost exclusively on those insects (Cramp 1985; Gorman 2004).

The causes for its decline are not fully understood. Habitat loss has been reported as causing the greatest impact (Gorman 2004). In farmland, agricultural intensification has been the main cause of Wryneck decline, as it leads to a reduction of nesting sites and perches used for hunting, in particular large isolated trees (Coudrain et al. 2010; Roux et al. 2015). Similarly, high-stem orchards, which used to be a preferential habitat, have disappeared in large parts of Europe (Herzog 1998; Kizos et al. 2012). In parallel, the same pattern of intensification has caused a reduction in prey availability: on one hand, agricultural intensification determines the reduction of ant abundance in the agroecosystem (by e.g. intensive use of insecticides), whereas on the other hand, the denser cover of ground vegetation due to the intensive use of fertilizers negatively affects ant detection by the species (Mermod et al. 2009). Similarly, wryneck declined in woodlands and forests. The causes of the decline in those habitat have been identified in the intensification of woodland management (which reduces nest sites), and in the thickening of forest undergrowth due to air-borne nitrogen deposition, which reduces forest openings and then impacts on the availability and accessibility of preys (Gorman, 2004; Mikusinski & Angelstam, 1997). Additionally, as is the case for other species wintering in sub-Saharan Africa, climatic and land use changes in western Sahel might have impacted the species via reduced survival (Sanderson et al. 2006; Zwarts et al. 2009). However, recent evidence suggests that Wrynecks breeding in central Europe (and probably, as a consequence of leap-frog migration, also in the Mediterranean region) mainly winter in the Mediterranean basin (van Wijk et al. 2013); thus factors acting on Palearctic breeding grounds are likely to be crucial.

A recent study carried out in Switzerland showed that Wrynecks could also persist in intensive permanent crops (orchards and vineyards), where a heterogeneous habitat matrix with some bare ground patches occurs, as long as ants and nest sites are available (Mermod et al. 2009). This study was carried out in an area where hundreds of nest boxes were installed for conservation purposes (Arlettaz et al. 2010; Zingg et

al. 2010), but the species had also been found to occur in abundance in intensive vineyards elsewhere (Coudrain et al., 2010; Assandri et al. 2016). However, how Wrynecks could find nesting sites in very intensive vineyards is still unknown, but this kind of knowledge is of key importance considering both the Europe-wide wryneck decline and the increasing share and intensification of vineyards over the continent.
In this paper, we investigated for the first time habitat selection at the territory scale in a Wryneck population breeding in a vineyard-dominated landscape (without systematic nest-box supplementation) in north-eastern Italy in response to landscape structure and management practices. We collected information on the breeding biology of the species focusing on an area where the intensification of management practices and the conversion of natural habitats into vineyards have created largely homogeneous monocultures (Assandri 2017b), similar to other sites in the Mediterranean basin and nearby areas (Martínez-Casasnovas et al. 2010), where intensification determined harsh impacts on biodiversity (Viers et al., 2013). Considering the concerning decline of the species across its breeding range, further knowledge on its ecology is urgently needed. Our specific aims were thus i) to investigate the habitat factors driving habitat selection in vineyard-dwelling Wrynecks; it was predicted that non-vineyard habitats could be less important than the characteristics associated with vineyard management in the homogeneous landscape of the vineyard-dominated area considered; ii) to understand how this secondary cavity breeder could nest in this simple and intensively exploited landscape that is apparently deprived of suitable nesting sites (it was expected that Wrynecks have found surrogate cavities for breeding); iii) to evaluate its breeding success in this agroecosystem, and considering the intensive agriculture of the area, a reduced reproductive outcome was expected.

2. Materials and methods

2.1 Study area

The study was performed in the Trento province (South-eastern Alps, Italy), in an area characterized by partly urbanized valley bottoms intensively exploited for permanent crop cultivation and mountainsides covered by woodlands interspersed with pastures, apple orchards, and in particular, vineyards (up to 900 m a.s.l.). For further details on the study area see Assandri et al. (2016, 2017a). We focused on 3 macro-areas (Piana Rotaliana, Cembra Valley, and the eastern side of Adige Valley) with different environmental and topographic characteristics mirrored in different local agricultural practices. They displayed a strong contrast in land usage with highly intensive cultivation in the most accessible and flat areas and more extensive farming elsewhere.

