

Diet and foraging ecology of the Hoopoe *Upupa epops* in a Mediterranean area of Central Italy

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Abstract - During the breeding season, the Hoopoe *Upupa epops* inhabits traditional and diversified rural habitats with high availability of bare ground and short grass areas where it forages. Only a few studies addressed the breeding diet of this species. Most of them were conducted in the intensively cultivated plains of southern Switzerland, where *Gryllotalpa gryllotalpa* represents the most common prey. In contrast, limited information is available for Mediterranean habitats. To fill this knowledge gap, we investigated the foraging behaviour of the species in a Mediterranean heterogeneous agricultural area in Central Italy during the 2020-2021 breeding seasons. 1123 prey items brought to the nest by adults were identified using camera traps positioned near four natural nests. Insect larvae constitute 84% of the diet, of which 61% are represented by *Cicada orni* nymphs. The importance of cicadas in the Hoopoe diet has been never described in the literature before. *C. orni* seems to substitute *G. gryllotalpa* in the more arid and hard soil of Mediterranean areas. The observed provisioning rate to clutches showed a maximum daily mean of over 14 prey per hour. To investigate Hoopoe foraging microhabitat selection, six different microhabitat variables were measured at 64 1 m² plots located at an equal number of foraging and random control points, by using a grid of 100 squares (10x10 cm each). Habitat selection analysis indicates that short herbaceous sward and low herbaceous cover are the fundamental factors driving foraging microhabitat selection. Our study contributed to enhancing the limited knowledge of the Hoopoe diet and foraging ecology in Mediterranean habitats and demonstrates, for the first time, the importance of *Cicada orni* nymphs in the diet of the species in this biogeographical region.

Keywords: nestling diet, trophic ecology, *Cicada orni*, provisioning rate, foraging habitat selection.
Short title: Hoopoe foraging ecology

INTRODUCTION

In Italy, the Hoopoe *Upupa epops* is a regular breeder, migrant and sometimes winterer species (Bricchetti & Fracasso 2015, Baccetti et al. 2020). Landscapes modelled by low-intensive and traditional anthropogenic activities (i.e. extensive animal husbandry and low-intensive agriculture) are often favoured by Hoopoes (Martín-Vivaldi et al. 2016). In fact, during

the breeding period, Hoopoes favour open countryside with scattered trees such as pastures, parkland, fruit orchards, heathland, olive groves or vineyards (Krištín & Kirwan 2020). The species avoids closed forests, especially coniferous ones, and favours landscape and local habitat heterogeneity (Barbaro et al. 2007, Schaub et al. 2010). Old traditional olive groves are important nesting habitats for the species in the

Mediterranean, as the thick trunks of these trees are plenty of cavities (Martín-Vivaldi et al. 2016). Indeed, this species strongly depend on suitably sized cavities for nesting (Martín-Vivaldi et al. 2016), although it was reported to have great versatility in using different types of holes, whether in trees, buildings, walls, heaps of stones, and nest boxes. Bare or sparsely vegetated land such as grasslands, forest clearings, field margins, or roadsides presenting short and sparse herbaceous swards are the preferred foraging places (Barbaro et al. 2007, Tagmann-Islet & Arlettaz 2007, Schaub et al. 2010). This bird species mostly forages on large terrestrial insects (Krištín 2001). Prey items are captured with the long beak after being located under the ground or stones (Cramp 1985, Krištín 2001). Most of the few studies on the nestling diet of this species were carried out in the cultivated plains of Switzerland (Fournier & Arlettaz 2001, Schaad 2002, Duplain et al. 2015, Guilloid et al. 2016) where Mole cricket (*Gryllotalpa gryllotalpa*) represents the main prey in term of biomass provided to nestlings. In contrast, in the Veronese Prealps and the Euganean Hills (N Italy) and south-western France, the Lepidopteran *Thaumetopoea pityocampa* pupae are the main prey items in pine plantations (Battisti 1986, Battisti et al. 2000, Barbaro et al. 2007); observations of predation on this insect were also recorded in Spain (Stefanescu 1997).

The Hoopoe has experienced a long-term decline, especially in central and eastern Europe, including northern Switzerland (Arlettaz et al. 2010b, Barbaro 2020) as well as Italy where its decline has been considered moderate in the last 20 years (Rete Rurale Nazionale & Lipu 2021). The main threats to the species are represented by agricultural intensification and urbanization, which trigger widespread habitat loss (Barbaro 2020). The removal of old rotting trees in farmland causes the loss of suitable nesting sites (Arlettaz et al. 2010a) and the use of insecticides could even lead to local extinctions if invertebrate prey strongly reduces (Martín-Vivaldi et al. 2016). Climate change may lead to lower reproductive success, especially during cold and rainy springs (Arlettaz

et al. 2010a). The population fluctuations attributed to climate change seem to be more pronounced in Middle Europe than in Mediterranean populations (Cramp 1985).

