

Diet heterogeneity and antioxidant defence in Barn Swallow *Hirundo rustica* nestlings

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Abstract – Populations of several farmland bird species have suffered sharp declines linked to increased environmental homogeneity and reduced biodiversity, particularly of insects, upon which several farmland birds feed. Diet, in turn, has a crucial role in organism fitness. Antioxidants acquired through diet, in particular, help by protecting the organisms against the effects of Reactive Oxygen Species, which originate as a natural by-product of metabolism. Here we investigated the relationships among environmental heterogeneity, diet composition, and oxidative status by using Barn Swallow (*Hirundo rustica*) nestlings as a model. By analysing chitin fragments extracted from faecal sacs, we found that nestlings' diet was mainly composed by four insect families: Formicidae (Hymenoptera), Aphodidae (Coleoptera), Tabanidae and Syrphidae (Diptera). We also observed body parts of *Diabrotica virgifera*, the most important insect pest of maize (*Zea mays*) in the world. Nestling diet composition varied with environmental heterogeneity in the foraging range of adult Barn Swallow (i.e. 200 m from each colony). The antioxidant capacity (AOC) of nestlings, which was assessed using the OXY-Adsorbent test on blood plasma samples, peaked at intermediate values of diet diversity, suggesting that it can be mediated by the composition of the nestlings' diet. Heterogeneous environments may offer a wide array of prey, and this may allow foraging Barn Swallows to feed their nestlings with selected prey that may enhance their oxidative status. Similar mechanisms may act for a wide array of farmland birds, thus shading light on the mechanisms that link habitat homogenization and bird population declines.

Key-words: agroecosystem, environmental heterogeneity, farmland birds, insects, oxidative status.

INTRODUCTION

In the last decades, populations of several farmland bird species have suffered sharp declines, concurrent to the introduction of modern intensive agricultural practices (Fuller *et al.* 1995; Donald *et al.* 2001, 2006; Laiolo 2017). Massive use of fertilizer and agrochemicals, coupled with the spread of monocultures and more intensive mowing of grasslands and pastures have greatly reduced biodiversity in agro-ecosystems (Vickery *et al.* 2001; Aviron *et al.* 2005; Tschardtke *et al.* 2005; Devictor & Jiguet 2007; Billeter *et al.* 2008; Fahrig *et al.* 2011). These practices have particularly damaging effects on insects, as shown by studies conducted in both Europe and North America, which indicated that insect diversity decreases with environmental homogeneity (Jonsen & Fahrig 1997; Benton *et al.* 2003; Geslin *et al.* 2016; Gillespie *et al.* 2018). The abun-

dance and diversity of insectivorous birds, in turn, follows strictly the environmental availability of insects. Indeed, the increase of both insect and bird diversity with environmental heterogeneity (Freemark & Kirk 2001) highlights the importance of heterogeneous environments to maintain high biodiversity in agroecosystems (Britschgi *et al.* 2006; Di Giulio *et al.* 2001; Fahring *et al.* 2011).

The fitness of organisms varies through space and time as a result of the combined effects of extrinsic abiotic conditions (e.g., temperature; Bryant 1978; van Noordwijk *et al.* 1995; Buse *et al.* 1999; Thessing 2000) and biotic factors, including food quality and availability (Bryant 1975; Quinney *et al.* 1986; van Noordwijk *et al.* 1995). Diet, in particular, has a crucial role in several components of fitness, including survival, breeding success and offspring development and quality. For example, in the Northern Bobwhite (*Colinus virginianus*) the number of fledglings

is influenced by food availability, while immune function, which may affect survival prospects, is affected by specific components of diet (Lochmiller *et al.* 1993). Many substances necessary for metabolic activities are assumed through diet: for instance, antioxidants acquired with diet act synergistically with endogenous mediators (i.e. enzymes) for protecting the organisms against oxidative damage (Surai 2002; Saino *et al.* 2011). Indeed, Reactive Oxygen Species (ROS), which originate as a natural by-product of metabolism, if not neutralized, may damage cellular structures. During a physiological increase of the metabolic rate, such as that occurring during growth (Alonso-Alvarez *et al.* 2007), the high concentration of ROS causes a rise of cellular oxidative stress (Finkel & Holbrook 2000; Saino *et al.* 2011). Diet is a source of antioxidants, such as vitamin E, carotenoids and polyphenols, which may help the organism to mitigate the damaging action of reactive species (Surai 2002; Catoni *et al.* 2008). The diet is also a source of substances that do not have antioxidant properties, but that may indirectly affect the organism's resistance to oxidative stress. For example, protein intake might affect the synthesis of some antioxidants (e.g., thiols, enzymes) whose production depends on the availability of amino acids (Li *et al.* 2014). Environmental conditions can also affect the oxidative status of organisms in different ways. For instance, they can influence food abundance, diversity and availability and, consequently, diet and oxidative status of organisms (Costantini *et al.* 2014). Abiotic factors such as temperature, metal ions and solar radiation, can also directly affect the oxidative balance regulation of organisms (Costantini 2014). Antioxidant defence is thus necessary to contrast the oxidative damage, and it is considered a good indicator of individual quality (Boncoraglio *et al.* 2012).