Piana Rotaliana is an alluvial plain (200-230 m a.s.l.) with land use dominated by intensive vineyards (see Assandri et al. (2017b) for further details).

In Cembra Valley, vineyards are the dominant land use between 370 and 900 m a.s.l. in the southern-exposed valley side. High acclivity prevented widespread agricultural mechanization, and viticulture is associated with a massive system of terraces supported by stone walls (Agnoletti 2013).

The third macro-area is the eastern side of the Adige Valley from San Michele all'Adige to Trento, an exposed hilly area largely covered by vineyards (which are still expanding at the expense of the forest). This area displays an intermediate level of viticulture intensification between the two previous areas.

For each of the three macro-areas, eight sample sites were selected (totally accounting for 400 ha; mean sample site surface ± sd: 15.8 ± 3.4 ha; range: 10.8-22.8 ha; Figure 1), that were: i) representative of the environmental characteristics of the main area; ii) small enough to survey three of them in a morning; iii) easy to survey (i.e. without any parts hidden when walking along a pre-defined route).

2.2 Territory survey

2.2.1 Field mapping

Territory mapping was conducted in each of the 24 sample sites during 4 visits during the breeding season in 2015 (10.04-17.04; 05.05-12.05; 29.05-05.06; 27.06-05.07).

During each visit, the same observer (G.A.) followed the same route inside the site, walking at a slow pace and thoroughly surveying the whole site.

All contacts with Wrynecks were recorded inside the sample sites as precisely as possible by using updated aerial photographs (scale 1:2500 m) and starting from the first location. If a Wryneck moved spontaneously (i.e. not disturbed by the observer), we also recorded its subsequent location(s) until it continued the same activity for at least 10 minutes (e.g. feeding, staying in a hole, singing from the same perch, etc.). Individuals' behaviours and interactions (e.g. aggressive behaviour, courtship, cavity showing, etc.) were accurately recorded in order to ease the subsequent task of territory definition.

Three sites per day were censused from dawn to a maximum of six hours afterwards (5.30 – 11.30 a.m. in spring), when Wryneck song activity is highest. Bad weather conditions (e.g. strong wind, rain) were avoided.

Census order across sites was changed from one visit to the following, to ensure variability in the census time within the morning.

2.2.2 Definition of territories and control plots

In studies dealing with resource selection by birds, several methods have been adopted to define territories (Bibby 2000). Circular buffers (e.g. around the nest) are frequently assumed to represent the territory defended by territorial species (e.g. Jedlikowski et al. 2016; Martinez et al. 2010).

Environmental variables were measured within 2.07 ha circular buffers (radius=81 m), defined by means of a two-step procedure and representing territories defended by pairs.

We initially built the minimum convex polygon based on the locations attributed to the same Wryneck pair and paying particular attention to simultaneous locations and interactions between individuals. The records potentially attributable to migrant individuals (e.g. birds feeding in unsuitable habitats during the early part of the study season and no longer contacted in the same site during subsequent visits) were discarded.

In the first step, the centroid of each polygon and the mean surface of the polygons that were based on more than 3 points (N=12) were calculated. The latter analysis suggested an average territory size equal to 0.69 ha, corresponding to a circular plot with a radius 47 m. In cases in which a nest was found, this was considered the final centre of the territory.

As a second step, we calculated the distance between the nearest neighbouring centroids (in the same sample site) and divided it by two, obtaining a value of 115 m (N=36).

We finally averaged the two values obtained by the two-step procedure (radius of the circular plot corresponding to the average polygon surface and half of the average distance between neighbouring centroids), and assumed the result (81 m) as the final radius of a hypothetical mean Wryneck territory. We used this distance to buffer all available centroids (N=44) and considered the resulting plots as territories in the analyses.

In Switzerland, Coudrain et al. (2010) and Mermod et al. (2009) used an average radius of 111 m based on previous telemetry data on seven Wrynecks (Weisshaupt et al. 2011), whereas in other studies on territorial species at a wider scale, reference values obtained from literature were applied (Martinez et al. 2010; Brambilla et al. 2010). Our method seemed to be a good trade-off between accuracy and the inclusion of a wider area.

