

Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies

Research Article

Cite this article: Gameiro J, Veiga J, Valera F, Palmeirim JM, Catry I (2021). Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies. *Parasitology* **148**, 904–912. <https://doi.org/10.1017/S0031182021000470>






Received: 11 January 2021
Revised: 11 March 2021
Accepted: 11 March 2021
First published online: 17 March 2021

Key words:

Carnus hemapterus; chewing lice; dilution effect; haematophagous mites; host–parasite interaction; louse flies

Author for correspondence:

João Gameiro, E-mail: jgameiro92@gmail.com

João Gameiro¹ , Jesús Veiga² , Francisco Valera² , Jorge M. Palmeirim¹ 
and Inês Catry^{3,4,5} 

¹cE3c – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal; ²Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (EEZA-CSIC), Almería, Spain; ³CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Vairão, Portugal; ⁴CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal and ⁵School of Environmental Sciences, University of East Anglia, Norwich, UK

Abstract

Coloniality in birds is often associated with an increase in parasite burden, but whether the co-occurrence of several host species influences the prevalence and abundance of ectoparasites and their relationship with colony size or density remains poorly known. Here, we studied mixed-species breeding colonies formed after the provision of artificial breeding structures for restoring the lesser kestrel (*Falco naumanni*) population in Portugal, to investigate the influence of colony traits on ectoparasite infestation. We sampled four groups of ectoparasites (carnid flies, haematophagous mites, louse flies and chewing lice) in four hosts: lesser kestrels, European rollers (*Coracias garrulus*), feral pigeons (*Columba livia*) and spotless starlings (*Sturnus unicolor*). Each host species had a distinct infracommunity of ectoparasites, regardless of colony traits such as size, density or host richness. The abundance of the most common ectoparasite, *Carnus hemapterus*, was influenced by colony composition – number of nests of each host species – rather than by colony size or density, with its abundance being diluted with increasing numbers of less suitable hosts such as starlings. The increased contact between multiple species of hosts in breeding colonies may complexify host–parasite interactions and challenge our current knowledge on the ecological relationships between host sociality and parasitism.

Introduction

Avian colonial breeding is often associated with higher parasite prevalence and intensity, as the increased proximity and contact between different group members facilitate ectoparasite transmission (Brown and Brown, 1986; Côté and Poulin, 1995; Tella, 2002; Patterson and Ruckstuhl, 2013). This pattern differs according to the mode of ectoparasite transmission, with contact-transmitted parasites (e.g. mites or lice) being positively correlated with group size, whereas no correlation is expected for mobile parasites (e.g. biting flies and mosquitoes) due to encounter dilution effects (Patterson and Ruckstuhl, 2013, but see Veiga *et al.*, 2020). Parasites can directly or indirectly affect the reproductive and survival components of individual fitness by decreasing nestling body condition and survival, or by reducing adult fecundity (Brown and Brown, 1986; Merino and Potti, 1995; Arriero and Møller, 2008; Hoi *et al.*, 2018). This may consequently impact avian population dynamics, for example by decreasing breeding-site fidelity and foster both the formation and extinction of colonies (Brown and Brown, 2004; Calabuig *et al.*, 2010; Brown *et al.*, 2017; Sanz-Aguilar *et al.*, 2020). Group living may also result in increased physiological social stress due to increased competition for resources, which synergizes with host susceptibility to parasite infestation (Beldomenico and Begon, 2010; Kappeler *et al.*, 2015). However, most studies assessing the relationship between parasitism and colonial breeding targeted monospecific colonies or the interaction between a single host and a single parasite species, overlooking the likely interactions among different hosts, or different parasites within the same host – the parasite infracommunity (Bush *et al.*, 1997; Holt *et al.*, 2003; Poulin, 2007; but see Whiteman and Parker, 2004; Veiga and Valera, 2020). In fact, bird colonies are often composed of different species, resulting in mixed-species colonies, that reshape the structure and functioning of communities through the increased interaction between the grouping species (Gaglio *et al.*, 2018; Catry and Catry, 2019). The formation of mixed-species colonies may allow species to acquire the benefits of group living while reducing the costs associated with intraspecific competition (Møller *et al.*, 1993; Campobello *et al.*, 2012), although multi-species associations may also result in costs through factors such as kleptoparasitism or interspecific competition (Gaglio *et al.*, 2018; Catry and Catry, 2019).