Birds are considered good model species for investigating the effects of oxidative stress in the wild (Costantini 2008). Birds, on average, live longer than mammals of equivalent body mass despite their higher metabolic rate, which should accelerate tissue damage and senescence (Costantini 2008), particularly during growth (Alonso-Alvarez *et al.* 2007). Some studies have analysed the oxidative status of adult birds in different environments (Olson & Owens 2005; Cohen *et al.* 2009; Herrera-Duenas *et al.* 2017), but very few have investigated the oxidative status of nestlings growing in different environmental conditions (Arnold *et al.* 2010). In addition, to the best of our knowledge, no study so far has directly investigated the relationships among environmental conditions, diet composition, and oxidative status in any bird species. Here, we aim to fill this knowledge gap using the Barn Swallow (*Hirundo rustica*) as a model species. The Barn Swallow

is an insectivorous passerine and a farmland bird that nests semi-colonially in human buildings (Turner 2006) and extensive studies have been conducted on the effect of oxidative damage in this species. For instance, high levels of antioxidant protection positively predict long-term survival of adult Barn Swallows (Saino *et al.* 2011). Here, we focus on nestlings, because they are exposed to high cellular oxidative stress because of their high metabolic rate during growth, which determine high ROS concentration (Alonso-Alvarez *et al.* 2007; Finkel & Holbrook 2000; Saino *et al.* 2011). Oxidative damage is considered to have a strong impact on nestlings and potentially pervasive consequences on their life history and viability (see above), and it is therefore considered an excellent marker of general condition of Barn Swallow nestlings (Boncoraglio *et al.* 2012). In addition, experimental manipulation studies have suggested that antioxidants may be available in limited amounts to Barn Swallow nestlings. This may occur because the diet that parents provide to their offspring may be limited in the amount of micronutrients, such as vitamin E, that act as antioxidants for vertebrates (de Ayala *et al.* 2006). Finally, large hayfields and highly heterogeneous environments are usually associated with high insect availability and diversity. We therefore hypothesized that Barn Swallow nestling diet varies according to environmental heterogeneity and hayfield extent around breeding colonies and, in particular, it is more diverse in heterogeneous environments and in nesting sites surrounded by large hayfields. We also expected an increase in nestling antioxidant defence with diet heterogeneity.

MATERIALS AND METHODS

Study species

The Barn Swallow is a semicolonial, socially monogamous and insectivorous passerine with biparental care of altricial offspring. Barn Swallows breed almost exclusively in rural buildings, often in association with livestock, and they forage for invertebrates on the wings close to their breeding sites, particularly on hayfields and meadows (Møller 1994; Møller 2001; Ambrosini *et al.* 2002a, b; Turner 2006) and where field margins have been sown with wildflowers (McHugh *et al.* 2018). More than 50% of foraging activity by Barn Swallow occurs within of 200 m of breeding sites, approximately 95% occur within 400 m and only occasionally Barn Swallow forages beyond 400 m from their breeding site (Ambrosini *et al.* 2002a; Sicurella *et al.* 2014) and up to 600 m from the nest (Bryant and Turner 1982). This species is declining at continental scale and in northern Italy, where this study was conducted. Particularly, in our

study area, Barn Swallow population declines are linked to declines of livestock farming (Ambrosini *et al.* 2012; Musitelli *et al.* 2016). However, land use around nesting sites, particularly hayfield extent, seems to play a role in modulating colony decline, probably through variation in insect food availability (Sicurella *et al.* 2014).

Selection of sampling sites

The study was conducted in April-July 2012 at 20 Barn Swallow colonies located in different farms in the Parco Regionale Adda Sud, in northern Italy (see Ambrosini *et al.* 2002a for a general description of the study area; Fig. 1). Each colony was considered independent if nests occurred in farms separated by more than 100 m to one another (see Ambrosini *et al.* 2002a). Since Barn Swallows forage within 400 m from each colony (Ambrosini *et al.* 2002a), foraging ranges of nearby colonies may overlap. However, only three colonies were at less than 400 m to one another. Hayfields and maize (*Zea mays*) fields are the two main land uses in the study area within 400 m from the study colonies (Ambrosini *et al.* 2002a; Sicurella *et al.* 2014). Colonies surrounded both by extremely large extent of either hayfields and maize fields show low values of environmental heterogeneity, while those with small extent of both the prevalent land uses in their surroundings occur typically in a mosaic of different land uses, and therefore show large values of habitat heterogeneity (see Fig. 1d).