Considering the limited information about the Hoopoe diet and foraging ecology in southern Europe, and the likely conservation relevance of this information, we decided to address these topics in the Mediterranean biogeographical region, working in a heterogeneous rural landscape of Central Italy. Specifically, we investigated two aspects: i) the nestling diet and the adult provisioning rate to nestlings, which were assessed working on natural nests; and ii) the foraging microhabitat selection of provisioning adults.

MATERIALS AND METHODS

Study area

The study was performed in Castel di Guido, near Rome (Central Italy), within the National Natural Reserve of the Roman Coast, 21-86 m above sea level (Fig. 1). Castel di Guido Farm is managed by Rome Municipality since 1978 and produces mainly cereals but also bovine dairy products and meat. Animals are raised both in enclosures and in the wild (Pizzuti Piccoli et al. 2019). The area is bioclimatically part of the transitional Mediterranean region (Blasi 1994). The study area is characterized by a great diversity of vegetation communities and extends for 1966 ha. According to the data provided by the Farm in 1999, 17% of the area (366 ha) is occupied by crops of durum wheat, corn, barley, olive groves, and alfa-alfa, 22% by natural forests (430 ha) with oak prevalence, 22% by pastures, 28% by pine plantations and reforestation areas, and the remaining part of the territory is occupied by roads, rural buildings, stables, irrigation channels, and other artificial infrastructures (Filesi 2001, Bartolucci & De Lorenzis 2004). The land cover of the study area remained quite stable in the last decades.

Nest survey

During the breeding seasons 2020-2021 (between

April and August), to study the nestling diet and provisioning rate, natural nests were searched within the study area. Adult movements toward suitable sites, such as tree rows, olives groves, isolated mature trees and agricultural buildings were investigated through direct observations using binoculars and telescopes. To increase nesting site availability and therein the survey sample, in early 2020, 22 wood handmade nest boxes were installed on trees or rural buildings within two meters of height, near farmhouses, tree rows or crops, and open areas such as pastures (Fig. 1). The entrance hole of the nest boxes was 6.5 cm and the internal space was 18 x 20 x 45 cm.

Nestling diet and provisioning rate

Camera traps with motion sensors were placed in front of the entrance of four natural nests. The cam-

eras have been set to produce ten-second-long movies with 1920x1080 (Full HD 1080p) resolution and a motion detection interval of 15 seconds. Cameras were active from mid-May to mid-July 2020-2021. This video material was used to taxonomically identify the prey supplied to the chicks from the first days of life to the last days before the flight and to determine their relative frequency. Prey has been identified mainly at the Order and sometimes Family level, descending in some cases to hierarchical levels less inclusive when the video quality allowed it.

To determine the nestling diet, 9,172 videos were processed. 1,123 were selected for prey identification while movies in which the prey was not easily visible in the parent beak were discarded (87.76%). The video material was collected during 69 different days covering two years and relative to all the nests.