Environmental variables were measured in the 44 territories and in 44 control plots defined starting from random points scattered within the 24 surveyed sites at locations where Wrynecks were never recorded. Overlapping between different territories was limited to 4.44%. QGIS 2.14.2 (QGIS Development Team 2016) was used for all the spatial analyses.

2.2.3 Environmental variables collection

Land-cover variables were measured by means of an accurate photointerpretation of aerial photographs, validated and updated in the field. We defined nine habitat categories: woods, apple orchards, urban areas, hedge and tree rows, paved roads, open areas, fallow land, vineyards, and field margins and calculated their percentage of cover for each territory. Land-cover types related to agricultural uses were measured at the parcel scale (field with the same crop, spatial arrangement, and management characteristics, see also Coudrain et al. (2010)), and within each vineyard parcel, management variables were collected by means of targeted field surveys.

In particular, we distinguished the two vineyard trellising systems occurring in the study area: *spalliera* and *pergola*. *Spalliera* (espalier) is the globally widespread vineyard arrangement, in which low vines (generally less than 2 m) are supported by wires held between poles. Rows are generally spaced less than 2 m apart. *Pergola* is the traditional and predominant form in the region, accounting for about 80% of the overall vineyard surface in Trentino (Chemolli et al. 2007). It consists of tall vines (up to 2.5 m when considering the secondary branches, growing in a dense leaf "roof"), aligned in rows spaced up to 5 m apart and supported by a robust structure of poles and beams. Beams could be metal irrigation pipes of various diameters (generally 7 cm) or made of wood (Figure 2). The first system is widespread in modern and intensive vineyards, the latter in old and traditional ones. In *pergola* vineyards, some typologies of mechanical activities (e.g. mechanical harvesting and pruning) are not possible, but there are no other differences in terms of general management between the two types. We attributed each vineyard in the study area to one of these two systems and used the percentage cover of *spalliera* among explanatory variables.

In our study area, vineyard and apple orchard grounds are extensively covered by a dense grass sward with the exception of the vine and tree base (a strip of about 1 m), where herbicides or mechanical grass removal are applied (mean ground grass cover in vineyard/apple orchards of the study area: 91.5%, our unpub. data). However, we distinguished between vineyards and apple orchards chemically weeded/ploughed and with a full grass cover by evaluating each single parcel in the field. The percentage of cover for chemically weeded/ploughed vineyards and orchards in each territory/control was used as an explanatory variable.

For each territory, we measured the average area of the vineyard parcels included (totally or partially) within the buffer, which is a proxy for intensive (larger fields) or extensive (smaller fields) agriculture.

Wrynecks are secondary cavity breeders that require holes for nesting. We quantified the availability of potential nesting sites within each territory by counting: the number of isolated trees with a diameter at breast height >20 cm (see Coudrain et al. 2010); the number of nest-boxes (occasionally supplied by farmers in their fields); the number of holes provided by pipe beam ends in *pergola* vineyards. The latter was measured, because there were anecdotal records of Wrynecks using these kinds of vineyard supports for nesting. Since pipes are typical of intensive and modern vineyards (in traditional, non-intensive cultivations, supports are often made of wood), we were interested in their effect in contrasting landscapes, so we divided our 24 sample sites into two landscape typologies following Batary et al. (2011), i.e. simple and complex landscapes. Landscapes with >20% of semi-natural areas (e.g. wood, hedgerows, tree lines, fallow lands, meadows, field margins), that are typical of traditional agriculture were considered as complex, whereas landscapes with <20% of those habitats were considered as simple.

Following that criterion, 10 sites out of 24 were classified as simple landscapes (mean cover of semi-natural areas: 12.02 ± 5.80%), whereas 14 were complex (mean cover of semi-natural areas: 29.91 ± 5.82 %), including all the sites on the eastern side of Adige Valley, except two (Fig. 1). In the simple landscapes, viticulture is more intensive compared with complex landscapes where agriculture is conducted in a more traditional and extensive way.