Thus, the colonies we selected could be ordered along two environmental gradients, which were also almost uncorrelated to one another, going respectively, from colonies surrounded by large hayfields to colonies surrounded by large maize fields, and from colonies surrounded by rather homogeneous habitats to colonies surrounded by heterogeneous habitats (i.e. increasing environmental heterogeneity; Fig. 1d). Livestock was present on 16 of the farms that hosted the investigated colonies and the four ones without livestock were all surrounded mainly by maize fields. Sample size was therefore too low to investigate the effect of livestock presence on nestling diet. For practical reasons, not all analyses were performed on all colonies (see Results for details on sample sizes).

General field procedures

Colonies were visited weekly starting on 1 April to identify egg laying and every day close to the estimated hatching date (i.e. 15 days after the laying of the penultimate egg in a clutch) to precisely identify hatching date and therefore nestling age. We selected one to three nests in each of the premises of a farm where Barn Swallow nests occurred. This allowed sampling nests approximately proportionally to colony size. At 8, 9, 10, 11 or 12 days we collected blood samples in heparinized capillary tubes from individual nestlings by puncturing their brachial vein for molecular analyses. Faecal samples were collected to

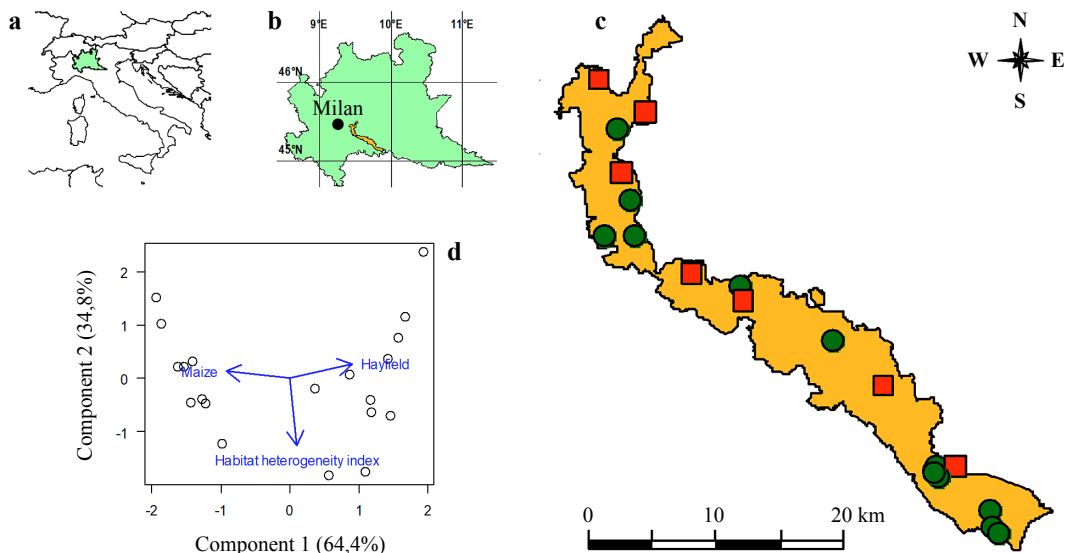


Figure 1. a) Lombardy in Italy and Europe and b) the Parco Regionale Adda Sud in Lombardy. c) Location of the farms included in the present study in the Parco Adda Sud. Different symbols indicate farms where we collected data on nestling diet only (green dots), or both data on nestling diet and antioxidant capacity (red squares) d) Biplot of PCA on the extent of hayfields, maize fields and the habitat heterogeneity index within 200 m from the farms. All variables were standardized before the analysis. Each dot represents a farm. The habitat heterogeneity index is clearly orthogonal to the extent of both hayfields and maize fields.

analyse nestlings' diet composition and diversity. We considered diet composition as the relative abundance of each insect family found in each faecal sac, while a "diet diversity index" was measured using the Shannon index (base e) (Shannon 1948) on the abundance of each insect family in each faecal sac. In the colonies where we collected faecal samples, nestlings were individually put in small plastic cups when they were 9-, 10- or 11-day-old and left there until they naturally defecate, which, in most cases, happened almost immediately in response to handling. Alternatively, faecal samples were collected when nestlings were 15-, 16- or 17-day-old. We never removed all nestlings from a nest to prevent nest desertion by parents and each nestling was returned to its nest in 5 to 7 min. In our experience of more than twenty years of study on Barn Swallow nestlings in this area, this manipulation procedure has no adverse effect on fledging success and never caused nest abandonment. Faecal and blood samples were then stored in a cool bag in the field. Once in laboratory, faecal samples were stored at -20 °C, while blood samples were centrifuged (11500 rpm for 10 min) and plasma was separated from red blood cells and stored at -20 °C. Nestlings sampled to collect faecal and blood samples varied from one to four (two in most cases) per nest, randomly chosen in order to avoid nest desertion by parents.