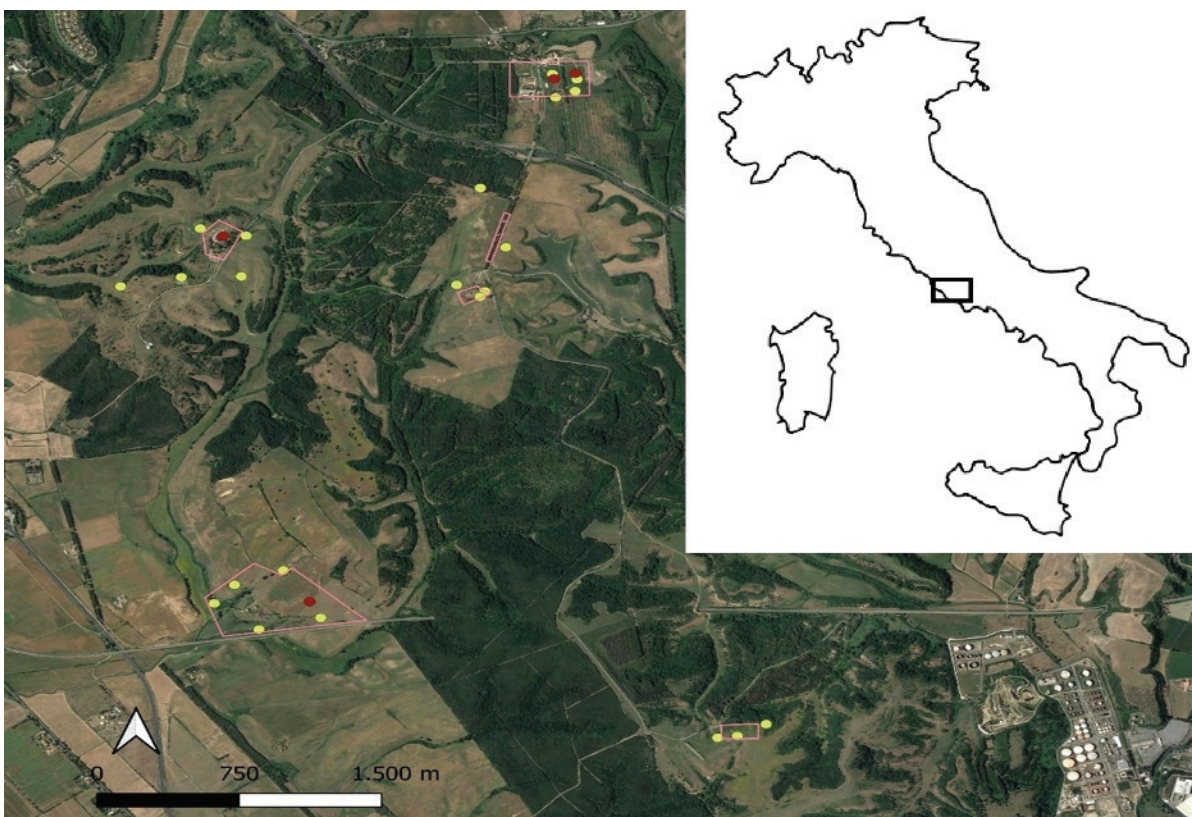


Figure 1. Location of the study area and position of Hoopoe *Upupa epops* natural and artificial breeding sites within the study area. In the inset is shown the location of the study area (rectangle) in Italy. Red points in the main map represent natural breeding sites, yellow points nest boxes, and pink polygons the areas within which foraging plots were located. Base map: orthophoto © 2020 Google.

Furthermore, through the videos recorded by the camera traps, it was also possible to estimate the provisioning rate (i.e., the number of prey items brought to the nest in an hour). Considering that the Hoopoe carries only one prey at a time to the nest, each movie of an adult carrying a prey (identifiable or not) to the nest was counted as one prey. The estimation of the provisioning rate was measured at three nests (N1, N2, N3) until the last chick flew, starting in N1 from the third day since the deposition of the first egg, or the 11th (N2) and 13th (N3) day of age of the first chick. The video material to estimate the provisioning rate was collected during 81 different days covering the two years of the study and relative to the three nests.

Foraging microhabitat selection

To investigate foraging microhabitat selection, six microhabitat variables were measured at 32 1 m² plots placed on the ground where the Hoopoes were seen foraging during the breeding period (from March to August 2021). These plots were mostly located around active nests and at several other potentially suitable areas (Fig. 1). We chose the microhabitat variables according to a comprehensive study on the Hoopoe habitat selection (Barbaro et al. 2007) and hypothesized which were the microhabitat characteristics that could influence the prey density and their accessibility in our study area. The microhabitat variables measured within the plots were: (1) bare soil percentage cover, (2) herbaceous vegetation height, (3) biological debris (dead wood, leaves and other organic material) percentage cover, (4) herbaceous vegetation percentage cover, (5) tree and shrub vegetation percentage cover, and (6) pebble percentage cover. The percentage cover of each variable was measured with the help of a grid consisting of 100 squares (10x10 cm each) centred at the point where the adult extracted prey or probed the soil with its beak. In addition, the same variables were measured at an equal number of control plots of equal size, selected 25 m away from each foraging point, in a randomly chosen direction. Microhabitat selec-

tion analysis was performed using Generalized Linear Models (GLM) with a binomial error distribution and a logit link. The plot type (1: foraging; 0: control) was entered into the model as a binomial response variable. We used Pearson's correlation coefficient (*R cor.test* function) to assess predictor correlation and reduce multicollinearity issues. Bare soil and biological debris cover resulted to be significantly negatively correlated with herbaceous vegetation height and cover (Tab. 3) and were thus removed from the statistical analysis to avoid multicollinearity issues. Model selection was conducted using a stepwise approach using the AIC through the R function *stepAIC* in the *MASS* package (Venables & Ripley 2002). All the analyses were performed using R version 4.1.2 (R Development Core Team 2021).