We additionally measured mean elevation and mean direct solar radiation for each territory from a 1-m resolution digital elevation model (DEM). Solar radiation was calculated on the 21st of June using the r.sun function from GRASS 7.0.2 and taking the shadowing effect of the topography into account (Neteler et al. 2012). For further details on explanatory variables, see Table 1.

2.2.4 Statistical analysis

Our explanatory variables were divided into three groups, which were separately considered when building models: land-cover/topographic, management, and nest-site predictors (see Table 1). This approach was adopted in similar studies when the variables' nature differed a lot and information embedded in different sets of variables partially overlapped (see for example Coudrain et al., 2010, Assandri et al., 2017c).

We carried out an accurate data exploration for each group of predictors in order to avoid common statistical problems (e.g. collinearity), following Zuur et al. (2010).

Vineyard cover was included in the management group (instead of land-cover) to correct for their cover within territories/control for plots when evaluating the effect of the vineyard management variables, as well as to remove collinearity among covariates in the land-cover group.

All the explanatory variables were standardized before entering them into the models to allow comparisons of their relative effects (Schielzeth 2010), and since recent literature has highlighted the importance of this procedure to control for multicollinearity in model averaging in order to obtain reliable predictor estimates (Cade 2015).

To test the effect of the covariates on Wryneck occurrence probability, we used GLMMs with a binomial error distribution and a logit-link function. Mixed models were used due to the nested nature of our experimental design (i.e. to account for potential non-independence of territories within the same sample sites). The response variable was Wryneck occurrence, and explanatory variables were the ones included in the three groups mentioned above (land-cover/topographic, management, and nest-site) and the random intercept was the sample site. In the nest-site model, we included an interaction between pipes and landscape typology (simple vs. complex). GLMMs were run with the R package glmmADMB (Skaug et al. 2015).

We worked within an information-theoretic framework (Burnham and Anderson 2002) using the dredge function in the R package 'MuMIn' (Barton 2015) to build all the possible models for each set of explanatory variables separately.

Models were ranked based on their AICc, and we selected only the most parsimonious models (i.e. ΔAICc < 2). We then averaged across these most supported models within each group of predictors to obtain model-averaged coefficients, their relative standard errors, and the relative variable importance (Johnson and Omland 2004) for each explanatory variable. In that process, 'uninformative parameters' (Arnold 2010), i.e. the variables included only in models comprising more parsimonious nested models, were discarded (Richards 2008; Richards et al. 2011).

Finally, we built a synthetic model starting with the variables selected according to the above procedure for each individual group, and adopting the same AICc-based ranking and model-averaging procedure (Koleček et al. 2014). All the analyses were performed with R version 3.2.0 (R Core Team 2016).

2.3 Nest survey

During the breeding season of 2016, we searched for Wryneck nests within the eight sample sites of Piana Rotaliana (all classified as simple landscapes). Territories were mapped in the same way as in 2015, but each sample site was visited seven times between 22 March and 13 May. We then created an 81-m buffer around each Wryneck contact location (see above), defining an area of "potential nest presence", and then carried out two sessions of nest-searching, one for the first brood (25 May – 10 June) and one for the second (9-27 July), since the Wryneck is generally reported to be a double brooded species (Gorman, 2004).

Nests were searched for in the entire vineyard parcels totally or partially overlapping the eight sample site areas and with the "potential nest presence area" using an "Explorer Premium" digital endoscope, which allowed us to survey all the pipe holes and the nest-boxes occurring in this area. An area of 272 ha and approximately 3,000 pipes and 18 nest-boxes occurring there were surveyed. This area is almost completely covered by vineyards (92.3% of the land cover with the remaining part mainly constituted by roads, field margins, and apple orchards), thus all the nests occurring within the area were virtually found.

After finding a nest, it was checked periodically to assess breeding success and collect reproductive parameters (i.e. number of eggs and the relative status - intact or damaged, number of nestlings, and the relative status -alive or dead).

To evaluate the environmental conditions occurring in pipes, four "Ibutton" data loggers were placed at pipe entrances and pipes were selected close to pipes with Wryneck nests and sharing the same characteristics with the latter (same conditions of solar exposition, same colour and material, same hole diameter). The loggers recorded temperature every minute between the 10th May and the end of June (thus during the period of Wrynecks' first brood, from nest site selection to chick rearing). The minimum and maximum pipe temperatures were compared with the air temperatures in the same period using values measured at a meteorological station found in the study area (Maso delle Part, Mezzolombardo, TN).