In multi-species assemblages, intra- and interspecific social contacts likely increase and complexify the interactions between different host and parasite species (Valera *et al.*, 2003;

Keesing *et al.*, 2006). High host diversity could decrease infestation risk through dilution effects, as different host species may be differently susceptible and/or competent to different parasite species, but this effect may not always occur and likely depends on specific community compositions (Keesing *et al.*, 2006; Randolph and Dobson, 2012; Civitello *et al.*, 2015; Halsey, 2018; Martin *et al.*, 2019). Mixed-species assemblages may also promote interspecific parasite exchange, especially within generalist parasite species. Whether the occurrence of several host species in bird assemblages increases or decreases the prevalence and abundance of parasites and their relationship with colony size or density remains poorly studied (Tella *et al.*, 1998; Valera *et al.*, 2003; Veiga *et al.*, 2020).

Study of the ecological relationship between parasites in mixed-species colonies may be harder than in mono-specific groups due to the complexity of addressing several species and their interactions, with the solution often being to simplify the system into one–one actors. In this study, we investigate host–parasite relationships in mixed-species colonies, by considering several host and parasite species and by simultaneously looking at several colony traits that may influence the prevalence and abundance of ectoparasites. In southwestern Iberia, colonial lesser kestrels *Falco naumanni* breed in man-made structures that attract other species, including common kestrels *Falco tinnunculus*, European rollers *Coracias garrulus*, barn owls *Tyto alba*, little owls *Athene noctua*, jackdaws *Corvus monedula*, spotless starlings *Sturnus unicolor* and feral pigeons *Columba livia*; thus forming mixed-species colonies (Catry and Catry, 2019). These multi-species assemblages provide an ideal opportunity to understand the ecological relationships between multiple host and parasite species (Valera *et al.*, 2003). Here, we study how colony traits such as colony size, host species richness, density, and composition, influence the ectoparasite infracommunities. Specifically, we aim to: (1) describe the ectoparasite infracommunity of different avian host species breeding in mixed-species colonies; (2) determine the main colony traits potentially affecting ectoparasite infracommunity composition and (3) assess how colony traits drive the abundance of *Carnus hemapterus*, a widespread haematophagous fly parasitizing at least 64 host species from 24 avian families (Grimaldi, 1997; Brake, 2011) and the most common ectoparasite in our study area. For this, we study the ectoparasites in nestlings and nests of the four main common bird species in 30 mixed-species colonies.

Materials and methods

Study system: hosts and parasites

This study took place in the Castro Verde Special Protection Area, Southern Portugal (~37°43'N, 7°57'W) (Fig. 1). In the framework of European LIFE projects to recover lesser kestrel populations, more than 800 artificial nests were provided in the study area, including new cavities opened in abandoned rural buildings, artificial cavities in newly built breeding walls and towers with up to 90 cavities, wooden nest-boxes and clay pots (Catry *et al.*, 2009). Given the low availability of nest-sites in the area, nest-site provisioning was very effective at increasing the lesser kestrel population and attracted other bird species to nest in these structures (Catry *et al.*, 2009; Catry and Catry, 2019; Gameiro *et al.*, 2020).

Mixed-species colonies occur in adobe-built abandoned farmhouses (nests located in cavities that appear with building degradation – ‘natural cavities’) or in artificial nest structures. Here, ‘colony’ was defined as a site with at least two active nests – usually a single building, or a main building with few smaller, annex structures (e.g. a farmhouse with a separated shed). Because nests occur inside cavities, the maximum size of the colony is