RESULTS

Four different natural Hoopoe nests were found during the two study years (Fig. 1). Two nests were found in tree cavities located within one meter from the ground and two were in root splits at the ground level. Only one successful brood per nest was raised during each season. On average, nestlings fledged within 30 days of age. None of the 22 installed nest boxes was occupied by the Hoopoe, while they were occupied by Starlings *Sturnus vulgaris* (13.6%) and Great Tits *Parus major* (4.5%), as well as by several Hymenoptera species.

Nestling diet and provisioning rate

The nestling diet consisted of Insecta (93.7%), Arachnida (3.9%), Clitellata (0.3%), Malacostraca (0.2%), Chilopoda (0.1%), Reptilia (0.1%), and unidentified prey (1.7%). The larvae constituted a large part of the prey items (84.2%) and they were mainly represented by *Cicada orni* (61.4%). The Cicada's nymph number ranges from a minimum of 2.25% in an early brood that ended at the beginning of June, when the natural availability of these nymphs is low, to a maximum of 88.7% in a brood concluded at the end of the same month. The remaining larvae (22.8%) were Lepidoptera, Diptera, Coleoptera, and other

unidentified insects. The insects preyed upon in the imago phase were Coleoptera (8.2%) and Orthoptera (1.2%), with only one Mole cricket detected. All the Arachnida were spiders. 15.5% of Insect larvae were not identified at a lower taxonomic level due to low video quality. Table 1 summarizes the data collected on the four reproductive sites for the breeding seasons 2020-2021.

The average provisioning rate during incubation was 5.4 prey/h (minimum 3.7 on the first and ninth incubation days; maximum 8.3 on the eleventh day). Food provisioning average frequency was 6.35 prey/h in N1 (minimum 0.9 at day 30 of age; maximum 13.1 at day 9), 9 prey/h in N2 (minimum 0.3 at day 30 of age; maximum 14.4 at day 15), and 8.33 prey/h in N3 (minimum 0.1 at day 30 of age; maximum 13.2 at day 19). To grow a brood of five chicks (of which three fledged), we estimated a total of 3047 prey items

Table 1. Hoopoe nestling diet in Castel di Guido (Rome, Italy). We reported the absolute number (N) and relative percentage (%) of prey items provided to nestlings. Data refer to 69 different sampling days at four nests during the breeding seasons 2020-2021.

Taxon	N	%
Hemiptera		
<i>Cicada orni</i> (nymphs)	689	61.4
Unidentified Insect larvae	174	15.5
Lepidoptera (larvae)	34	3.0
Coleoptera (imago)	92	8.2
Coleoptera (larvae)	21	1.9
Scarabaeidae (larvae)	5	0.4
Diptera (larvae)	5	0.4
Tipulidae (larvae)	17	1.6
Orthoptera	14	1.2
<i>Gryllotalpa gryllotalpa</i>	1	0.1
Araneae	44	3.9
Clitellata	4	0.3
Malacostraca	2	0.2
Chilopoda	1	0.1
Lacertilia	1	0.1
Unidentified prey	19	1.7
Total prey	1123	100

were brought to the nest in thirty-one days (N1), with a maximum of 197 prey/day (N1), 216 (N2), and 198 (N3). In N2 and N3, it was not possible to obtain data on the provisioning rate for the full period of incubation and chick growth, because of technical problems with the camera traps (Fig. 2).

Foraging microhabitat selection

Foraging plots were characterized by a shorter herbaceous sward, a lower herbaceous vegetation cover and absence of trees and shrubs, and a higher cover of bare ground, pebbles, and biological debris compared to random plots (Tab. 2).

Herbaceous vegetation height and cover were the only statistically significant variables according to the parsimonious binomial GLM (Tab. 4). The other variables were excluded from the backward stepwise selection or resulted to be non-significant (Tab. 4).

DISCUSSION

Our work represents the first study on the Hoopoe diet in a heterogeneous agricultural Mediterranean landscape during the breeding season and the results indicate that *C. orni* is a very important food resource in this habitat, comparable to the Mole cricket in the Swiss intensive agroecosystems, where it represents the main prey provided to nestlings in term of biomass (Fournier & Arlettaz 2001). Our results showed that over 61% of the nestling diet consisted of nymphs

Table 2. Microhabitat variable mean values \pm SD at foraging and control plots.