3 Results

3.1 Territory survey

The most parsimonious among land-cover/topographic models only retained the topographic variables (i.e. solar radiation and elevation), whereas all the land-cover categories were excluded as not comprised in the supported models (ΔAICc<2), or being uninformative (see supplementary materials online, Table S1-S2). Considering management variables, the cover of *spalliera* vineyard and the mean area of vineyard parcels were retained, whereas chemically weeded or ploughed field cover and vineyard cover were not (Table S3-S4).

Among the potential nest-site predictors, only the interaction between pipes and landscape typology was retained, whereas isolated trees and nest boxes were discarded (Table S5-S6).

Among the individual groups, the land-cover/topographic best model (AICc=114.6) and the nest-sites model (AICc=114.3) had fully comparable support, whereas the management one was less supported (AICc=118.6). The synthetic model, combining variables from different groups, was slightly more supported (AICc=113).

Despite a moderate collinearity among the retained predictors (higher gVIF=4.18), all of them were entered in the final synthetic model. No odd effect imputable to collinearity was detected in the model output, and parameter estimates were biologically meaningful and comparable with individual group model outputs, so the statistical issue of possible collinearity was considered of minor concern in this case.

Support was found for nine synthetic models, and all the variables were informative with the exception of the mean area of vineyard parcels (Table 2).

Overall, without considering landscape typology in interaction with other covariates, Wryneck had a higher probability of occurrence in simple landscapes than in complex ones (Table 2).

Solar radiation had a positive effect on Wryneck occurrence, whereas *spalliera* vineyard cover and elevation had negative effects, the latter being barely uninfluential, as suggested by the parameter estimate being very close to zero (Table 2).

The interaction between pipes and landscape types was well supported (retained in the most parsimonious model) and suggested a strong positive effect of pipes, especially in simple landscapes (Table 2, Figure 3).

3.2 Nest survey

In Piana Rotaliana during spring 2016, we defined 17 territories defended by Wryneck pairs. In 2015, the same area hosted 25 territories. We found 11 clutches (plus a replacement clutch) during the first brood period (6 in pipes (Figure S1) and 5 in nest boxes), and 2 clutches during the second, both in nest boxes. Only 4 of these 11 clutches occurred inside one of the 17 defended territories.

All the clutches in pipes were abandoned, 4 after the deposition of the first egg, one with 3 eggs and one with 6. In nest boxes, 3 clutches failed (due to abandonment or predation), 3 were partially successful (at least 13 juveniles fledged over 37 eggs laid). One containing 6 eggs was predated, and subsequently the (same?) female laid a further 4 eggs which hatched and the nestlings fledged.

The mean temperature in pipes, as measured by the data loggers, was 22.0° C, the overall mean of the minimum temperature recorded was 6.6° C, and the mean of the maximum was 43.1° C (N=4). Temperature measurements above 40°C accounted for the 6.7% of the sample. For comparison, the air temperature in the same area and in the same period registered a minimum of 3.4° C and a maximum of 33.4° C.

4. Discussion

In our vineyard-dominated study system, Wrynecks seemed not to select particular habitat features, but set territories in sunny areas with *pergola* vineyards with a high availability of pipe holes (i.e. potential nesting sites) and simple landscapes, i.e. landscapes with natural remnants covering less than 20% of the area (Batáry et al. 2011).

In Trentino vineyards, Wryneck abundance is positively affected by vineyard cover at a landscape scale (our unpub. data), possibly because vineyards recall the natural habitat to which Wryneck is generally associated with, i.e. sunny open forests in warm climates (Cramp 1985; Gorman 2004). Our results showed that at a finer spatial scale (i.e. territory), specific vineyard characteristics likely have a greater importance than land cover. In particular, the availability of nesting sites, which act as a limiting resource in this intensive crop, seemed particularly important. Consistent results came from other studies performed in intensive farmlands (orchards and vineyards), which showed that territory establishment and reproductive output in Wrynecks are driven by specific limiting factors, such as food (in particular ant) availability and detectability (critically affected by the occurrence of bare ground) and, in particular, nesting site availability, rather than by habitat composition (Mermod et al. 2009; Zingg et al. 2010; Coudrain et al. 2010; Weisshaupt et al. 2011).