We quantified the extent of different land uses in a radius of 200 and 400 m around each farm, as Barn Swallow forage mainly in that range (Ambrosini *et al.* 2002a; Møller 2001; see also above). Land use was assessed by direct observation and recorded on maps 1:10.000; the following land uses were identified: maize, hayfield, wheat (*Triticum ssp.*), alfalfa (*Medicago sativa*), soybean (*Glycine max*), poplar (*Populus spp.*) plantations, woods, uncultivated land, other cultures, rivers and human settlements. The area occupied by each of these land use categories was measured by superimposing a standard grid of equidistant dots (each dot corresponding to ~0.25 ha) onto the map and counting the number of dots in each land use (Ambrosini *et al.* 2002a). This information was then summarized in a "habitat heterogeneity index" corresponding to the Shannon index (base e) (Shannon 1948) calculated on the proportional extent of all land use categories (see Ambrosini *et al.* 2002a for a similar approach).

Faecal analysis and diet determination

Faecal sacs were defrosted, spread on Petri dishes filled with ethanol 70%, and inspected under a stereomicroscope (50×) in order to extract each chitin fragment and each insect body part (e.g. heads, thorax, legs, elitrae, abdomens etc.). Since Barn Swallows, as all birds, are not able to digest chitin, fragments of chitin parts and, generally, in-

sect body parts found in the faeces can be used for taxonomic identification of invertebrate prey and for assessing the number of prey items from each taxon (Orlowsky & Karg 2011). For this latter task, we applied the rule of summation of different chitin parts to the level of one individual in accordance with previous studies (Orlowsky & Karg 2013a, b; Orlowsky *et al.* 2014). Insect part identification was performed using the identification keys in Gobbi & Latella (2011), Latella & Gobbi (2015), Pesarini (2004). In any dubious case, insect body parts were compared with the insects stored in the dry collections of the MUSE-Science Museum of Trento (Italy). We could identify 94.4% of items at the family level, 70.9% at the genus level and 23.2% at the species level. In the analyses, we therefore decided to describe nestling diet as the number of prey items in each family because this taxonomical level allowed having a reasonable sample size with a small loss of information on functional diversity of prey items. We also calculated a "diet heterogeneity index" corresponding to the Shannon index (base e) of the number of prey items of each family.

Analysis of faeces is likely to yield a reliable picture of the Barn Swallow diet. Indeed, experimental feeding of a Barn Swallow nestling conducted by Waugh (1978) showed that the proportions of different prey types ingested (including soft bodied prey like small Diptera) and the proportions recovered in the faeces are in very close agreement. Hence, Barn Swallows seem not to digest differentially prey types with soft bodies and flexible wings or heavily chitinised prey (Waugh 1978, Orlowsky & Karg 2013a; Orlowsky *et al.* 2014).

Plasma antioxidant capacity (AOC)

Blood samples from two randomly chosen nestlings from each nest were used to determine an index of overall plasma antioxidant capacity (AOC). AOC was measured using the OXY-Adsorbent test (Diacron, Grosseto, Italy). This test performs a colorimetric determination of the capacity of the plasma antioxidant barrier to cope with oxidation by the hypochlorous acid (HClO) (Saino *et al.* 2011). Through this test, we can measure the non-enzymatic antioxidant capacity, to focus the attention on the exogenous antioxidants supplied by diet.

Plasma sample (5 µL) was diluted 1:100 with distilled water. A 5 µL aliquot of the diluted plasma was added to 200 µl of a titred HClO solution. The solution was mixed and incubated for 10 min at 37 °C. At the end of the incubation time, 5 µL of an alkyl-substituted aromatic amine solubilized in a chromogenic mixture, was added. This amine is oxidized by the residual HClO and transformed into a pink-coloured derivative. The concentration of the

coloured complex is directly proportional to the HClO excess and inversely related to the antioxidant capacity of tested plasma. The intensity of the coloured solution was measured at 492 nm using a photometer (Multiskan EX, Labsystem). One standard sample of known antioxidant capacity used as reference and one blank sample (5 μ L of distilled water) were both processed as normal samples. In all the analyses, antioxidant capacity is given as μ mol HClO mL⁻¹ neutralized.

Because the different components of the antioxidant barrier do not necessarily act in additive way, total antioxidant capacity, measured through OXY-Adsorbent test, is not simply an additive function of the concentration of individual antioxidants, and overall measures of antioxidant capacity are thus more representative of the redox status of an individual (Cohen *et al.* 2007; Monaghan *et al.* 2009).