Microhabitat variables	Foraging plot	Control plot
Bare soil cover (%)	36 \pm 25	5.4 \pm 11
Herbaceous vegetation height (cm)	6.64 \pm 3.55	57.0 \pm 46.4
Biological debris cover (%)	29 \pm 35	16 \pm 27
Herbaceous vegetation cover (%)	35 \pm 28	73 \pm 34
Tree and shrub vegetation cover (%)	0 \pm 0	6 \pm 21
Pebble cover (%)	7 \pm 16	0.3 \pm 1

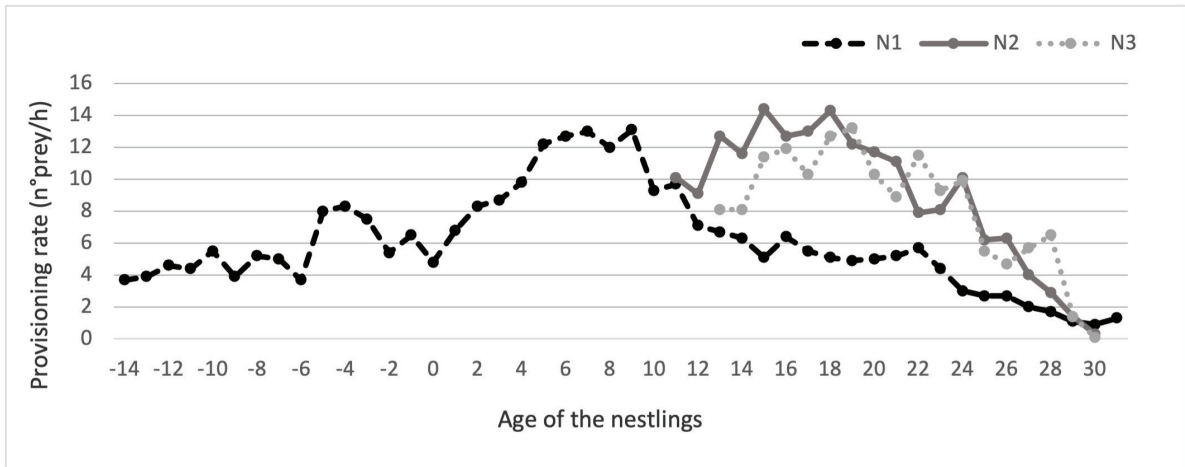


Figure 2. Provisioning rate (n°prey/h) at three Hoopoe nests during the breeding season in Castel di Guido (Rome, Italy). On the x-axis, the day 0 corresponds to the hatching of the first egg. Different lines represent different nests.

Table 3. Correlation table of the six micro-habitat variables measured in the field. Pearson Correlation Coefficient is reported and the significance of the correlation between paired samples is reported as follows: *** P < 0.001, ** P < 0.01, * P < 0.05.

	Bare soil cover	Herbaceous vegetation height	Biological debris cover	Herbaceous vegetation cover	Tree and shrub vegetation cover	Pebble cover
Bare soil cover		-0.48**	-0.22	-0.43***	-0.17	0.28*
Herbaceous vegetation height			-0.31*	0.45***	0.37**	-0.15
Biological debris cover				-0.69***	-0.07	-0.19
Herbaceous vegetation cover					-0.24*	0.00
Tree and shrub vegetation cover						-0.07

Table 4. Microhabitat foraging habitat selection of breeding Hoopoe in Castel di Guido (Rome, Italy). Summary of the parsimonious best binomial GLM obtained with a backward stepwise procedure. ** P < 0.01, * P < 0.05, ns = not significant.

	Estimate	Standard error	z-value	P-value
Intercept	7.117	2.503	2.843	**
Herbaceous vegetation height	-0.588	0.226	-2.599	**
Herbaceous vegetation cover	-5.266	2.240	-2.351	*
Pebble cover	1.917	3.138	0.611	ns

of *C. orni*, which has not been listed in literature until now as a preferential Hoopoe prey. We observed the Hoopoe actively searching on the ground for tunnels that the *Cicada* nymphs dug to emerge, and once found, inserted their long bill into the galleries to extract them. The nymphs of this insect begin to be prevalent in the nestling diet in the first days of June, when they start raising from the underground and become available for Hoopoes. Before cicadas become available in the environment, we observed that the other groups of terrestrial larvae (Lepidoptera, Coleoptera and Diptera) are dominant in the diet of the chicks. Conversely, Mole crickets are irrelevant in our study area as food provided to nestlings, probably because the soil is quite hard and dry, and therefore less suitable for this insect, which prefers moist and soft soils where it is facilitated in digging tunnels (Hertl & Brandenburg 2007). Indeed, as previously suggested by Fournier & Arlettaz (2001), our study confirms that the Hoopoe is mainly specialized in hunting Insect larvae (over 84% of their diet).