The number of holes available in a territory had been reported to be correlated with territory quality in Wrynecks and other cavity nesting species, since several holes allow birds to tune nest choice according to changing environmental conditions or to predation pressure (Tomé et al. 2004; Zingg et al. 2010; Coudrain et al. 2010).

In our study system, Wrynecks seemed to be attracted by pipe holes and defended territories with a higher availability of these artificial structures. In fact, our extensive nest search showed that the effective breeding attempts in pipes were very few, especially when compared with their extremely high availability and all attempts occurred during the first part of the breeding season (i.e. the time of the first brood). All the breeding attempts occurring in pipes failed during egg deposition, suggesting pipes were unsuitable for reproduction. One of the possible causes for the widespread failure recorded in pipes could be the high maximum temperature reached within them, approximately 10°C higher than outside. Additionally, a metal pipe with a round section of 7 cm could have offered inadequate conditions for effective egg incubation. We acknowledge our low sample size, and thus our results should be considered preliminary findings. Nevertheless, the low number of nests in pipes despite the high number of pipe holes available and surveyed clearly suggested that nesting in pipes is relatively rare.

In short, Wrynecks selected territories on the basis of the number of pipe holes, but then apparently did not find suitable nesting sites or were forced to nest in unfavourable sites (i.e. in pipes). This behaviour could be possibly due to juvenile/inexperienced individuals with the more experienced (or the dominant) individuals ultimately exploiting the few favourable available nesting sites (e.g. nest boxes), and in general this pattern was likely to be due to the general scarcity of potential breeding sites.

Even if the number of nest boxes was not selected among the informative predictors of Wryneck occurrences, the nest survey revealed their key importance as breeding sites in simple landscapes with 39% of boxes occupied. This is a high occupation rate especially considering that, in several cases, nest-boxes occur in small clusters and that some of them were damaged or very small. Thus, several nest boxes were likely unsuitable for the species. Additionally, nest boxes harboured the only four pairs that successfully reared juveniles in the whole study area. The lack of effect in the analysis of territory selection could be an effect of the clustered distribution and the very low density at which they occurred in the study area (0.055 nest-boxes/ha in 2015; 0.066 nest-boxes/ha in 2016).

We also found no effect of the number of isolated trees at the territory scale, even if they had been reported to favour Wryneck territory occupancy (Coudrain et al. 2010) and farmers reported that big willow trees (traditionally kept and pruned to produce cords to tie the vines, but now almost completely removed) used to be occupied by Wrynecks for nesting in the study area. Also for isolated trees, the low rate at which they occurred (0.145 trees/ha) could have led to an apparent lack of effect in the model.

Pipe hole distribution likely also explains why the species had both a higher probability of occurrence in *pergola* than in *spalliera* vineyards (because the latter do not have beams with holes) and in simpler landscapes than in complex ones. In fact, complex landscapes are characterized by more traditional and less intensive viticulture, and vineyards are usually supported by wood beams without any (or a few) holes; thus, the few Wrynecks in these vineyards likely depend on other cavities for nesting.