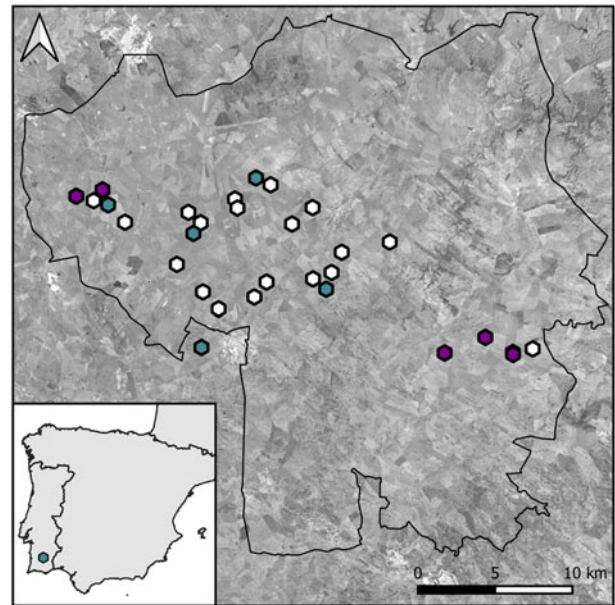


Fig. 1. Location of small (white), medium (light) and large (dark) colonies sampled in this study (See online for the colour version). Boundaries of the Castro Verde Special Protection Area (SPA) shown as a black line.

ultimately dependent on the number of available nest-sites, which can go from just a couple to more than a hundred cavities. Larger colonies (>40 breeding pairs) tend to have higher density of nests and a higher richness of host species and can be dominated by either lesser kestrels or spotless starlings (Table 1). Larger colonies usually also hold a few pairs of jackdaws and feral pigeons, one to four common kestrels and European rollers and one pair of barn owl and/or little owl (Catry and Catry, 2019). Distance to nearest colony was always greater than 100 m (min = 150 m, max = 4266 m).

This study focused on the four most common bird species in these mixed-species colonies: lesser kestrels, European rollers (hereafter rollers), spotless starlings (hereafter starlings) and feral pigeons (hereafter pigeons). Lesser kestrels and rollers are single-brooded, secondary cavity nesting birds with a trans-Saharan migration (Catry *et al.*, 2015). Lesser kestrels are typically colonial, with colonies reaching up to 80 breeding pairs in the study area (Catry *et al.*, 2009). They arrive at the breeding grounds in early February and typically lay four to five eggs in April–May. Nestlings are born with a down feather coat after a 28 days incubation and usually fledge at 36 days (Catry *et al.*, 2015). Rollers (up to four breeding pairs) are usually found breeding in lesser kestrel colonies but can also nest in isolated nests in farmhouses or in nest-boxes placed on trees or telephone poles. Egg laying is asynchronous with three to six eggs laid in May–June. Nestlings are born featherless after 17–19 days of incubation and fledge at 20–25 days (Catry *et al.*, 2015).

Starlings and pigeons are resident in the study area and lay several clutches along the breeding season. Starlings generally nest at high densities, with up to 32 breeding pairs in these mixed-species colonies (Table 1). Starlings lay three to six eggs, incubation takes ca. 12 days and nestlings fledge at 20–22 days old (Muriel *et al.*, 2013). Pigeons occur at lower densities, with up to eight breeding pairs in these colonies (Table 1). They lay up to two eggs, incubation lasts around 18 days and nestlings fledge at ca. 28 days old (Johnston and Janiga, 1995). Contrary to lesser kestrel and roller nests, which are usually just comprised of dirt and prey remains, starlings and pigeons build their nest with sticks, straws and other vegetable material, and pigeons also accumulate droppings inside the cavity.

Table 1. Colony traits of small (<20 pairs), medium (21–40 pairs) and large (>40 pairs) mixed-species colonies sampled for ectoparasites

	Small	Medium	Large
Colony host richness ^a	3 (1–5)	4 (4–5)	5 (3–6)
Colony size ^a	6 (2–11)	29 (27–30)	49 (46–62)
Colony density ^a	6.2 (2.0–22.6)	2.6 (0.8–5.6)	0.9 (0.8–4.4)
Colony composition			
Lesser kestrel	4 (0–10)	20 (17–24)	22.5 (8–47)
Roller	1 (0–2)	2 (1–3)	1 (1–3)
Pigeon	0 (0–5)	5 (0–5)	4 (0–8)
Starling	0 (0–1)	3 (0–3)	21.5 (1–32)
Colonies sampled	19	5	6
Nests sampled	56	61	144

Median (min–max) values are shown for host richness, colony size, density (average distance to the three active closest nests) and colony composition (number of active nests).

^aAlso includes other, less abundant host species (common kestrels, jackdaws, little owls and barn owls).