Statistical analyses

Variation in nestling diet composition was investigated by multivariate analyses. We used variation partitioning (Legendre & Legendre 2012) to assess the relative amount of variation in nestling diet among nestlings, broods and farms while accounting for the hierarchical structure of data. Indeed, nestlings from the same broods cannot be considered statistically independent as they share parents and rearing environment. To this end, we performed the variation partitioning analysis by means of a series of partial redundancy analyses (part-RDAs) because they allow quantifying the total variation at one level of a nested dataset while conditioning the analyses to immediately higher level. We proceeded as follows: first, we estimated the amount of variation in nestling diet composition among farms with a RDA with farm (fixed factor) as predictor. Second, we ran a partial RDA with nest identity (fixed factor) as predictor while conditioning the model to farm identity. Third, we obtained diet variation among nestlings in a RDA with nestling identity (fixed factor) as predictor while conditioning the model to nest identity (Legendre & Legendre 2012). These analyses allow partitioning the variance into independent quotas as demonstrated by the fact that the sum of the variances attributed by part-RDAs to the farm, nest and nestling levels sum to the same amount of variance explained by an RDA including nestling identity as the sole predictor. This variation partitioning analysis thus allowed assessing the contribution of each of these hierarchical levels to the variation in the diet of individual nestlings. All RDAs were based on the Hellinger distance among samples, which depends on the difference in the proportion of prey taxa between samples, decreases the importance of taxa abundance over occurrence and avoids the double-zero problem when comparing species compo-

sition between samples (De Cáceres *et al.* 2010; Legendre & Legendre 2012).

We then investigated variation in diet composition in relation to land use around farms by a RDA including as predictor the habitat heterogeneity index. In this analysis, we considered an average diet composition for all the nests of the same brood, equal to the mean number of prey items of the same family. This average diet was considered an estimate of the diet composition of all nestlings of the same brood, which we considered reflecting parental choice of food items for their brood. We also accounted for non-independence of data collected on the same farm by performing randomizations between farms only (Manly 1997). In details, we randomly shuffled the habitat heterogeneity index between farms and then assigned to all nestlings of a farm the same shuffled value. Finally, we used separate RDAs including Hellinger-transformed abundance of one prey family as dependent variable at time to assess abundance of which prey family changed according to predictors. Significance of these models was then corrected with the False Discovery Rate (FDR) procedure to account for multiple statistical tests (Benjamini & Hochberg 1995).

We used linear mixed models (LMMs) assuming a Gaussian error distribution, whereby nest and farm were included as nested random grouping factors, to relate antioxidant capacity of nestlings to the diet heterogeneity index (see above). In the models, we also included the quadratic terms of predictors whenever preliminary inspection of the data suggested the existence of non-linear effects. Potential outliers were identified by routine inspection of graphs of residuals performed for checking model assumptions, however results did not change (i.e. all significant results remained significant) when the analyses were re-run by excluding one potential outlier (details not shown). We therefore reported only the results of the analyses on the whole datasets. No other potential violation of model assumptions was detected.

Statistical analyses were performed using R 3.5.1 (R Core Team 2018), with packages BiodiversityR, car, vegan, lmerTest. The Electronic Supplementary Material (ESM) includes an Excel file with all data used in the analyses.

RESULTS

Diet composition

We collected faecal samples from 142 nestlings from 71 nests and 20 colonies. Overall, we extracted 518 prey items 503 of which were identified at family level. Barn Swallow

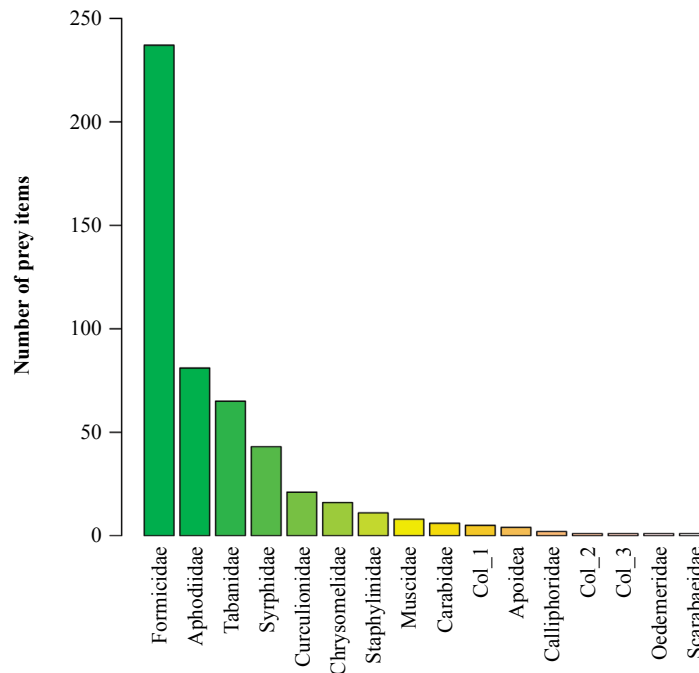


Figure 2. Frequency of different prey families, in decreasing order. “Col_1”, “Col_2”, “Col_3” indicate three different but unidentified families of Coleoptera.

nestlings diet was composed mainly by four insect families: Formicidae (Hymenoptera), Aphodiidae (Coleoptera), Tabanidae and Syrphidae (Diptera) (Fig. 2). Formicidae found in faecal sacs belonged to genera *Tetramorium* (sp. *caespitum*) and *Formica*. We found ten families of Coleoptera, including 11 individuals of the pest *Diabrotica vigifera* (Chrysomelidae), allocated in three faecal samples; however, the most common family of Coleoptera was Aphodiidae, genus *Aphodius*. Diptera belonged mainly to families Tabanidae and Syrphidae (Fig. 2; ESM 1).