Wrynecks have been reported to be dependent on bare ground, since it favours ant detectability. In previous studies in permanent agroecosystems, the availability of bare ground was a crucial predictor of Wryneck occurrences at the foraging scale with higher occurrences of foraging Wrynecks when the extent of bare ground was above 60% at the foraging site (Weisshaupt et al. 2011). Other studies performed at a territory scale, reported less clear relationships between Wryneck territory occupancy and bare ground availability, suggesting that at that scale bare ground availability might be not that crucial. Specifically, Mermod et al. (2009) detected only a marginal effect of the extent of bare ground (with an optimum at 20-30%), whereas Coudrain et al. (2010) found a stronger effect (with an optimum at 50%). In our study area, the ground in vineyards and apple orchards is almost completely covered by grass with a percentage of bare ground almost invariably much lower than the optimum reported in the above cited territory-scale studies. In fact, no more than 10-15% of bare ground occurs in vineyards/orchards in the study area and only in fields in which some herbicides or mechanical grass removal were applied. We still expected to find a relatively higher amount of fields with bare ground in Wryneck territories, but models suggested a lack of a noticeable effect. Although the methodology used to asses the bare ground extent in our study differed from the one adopted in the cited Swiss studies, apparently, in our study system the crucial drivers of territory selection are others (e.g. nesting site availability) than bare ground availability. Further studies in the area should asses the fine-scale foraging habits of the Wryneck to understand how this species could find prey and thus persist in this habitat, which presents a much lower extent of bare ground than the optimum reported by other studies in similar habitats (Mermod et al. 2009, Coudrain et al. 2010). In particular, factors affecting prey (in particular ant) detectability and abundance should be investigated to further shed light on the species ecology in this agroecosystem.

In conclusion, the territory setting for Wryneck in the study area was strongly dependent on a vineyard feature (pipe availability) characterising a simple (and intensive) landscape, which possibly provides nesting sites. In fact, this feature was unsuitable for reproduction and the species bred successfully only in the few nest boxes that sparsely occurred in the study area.

In areas characterized by intensive agriculture and in the absence of specific conservation measures (e.g. nest box provisioning, Zingg et al. 2010), such as the one investigated here, the persistence of a viable Wryneck population is likely to be strongly challenged. Our results suggested that particular structural features of the farmland, which provide potential nesting sites (e.g. pipes) attracted individuals, but turned out to be unsuitable for reproduction, and could potentially even exacerbate the impact of intensive management on the species, possibly leading to an ecological trap.

Results suggested that the primary limiting factor for Wryneck was nest-site availability, thus the prime conservation measure for its conservation should be the provisioning of nest boxes.

Nest box provisioning is a popular conservation measure to enhance secondary cavity nesting birds when natural cavities are lacking, e.g. due to the removal of large trees in response to agricultural intensification (Newton 1994a; Newton 1994b). However, when the general environmental conditions are not suitable for a species, providing nest boxes may create ecological traps (Mänd et al. 2005; Klein et al. 2007). Hence, this conservation measure should be tested on defined sample areas and followed by an assessment of the reproductive outcome in those areas. Furthermore, nest boxes should be provided in an adequate number to allow Wrynecks to choose the boxes in the most suitable territories.

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Figure captions

Fig.1 Location of the study area in Italy and the sample sites in the Trento province. The vineyard cover is shown in violet, and the 24 sites (numbered from 1 to 24) in which Wryneck territory mapping was performed are in black. The three macro-areas described in the study area section are also shown. Landscape classification of the sites: 1-9, and 12: simple landscape; 10,11, and 13-24: complex landscape.

Fig.2 Comparison of different beams found in *pergola* vineyards in Trentino. A. Metal beam generally found in simple landscapes made from an irrigation pipe (diameter 7 cm). In the inset: detail of the hole provided by this kind of beam. B. Wooden beam generally found in complex landscapes.

Fig.3 Graphical representation of the effect of pipes on the probability of Wryneck occurrence in contrasting landscapes (complex and simple) as predicted by the averaged synthetic models. Other predictors included in the models are kept constant at their mean value. 95% confidence intervals of the mean are shown in light grey. Quite large 95% confidence intervals are due to the choice of conducting model averaging on mixed models and to the presence of several outliers..N=88

Table 1. List of variables used in the analysis and their mean value and range in territories and control plots.