The most common ectoparasites found in hosts' nestlings in our study area were carnid flies (*C. hemapterus*, Diptera: Carnidae), haematophagous mites (Acari: Mesostigmata), louse flies (Diptera: Hippoboscidae) and feather lice (Phthiraptera); and they were considered in this study as four separate groups since: (i) identification at the species level and quantification of each species in each nest and host was not feasible, and (ii) working at the species level falls beyond the scope of this study, i.e. to investigate the influence of colony traits on the general patterns of ectoparasite infestation. Yet, some information about the identified species is provided in the 'Discussion' section.

The generalist *C. hemapterus* (hereafter *Carnus*) is a nidicolous, haematophagous fly infesting many bird taxa. *Carnus* loses its wings after finding a host, with peak infestations occurring during the mid-nestling stage, and with a resistance stage (pupa) that remains in the nest debris until the next breeding season when adult flies emerge (Valera *et al.*, 2006a; Calero-Torralbo and Valera, 2008). Despite being a mobile ectoparasite, it was found to increase with colony size and host density (Hoi *et al.*, 2010; Veiga *et al.*, 2020; but see Liker *et al.*, 2001). Mites are also generalist ectoparasites, feeding mostly on blood or skin tissue of nestlings and adults. Mite populations usually grow quickly in the nest during their host's breeding season and some individuals may overwinter in the nest (Burt *et al.*, 1991). Being contact transmitted parasites, they are expected to increase with colony size (Davis and Brown, 1999). Louse flies are also haematophagous parasites, but imagoes do not lose their wings and can fly between nests, and they have often a more restricted host range (Veiga *et al.*, 2019). Imagoes spend most of their time feeding on the host's body, and pupae are formed and apparently overwinter in the nest (Boyd, 1951). Louse flies are mobile parasites and should not be affected by host coloniality (Poulin, 1991). Feather chewing lice are permanent ectoparasites with a host range usually confined to species within the same family or genus (Clayton *et al.*, 2008). They live on the feathers and seldom leave their host except to transfer among individuals through direct contact (e.g. between parents and their offspring), and thus are likely influenced by host sociality (Clayton and Tompkins, 1995; Rózsa *et al.*, 1996; Whiteman and Parker, 2004; Ortego *et al.*, 2007).

Data collection

Ectoparasite estimation

Fieldwork was conducted during the breeding season of 2018, from mid-April to mid-July, by sampling unclean nests occupied by the four studied host species. Colonies and nests within colonies were randomly sampled during a lesser kestrel and roller monitoring programme. A total of 30 colonies were sampled (Fig. 1): seven with all four hosts; four with lesser kestrels, rollers and starlings; two with lesser kestrels, rollers and pigeons; six with lesser kestrels and rollers; two with lesser kestrels and pigeons; two with rollers and pigeons; five with lesser kestrels and two with rollers (Table 1). Overall, we sampled 261 nests: 141 lesser kestrel, 33 roller, 38 pigeon and 49 starling nests. Nests were not cleaned prior to this study for two reasons: (i) removing old nest detritus was not possible for most of these nests (especially for natural cavities) and (ii) unclean nests provide results that better resemble the natural conditions (Møller, 1989). Soiled nests may influence the prevalence and numbers of some ectoparasites in these colonies and may cause some unaccounted variability in the data, particularly when considering ectoparasites with most of their life cycle, including long diapauses, occurring in the nests (Veiga *et al.*, 2020). Thus, this potential bias was considered in the statistical approach (see 'Data analysis' section) and its influence was discussed.

The presence and number of ectoparasites were assessed by examining all nestlings in each host species nest. Each nest was sampled at two different periods: at mid-nestling stage (around 8–12 days old), and few days before fledging. During each of these two periods, each nestling was taken from its nest and placed in a transparent plastic bag to avoid losing mobile parasites (e.g. louse flies). The nestling was then taken from the bag and the number of carnid flies and louse flies on the bag and on the body surface and sheaths of the nestling were counted twice and then averaged (Roulin, 1998; Václav *et al.*, 2008). Feather lice were sampled by carefully scanning the nestlings' sheaths and feathers (Valera *et al.*, 2003; Ortego *et al.*, 2007). Mites were sampled by resting the observer's hand on the bottom of the nest for 1 min and then the number of mites were counted twice and then averaged. Nestlings were then carefully placed back on the nests. The number of each ectoparasite group was calculated as the sum of parasites in all nestlings from the same brood. The maximum number of parasites from both sampling periods was selected. All study protocols were approved by the relevant Portuguese authorities (Instituto da Conservação da Natureza e das Florestas).