We then calculated the number of prey items in each insect family for further analyses (see methods). The six faecal sacs whereby we could not determine the family of all prey items were discarded. Sample size was therefore 136 faecal sacs and 503 prey items from 77 nestlings at age 10 ± 2 days and 59 nestlings at age 16 ± 1 days. These nestlings were from 71 nest in 20 colonies.

Variation partitioning showed that nestling diet largely varied between nestlings (46.3% of variance) and then among nests (36.2%). Variation explained by differences among farms (17.5%) was minor compared to differences between nestlings and among nests, but was nevertheless significant ($F_{19,116} = 1.299$, $P = 0.032$). The statistical significance of the other components of variance cannot be tested (see Borcard *et al.* 2011 for details).

Diet did not differ between age classes ($F_{1,134} = 0.485$,

$P = 0.856$). However, the high variation between nestlings could reflect also temporal variation in prey abundance and availability, as suggested by the fact that nestling diet composition also varied significantly along the season, as shown by an RDA including sampling date as predictor ($F_{1,134} = 3.176$; $P = 0.017$). Separate models showed that Hellinger transformed abundance of both Formicidae and Carabidae (Coleoptera) tended to increase with date, but this variation turned statistically non-significant after FDR correction (Formicidae: $F_{1,134} = 7.574$, $P = 0.016$, $P_{FDR} = 0.124$; Carabidae: $F_{1,134} = 4.862$, $P = 0.011$, $P_{FDR} = 0.124$; $F_{1,134} \leq 7.756$, $P \geq 0.079$ in all the other cases).

Influence of land use on diet

We tested the influence of land use around farms on the mean diet composition of the nestlings of each nest calculated as the mean number of items of each family found in the faecal sacs of the nestlings. RDA revealed a significant variation in the mean diet composition of a nest with the environmental heterogeneity index ($F_{1,69} = 2.026$; $P = 0.030$). In addition, a LMM indicated that the diet heterogeneity index of the nest did not vary significantly with the habitat heterogeneity index ($F_{1,18,725} = 0.306$ $P = 0.587$). Thus, environmental heterogeneity was linked to a variation in diet composition but not in the overall diet heterogeneity. In this case, we did not consider the temporal var-

iation effect because in 46.5% of broods, nestlings were sampled at different ages, and so in different dates. When we repeated the analyses with land use within 400 m from each farm, we observed a non-significant effect of the environmental heterogeneity index on the mean diet composition of a nest in RDA ($F_{1,69} = 1.660$, $P = 0.101$). Similarly the effect of the environmental heterogeneity index within 400 m from each farm on the diet heterogeneity index was not significant ($F_{1,14,743} = 1.760$, $P = 0.205$).

Antioxidant capacity and diet heterogeneity

We tested the influence of diet heterogeneity on nestlings' antioxidant capacity on a sample of 24 nestlings from 16 nests in seven colonies for which information on both diet heterogeneity and antioxidant capacity was available. We found a significant non-linear relation between AOC and the diet heterogeneity index (Tab. 1, Fig. 3). Model coefficients indicated a maximum in AOC values for values

of the diet heterogeneity index of 0.578. AOC values also declined significantly after the maximum ($t_9 = -2.265$, $P = 0.049$), while the increase before the maximum was non-significant ($t_{5,458} = 1.104$, $P = 0.316$). When we repeated the analysis excluding one possible outlier, results did not change (Fig. 3).

DISCUSSION

Diet composition and heterogeneity

The diet of Barn Swallows nestlings was composed mainly by four insect families: Formicidae (Hymenoptera), Aphodiidae (Coleoptera), Tabanidae and Syrphidae (Diptera). Aphodiidae and Tabanidae are particularly associated to livestock as the former spend the larval phase in manure (Pesarini 2004) and the latter spend the larval phase in moist ground and some adults are blood-sucking (Ket-

Table 1. Coefficients of the fixed effects of the linear mixed model of antioxidant capacity (AOC) in relation to the first and second order polynomial term of nestling diet diversity index.