Variable name	Description	TERRITORIES (Mean and range)	CONTROLS (Mean and range)
Land-cover/topographic variables			
Woods	% cover of woodlands (large majority of broadleaved woodlands).	2.75 (0-28.00) %	5.14 (0-35.78) %
Apple orchards	% cover of intensive apple orchards.	5.02 (0-37.77) %	3.40 (0-55.67) %
Urban areas	% cover of urban areas (including isolated houses).	1.58 (0-23.70) %	2.68 (0-32.02) %
Hedge and tree rows	% cover of hedge and tree rows, defined as linear clusters of shrubs and/or trees, which were less than 15-m wide, isolated in the farmed landscape or originating from woodland remains but clearly isolated from the main woodland area.	1.41 (0-8.91) %	2.25 (0-11.72) %
Paved roads	% cover of paved roads.	2.01 (0-6.02) %	2.84 (0-7.88) %
Open areas	% cover of open areas (fields, meadows, extirpated wood crops).	2.11 (0-17.58) %	1.52 (0-19.12) %
Fallow land	% cover of fallow land (also including abandoned vineyards invaded by shrubs).	1.43 (0-24.65) %	1.25 (0-12.27) %
Field margins	% cover of field margins (also including unpaved roads and small rural buildings).	9.58 (0.97-23.08) %	12.03 (0.12-27.82) %
Altitude	Mean territory altitude	318 (204-727) m	409.58 (205-675) m
Solar radiation	Mean territory solar radiation on 21th June	8741 (8123-8968) W/m^2	8546 (7584-8973) W/m^2
Management variables			
Vineyards	% cover of vineyards	73.60 (30.70-95.46) %	68.10 (22.78-94.25) %
Spalliera	% cover of *spalliera* vineyards	7.12 (0-96.33) %	22.47 (0-100) %
Chemically weeded or ploughed fields	% cover of permanent crop fields (vineyards and apple orchards) with chemically weeded or ploughed rows (i.e. fields with at least some bare ground).	63.42 (0-100) %	50.68 (0-100) %
Mean area of vineyard parcels	Mean area of vineyard patches overlapping with a territory.	4200 (1005-8394) m^2	3295 (544-15966) m^2
Nest-site variables			
Isolated trees	Number of isolated trees (diameter at breast height >20 cm) per territory.	0.25 (0-3)	0.34 (0-3)
Nest boxes	Number of nest boxes per territory.	0.11 (0-3)	0.16 ± 0.48 (0-2)
Pipes	Number of holes originated by *pergola* pipe beam ends per territory.	20.47 (0-46)	11.79 (0-26)
Landscape typology	Categorical. Two levels: complex and simple.	-	-

Table 2. Most supported synthetic GLMM models on Wryneck occurrence. Models are ranked according to Akaike's information criterion corrected for small sample size (AICc) and only models within an interval of ΔAICc < 2 are shown. The difference in AICc from the best-supported model (ΔAICc), Akaike's weights (w_i), and -2 log-likelihood values (logLik) are also given. Negative (-) or positive (+) relationships between predictors and Wryneck occurrences are shown. For variable acronyms, see Table 1. N=88.

Model	df	logLik	AICc	ΔAICc	w_i
solar radiation (+) + pipes (-) *landscape typology	6	-49.996	113	-	0.16
solar radiation (+) + pipes (+)	4	-52.325		0.10	0.15
spalliera (-) + pipes (-)*landscape typology	6	-50.118		0.24	0.14
solar radiation (+) + *spalliera* (-) + landscape typology	5	-51.427		0.56	0.12
solar radiation (+) + landscape typology	4	-52.713		0.88	0.10
solar radiation (+) + *spalliera* (-)	4	-52.860		1.17	0.09
pipes (-) *landscape typology	5	-51.786		1.27	0.09
elevation (-) + irradiation (+)	4	-53.073		1.60	0.07
spalliera (-) + landscape typology	4	-53.254		1.96	0.06

Table 3. Model averaged standardized parameter (based on models with $\Delta AICc < 2$) and relative variable importance of predictors (measured considering the sum of the Akaike weights over the most supported models in which that variable appears) from synthetic models of Wryneck occurrence. Covariates are ranked according to cumulative weights. The reference value for landscape typology and its interaction is “complex landscape”, thus “pipes” coefficient refers to complex landscapes and “pipes*landscape” is the correction for simple ones. For variable acronyms see Table 1. N=88.

Variable	β	SE	$\sum w_i$
intercept (reference value for complex landscape)	-0.691	0.737	-
solar radiation	0.458	0.394	0.71
landscape typology (simple)	0.871	0.859	0.68
pipes	-0.273	0.769	0.55
spalliera	-0.219	0.329	0.42
pipes*landscape (simple)	0.683	1.031	0.39
elevation	-0.389	0.544	0.07