Mixed-species colony traits

The following variables were recorded for each sampled nest: host species identity, type of nest (natural cavities in farmhouses, artificial cavities, clay pots and wooden nest-boxes), brood size (number of nestlings) and the sampling date of the first sampling period, which was used as a proxy for ectoparasite seasonal effects (Calero-Torralbo *et al.*, 2013). The species occupying the focal nest in the previous year was also recorded, as some ectoparasites spend most of their life cycle in the nest and their occurrence and abundance may depend on previous breeding seasons (Valera *et al.*, 2006a). Each nest was also categorized according to four main colony traits: colony host richness (number of host species in the colony); colony size (number of active nests, i.e. nests with nestlings, of all species); colony density (the inverse of the average distance to the three active closest nests, in meters) and colony composition (four variables, each with the number of active nests of each of the four main host species) (Table 1). Colony size was grouped into three categories: small (up to 20 nests), medium (21–40 nests) and large (more than

40 nests) (Fig. 1). Similarly, colony density was grouped into low (average distance to the three closest nests >5 m), medium (1–5 m) and high density (<1 m). All traits (except for colony composition) acknowledged all nesting bird species, including less abundant species (common kestrels, jackdaws, little owls and barn owls).

Data analysis

The nest was used as the sampling unit and thus the term infracommunity refers to the community of ectoparasites in a given nest (see Veiga and Valera, 2020 for a similar approach). Accordingly, the prevalence and mean intensity of each ectoparasite group for each host species was calculated, respectively, as the proportion of infested nests among all nests sampled and the mean number of parasites of all infested nests. Because some nests were not sampled during both periods, prevalence and mean intensity of each parasite were calculated only for nests sampled at each parasite's peak infestation stage (assessed from our own dataset and the literature; see following sentences), so that comparisons could be made between the different hosts (see 'Results' section). *Carnus* infestation peaks at mid-nestling stage (prevalence of 87% and 20% for the first and second sampling periods, respectively; see also Václav *et al.*, 2008), while feather lice and louse flies are more common in fully-grown, feathered nestlings (lice prevalence of 2% and 86%, and louse fly prevalence of 26% and 47% for the first and the second sampling periods, respectively; see also Muñoz *et al.*, 1993). The prevalence of mites did not differ between the two sampling periods in our study (23% and 19% for the first and second sampling periods, respectively). Accordingly, prevalence and mean intensity values of carnid flies were obtained from all nests sampled in the first period, values for lice and louse flies from nests sampled in the second period and values for mites were obtained from all nests (sampled both in the first and/or in the second period).

Fisher's exact tests, and Kruskal–Wallis *H* test followed by bootstrap two-sample *t*-tests, were used for comparing parasite prevalence and mean intensity, respectively, among hosts, using 2000 replications for both estimation of confidence intervals and bootstrap *t*-tests (Rózsa *et al.*, 2000; Veiga *et al.*, 2019).

A principal component analysis was used to explore the potential correlation among the colony variables without constraints (random factors), prior to further analysis (Supplementary Fig. S1) (Borcard *et al.*, 2011; Václav and Valera, 2018). To examine how colony traits influence the ectoparasite infracommunity composition, a partial canonical correspondence analysis (CCA) was used including all sampled nests and conditioned by brood size, sampling date and colony ID (Borcard *et al.*, 2011). The presence–absence matrix of each parasite group in each nest was used as the response variable (nests without parasites were removed; Oksanen, 2020). Host species, nest type, the species using the nest in the previous year, and colony host richness, size, density, and composition, were used as the predictive variables. The variance inflation factor (VIF) was used to assess collinearity between predictive variables (all VIFs <10, min = 1.01, max = 6.61) and forward and backward selections were performed to choose the best CCA model (Borcard *et al.*, 2011; Václav and Valera, 2018).