Effect	Coef.	SE	df	<i>t</i>	<i>P</i>
Intercept	185.30	12.37	21	14.98	< 0.001
Diet Diversity Index	193.43	59.66	21	3.24	0.004
(Diet Diversity Index) ²	-165.84	57.69	21	-2.87	0.009

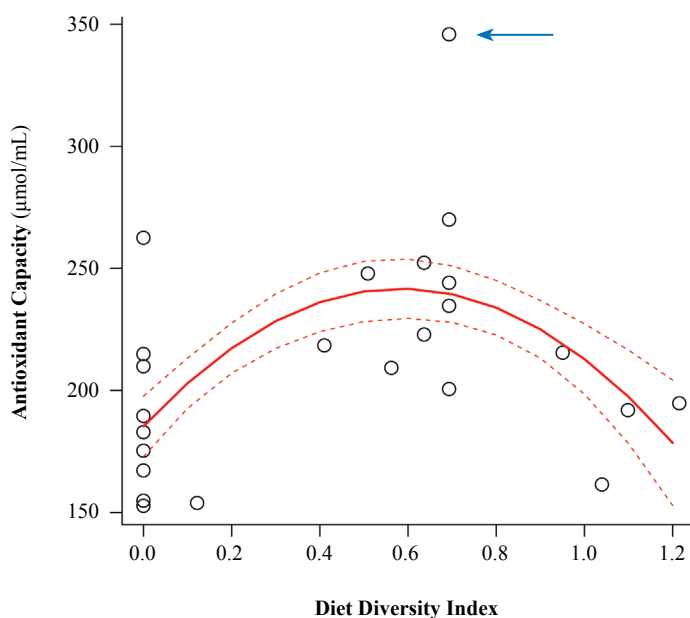


Figure 3. Variation of antioxidant capacity (AOC) in relation to diet diversity index. The regression function (solid line) and its standard error (dashed lines) were drawn according to model coefficients in Table 1. The arrow indicates the potential outlier whose removal from the analyses did not affect the results.

tle 1992). Formicidae are smaller than the others prey observed in Barn Swallow nestling diet, but they are particularly abundant during the second half of June, when, in our study area, they are flying in swarms (personal observation), with a high density of individuals. Syrphidae, famous for their Batesian mimicry (Edmunds, 2000), is a common family of Diptera in agroecosystem because of their role as pollinators (Burgio and Sommaggio 2007; Gobbi and Latella 2011). The high frequency of Syrphidae found in the faecal samples of the nestlings suggests that their Batesian mimicry strategy may not be very effective to prevent the predation by Barn Swallows. High abundance of Syrphidae was documented in Barn Swallow nestlings diet also in Poland (Orłowski & Karg, 2011). We can speculate that the population of the model species (e.g. Honey-Bee *Apis mellifera*) is smaller than the population of the mimic species, so Barn Swallows have a lower probability to encounter the model species and learn (or recall) the connection between signal and quality (unpalatability) than the connection between the signal and mimic (Lindstrom et al. 1997; Veselý & Fuchs 2009). Interestingly, in the faecal samples we found body parts of *Diabrotica virgifera*; to the best of our knowledge, only one other study has recorded vertebrate predators of the adult stage of this invasive pest insect (Cristiano et al. 2018), which is probably the most important insect pest of maize in the world (Lombaert et al. 2018). Human, livestock and agricultural pests have already been detected in the diet of the Barn Swallow, (McClenaghan et al. 2019), which suggests that this species can provide an ecosystem service by reducing pest number in agro-ecosystems.

In general, the diet of Barn Swallow nestlings in the Parco Adda Sud has a lower heterogeneity than that observed in other studies conducted in Northeastern Europe with similar methods, where insects of orders Hemiptera and Lepidoptera were also found (Møller 1994, Orłowsky & Karg 2013a, Orłowsky et al. 2014). These orders are generally frequent in Italian agroecosystems, but less so in intensively cultivated or urbanized area as the Po plain, where our study was performed and where pesticides and herbicides are used in large amount (Bonelli et al. 2011; Regan et al. 2017). Some previous studies performed either with morphological or DNA metabarcoding analysis of faecal sacs documented an even larger prey heterogeneity in Barn Swallow nestlings diet. For instance, Kozena (1979) recorded over 80 insect families in nestlings faecal sacs in Poland using morphological analysis of prey; McClenaghan et al. (2019) identified 130 insect families in the diet of nestling Barn Swallows of the *erithrogaster* subspecies nesting in Ontario (Canada) with DNA metabarcoding. Barn Swallow diet heterogeneity seems there-

fore rather low in our study area, probably because of the intensive agricultural practices or, less likely, because of geographical and environmental differences in diet between Barn Swallow populations. However, horseflies (Tabanidae) were among the most preferred prey both in our study and in Ontario (McClenaghan et al. 2019).

More generally, the diet of aerial insectivores that often co-occur in European farmland (the Barn Swallow, the House Martin *Delichon urbicum* and the Common Swift *Apus apus*) seems mainly based on crop insects, with a relatively large importance of coprophilous taxa (particularly for Barn Swallows and House Martins) (Orłowski et al. 2014), consistently with the finding of our study. This confirms the importance of organic farming or fertilizers as a substratum for the development of these important prey (Orłowski et al. 2014). In a broad review of the diet of European farmland birds, Holland et al. (2005) found that Carabidae, Chrysomelidae, Formicidae, Scarabeidae and Staphylinidae are among the most important invertebrate families in the chick diet, together with Curculionidae, Tipulidae, Aphididae and Tenthredinidae, which we did not record in Barn Swallow nestling diet.