Several previous studies indicate that Hoopoe feeds on below-ground pupae of the pine processionary moth (*Thaumetopoea pityocampa*) and it could also represent the dominant prey species provisioned to chicks in landscapes where open habitats are intermixed with pine forests (Battisti 1986, Battisti et al. 2000, Barbaro et al. 2007). Notably, in the intensively managed maritime pine plantation forest of southwestern France, the Hoopoe breeding success is linked to the *Thaumetopoea pityocampa* abundance (Barbaro et al. 2007). In our sample, we have not recorded any pupae of pine processionary moth; this could be due to the relative distance of the sampled nests from most of the pine forests since the Hoopoe does not usually move too much from the nest to forage (Barbaro et al. 2007).

All the works carried out to date on the Hoopoe foraging biology demonstrate that in landscapes and regions where Mole cricket are rare or absent, other ground-dwelling prey of likely similar energy content may become dominant in nestling diet: *Thaumetopoea pityocampa* near pine plantations (Battisti et al.

2000) or *C. orni* in the Mediterranean extensive rural areas (this study), suggesting that the Hoopoe can be quite adaptable in term of prey preference depending on local context and resulting prey availability. Further research should assess if *C. orni* is an important food resource also in other Mediterranean habitats and should investigate the relationship between provided *Cicada* biomass and breeding success.

In birds, foraging habitat selection results from an interaction between food abundance and accessibility, mediated by vegetation structure (Morris et al. 2001). Our foraging microhabitat selection analysis showed that the herbaceous vegetation height and cover are the only influential variable for the species. In particular, as grass height and cover increase, the likelihood that this bird chooses an area to feed decreases. However, as shown by the preliminary correlation analysis performed, when the herbaceous vegetation cover decrease, the bare ground increase (along with the organic debris). Therefore, it could be assumed that the bare ground also affects the choice of microhabitat, as demonstrated in the study of Tagmann-losset & Arlettaz (2007). Indeed, Hoopoes avoid sites characterized by extensive high vegetation cover, preferring open areas with bare soil alternated with scattered patches of sparse grass, probably because this mosaic provides a greater amount and diversity of prey compared to areas completely bare or completely vegetated (Schaub et al. 2010). Grass, especially if high, is however negatively selected as it constitutes an obstacle in probing the soil or otherwise making the below-ground insects less accessible; particularly, as vegetation height increases, prey location signals are likely less detectable (Butler & Gillings 2004). At the same time, sparse vegetation may decrease the predation risk (Whittingham & Evans 2004), because elements such as tall or dense vegetation could hinder predator perception and thus delay an escape response from peril (Devereux et al. 2006).

With regard to the complete lack of nest box occupation in our study area, we hypothesized that it

depends on the high heterogeneity and complexity of the landscape, which presumably offers enough natural breeding sites, even if increased nest box density may increase the Hoopoe population (Arlettaz et al. 2010a). This data could prove that the nest box installation in extensive rural areas may be much less important than in more intensive cultivable environments, where there is a lack of nesting cavities (Arlettaz et al. 2010a). Another complementary hypothesis is that the nest boxes colonization by Hoopoes may take longer than one year, even if this is not sufficiently documented in the literature. However, in the WWF oasis of Macchiagrande, approximately 10 Km from our study area, Hoopoes occupied nest boxes only in the second year since installation (Baldi & Sorace 1996).

Low-intensive anthropogenic activity, which includes mechanical removal of grass along crops or country houses, creation of dirt roads and dry-stone walls, extensive animal husbandry, and herbaceous firebreaks maintained low by cutting or grazing, in traditional cultural landscape (well exemplified by our study area) can contribute to create and maintain suitable environmental conditions for this decreasing species, which requires a microscale mosaic of different habitats to forage (Barbaro et al. 2007). We think that this evidence should be accounted for when designing conservation plans aimed at this species, or others with similar ecological needs (Schaub et al. 2010), also considering the strong context-dependent foraging habitat needs of insectivorous bird species in different regions (Assandri et al. 2022).

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