To assess how colony traits (richness, size, density, and composition) influence the abundance (i.e. including both infested and non-infested nests) of *Carnus*, the most common ectoparasite in our mixed-species colonies, a generalized linear mixed model (GLMM) was used. The model followed a negative binomial distribution of errors to account for the aggregated distribution

of *Carnus* among hosts (Václav and Valera, 2018). *Carnus* abundance in each nest was used as the response variable and colony ID as a random variable. The sample-to-variable ratio and the high correlation between some colony traits did not allow the inclusion of all variables in a single model (Supplementary Fig. S1). Because colony size, density and host richness were correlated, the number of variables were reduced by choosing the most meaningful traits. Colony size was removed in favour of colony density because the latter reports about the nest density around each focal nest, whereas colony size attributes the same value to all nests within the same colony. Colony composition was selected instead of colony host richness because it contains information about the identity of the host and its abundance, rather than just the number of species found in a given colony. However, because the abundance of pigeons and rollers was considerably lower than the one of lesser kestrels and starlings, and both were correlated with the number of starling nests (Supplementary Fig. S1), colony composition was restricted to the number of nests of the most abundant hosts, i.e. lesser kestrels and starlings. Nonetheless, different combinations of variables were tested, which also included the host species using the nest in the previous year, but did not provide additional or different outputs. The results shown here refer to the most biologically meaningful model, that includes the following, non-correlated, explanatory variables: host species, brood size, sampling date, type of nest, colony density (categorical), number of lesser kestrel nests and number of starling nests (highest VIF = 5.07, for type of nest). A model-averaging approach based on the Akaike information criterion (AIC) was used to obtain weighted average estimates for fixed parameters (Grueber *et al.*, 2011). Model averaging was performed on models with the cumulative sum of corrected AIC (AICc) weights >0.95.

All continuous explanatory variables were scaled and centred prior to analysis. All analyses were conducted with R software 3.6.1 (R Core Team, 2016), using the packages Vegan 2.5-6 (Oksanen, 2020), nlme 3.1-148 (Pinheiro *et al.*, 2020), lme4 1.1-23 (Bates *et al.*, 2020) and MuMIn 1.43.17 (Bartón, 2020).

Results

Prevalence and intensity of ectoparasites in mixed-species colonies

The composition of the infracommunity of ectoparasites differed among the various host species breeding in mixed-species colonies: lesser kestrels and pigeons had all four types of ectoparasites whereas starlings had no louse flies and rollers had no lice and almost no louse flies (Table 2).

Carnus was the most common ectoparasite in mixed-species colonies but its prevalence differed among the four host species (Fisher test: $P < 0.001$), being highest in lesser kestrels and rollers and lowest in pigeons. *Carnus* mean intensity was more than double in rollers than in lesser kestrels (bootstrap two-sample *t*-test: $t = 4.22$; D.F. = 29.65, $P < 0.001$) and lowest in pigeons (Table 2). Mites were the second most common ectoparasite in mixed-species colonies, reaching the lowest prevalence and intensity in lesser kestrels (Table 2). Rollers, pigeons and starlings had similar mite prevalence and intensity (prevalence; Fisher test: $P = 0.97$ intensity; Kruskal–Wallis *H*: 1.11, D.F. = 2, $P = 0.57$). Lice were almost exclusively found in lesser kestrels and pigeons, with similar prevalence and intensity (prevalence; Fisher test: $P = 1.00$; intensity; bootstrap two-sample *t*-test: $t = -1.45$, D.F. = 22.65, $P = 0.160$) and louse flies were mostly found in pigeon nests (Table 2).

Table 2. Prevalence (percentage of infested nests) and mean intensity (mean number of parasites found in infested nests) of ectoparasites found on nests of mixed-species colonies in southern Portugal (with 95% confidence intervals in round brackets and number of infested nests/number of sampled nests in square brackets).

Parasite		Roller	Lesser kestrel	Pigeon	Starling
Carnid fly	Prevalence	100% (87.7–100) [28/28]	97.7% (93.5–99.5) [129/132]	41.9% (24.5–60.9) [13/31]	76.9% (60.7–88.9) [30/39]
	Mean intensity	58.3 (40.1–75.8)	21.4 (17.7–25.2)	2.9 (1.3–4.6)	5.6 (3.9–7.3)
Louse fly	Prevalence	3.0% (0–15.8) [1/33]	2.6% (0.5–7.4) [3/116]	47.4% (24.4–71.1) [9/19]	0.0% (0.0–21.8) [0 /15]
	Mean intensity	1*	1 (1–1)	1.8 (1.1–2.4)	0
Lice	Prevalence	0.0% (0–10.6) [0/33]	84.5% (76.6–90.5) [98/116]	94.7% (74.0–99.9) [18/19]	6.7% (0.0–31.9) [1/15]
	Mean intensity	0	24.3 (17.4–31.1)	37.9 (19.5–56.3)	1*
Mite	Prevalence	33.3% (18.0–51.8) [11/33]	15.6% (10.0–22.7) [22/141]	31.6% (17.5–48.7) [12/38]	30.6% (18.3–45.4) [15/49]
	Mean intensity	18 (0–39.9)	5.0 (1.4–8.6)	18.3 (4.2–32.3)	19.1 (9.4–28.7)