Variation partitioning analysis showed that variation in diet occurred mainly among nestlings and then among nests. A minor but significant part of variation occurred among farms. Variation among nestlings may indicate that an important source of variation in diet may be related to food allocation decisions by parents (Saino et al. 2000; Royle et al. 2012). However, variation between broods may also reflect different foraging strategies or different foraging abilities among parents, while the significant diet variation among farms indicates an effect of environmental features around colony sites on nestlings' diet. Diet variation among sites as well as along the breeding season was detected also in Ontario, and is probably related to the fact that Barn Swallows, as other insectivores, are generalists with respect to taxonomy but select prey based on size (McClenaghan et al. 2019).

Diet and antioxidant capacity

Evans et al. (2007) pointed out that invertebrate abundance in agricultural landscapes changes strongly between crop types and, at the same time, Barn Swallow foraging activity follows aerial insect distribution patterns. During nestling rearing, Barn Swallows forage mainly within 200 m of breeding sites and only occasionally beyond 400 m (Ambrosini et al. 2002a; Sicurella et al. 2014). In addition, they usually do not forage inside farm buildings (Cramp 1988). Our results confirmed that the environmental heterogeneity around colonies, considering land use within 200 m from them, influenced diet composition, evaluat-

ed as the mean number of prey items of each insect family among nestlings of the same brood, which we considered a more consistent estimate of the prey items caught by parents for feeding their nestlings than the diet of a single nestling. Many studies indicated environmental heterogeneity as a fundamental element for the conservation of the biodiversity of agricultural landscapes (Devictor & Jiguet 2007; Fähring *et al.* 2011). Our results confirm this indication, as they show that environmental heterogeneity affects the diet composition of an aerial insectivorous typical of agroecosystems. These results also confirm previous findings indicating that land use within 200 m from the colony is important for Barn Swallow feeding activity (Sicurella *et al.* 2014).

Landscapes containing different habitat types are expected to host higher overall biodiversity (Fähring *et al.* 2011). However, contrary to our expectation, we did not find any positive association between environmental heterogeneity and diet heterogeneity. We can hypothesize that this lack of an effect may be due to prey selection from adult Barn Swallows. Many studies indicate that Barn Swallows catch large insects disproportionately more than small ones, even if the latter are abundant in the environment (Møller 1994; Turner 2010; McClenaghan *et al.* 2019). However, the antioxidant defence (AOC) of nestlings peaked at intermediate values of the diet heterogeneity. This may occur, for instance, because environments with low insect heterogeneity, like monocultures, can reduce Barn Swallow nestling diet heterogeneity, which, in turn, may reduce their antioxidant defence if the few available prey are also poor in antioxidants. However, if the habitat suitability for nestling Barn Swallow is strongly conditioned by the abundance and availability of preferred prey, also environments with high insect heterogeneity, but low abundance or availability of each prey species, may be sub-optimal. Indeed, in such conditions, parents may not be able to find a sufficient number of the preferred prey, and may therefore be forced to provide prey of poor quality to their nestlings. For instance, in Ontario, Barn Swallows feed their nestlings with more Chironomidae during the second brood, despite they were more abundant in the environment during the first brood, probably because frequently provisioned prey families decreased in abundance during the time that Barn Swallows had their second brood (McClenaghan *et al.* 2019). This higher abundance of alternative prey, in turn, can reduce their antioxidant capacity. Admittedly, a large number of factors may affect the composition of nestling diet, for instance, seasonal variation of prey as well as meteorological conditions (Turner 2010). During sample collection, meteorological conditions were generally good (B. Sicurella and R. Ambrosini, personal

observations), so we considered unlikely that they have affected our results. In addition, other confounding factors not included in the analysis like seasonal variation in insect availability (for instance ant swarming) should simply increase the variability in the nestling diet, rather than generating a pattern of relationship between antioxidant capacity and diet heterogeneity like the one we observed.

Another limit of our study was that we used only one faecal pellet per nestling, which may not exhaustively represent nestling's diet. Indeed, the AOC of an individual can be affected by its diet during a longer period than that represented in a faecal sac. However, such bias should have masked the association we observed between antioxidant capacity and diet heterogeneity. Hence, we are confident that our results are robust to these potential confounding effects.

The peak in antioxidant capacity we observed at intermediate levels of diet heterogeneity allows hypothesizing that a heterogeneous environment may offer a wide array of prey, among which foraging Barn Swallows may select the preferred ones to feed their nestlings. Heterogeneous rural habitats may therefore be beneficial to insectivorous farmland birds because they can provide the diet necessary to promote nestling antioxidant capacity and, ultimately, their fitness. Such mechanisms may thus help shading light on the links between habitat homogenization and bird population declines.

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