Influence of colony traits on ectoparasite infracommunity in mixed-species colonies

The partial CCA, conditioned by sampling date, brood size and colony ID, revealed that host species was the only predictor of parasite infracommunity (presence/absence), being the only variable selected following both forward and backward selection processes (final CCA adjusted $R^2 = 0.18$; $\chi^2 = 0.2$, $F = 18.2$, P value = 0.001). Conditioned and constrained partitioning explained 27.0% and 16.7% of the total inertia, respectively ('variance', total inertia = 1.11). The ectoparasite infracommunity of each host species was best described by the presence of louse flies, followed by lice and mites (Fig. 2). Louse flies were clearly associated with pigeons and lice commonly infested pigeons and lesser kestrels. Mites showed a positive association with starlings, rollers and pigeons, whereas *Carnus* was negatively associated with pigeons (see also Table 2).

Influence of colony traits on *C. haemapterus* abundance in mixed-species colonies

Host species had a significant influence on *Carnus* abundance, being highest in rollers and followed by lesser kestrels, starlings and pigeons (the reference level) (Table 3). Model averaging revealed that *Carnus* abundance increased significantly with brood size and marginally significantly with increasing numbers of lesser kestrel nests in the colony. In contrast, it decreased significantly with increasing numbers of starlings' nests. The abundance of carnid flies also decreased, although marginally significantly, in clay pots when compared to other types of nests. Colony density had no influence on *Carnus* abundance. The models with $\Delta AICc < 2$ after model averaging and the best two models can be found in Tables S1 and S2, respectively, in the Supplementary material.

Discussion

This study provides information on the ecology of avian parasitism in mixed-species colonies. To our knowledge, there is little information on the factors influencing host infestation by ectoparasites in colonies formed by multiple species of hosts and even less at the parasite infracommunity level. Four main ectoparasite groups – carnid flies, louse flies, lice, and mites – in four different host species were analysed, including the conservation reliant lesser kestrel and European roller (Gameiro *et al.*, 2020). It was found that the main driver for the differences in composition of

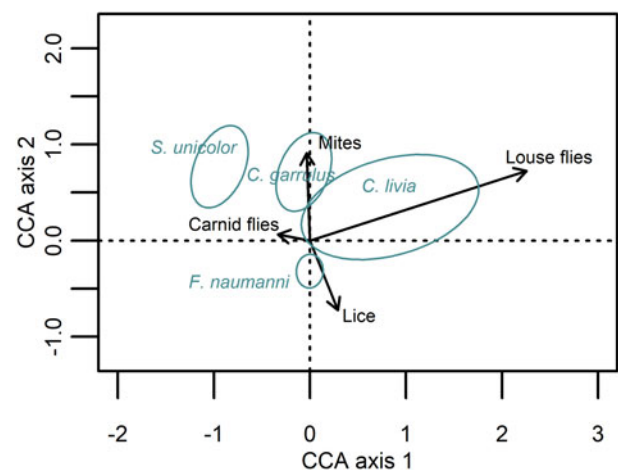


Fig. 2. Biplot (scaling 3) of the partial CCA showing the relationship between the occurrence of ectoparasites and host species, the only explanatory variable selected after forward and backward selections. Statistics: CCA1: $\chi^2 = 0.10$, $F = 29.0$, P value = 0.001; CCA2: $\chi^2 = 0.08$, $F = 24.9$, P value = 0.001. Sample size = 240 nests (139 lesser kestrels, 29 rollers, 33 pigeons, 39 starlings).

the ectoparasite infracommunity was the identity of the host species, regardless of colony traits such as size, density or richness. Accordingly, variation in the abundance of the most common ectoparasite (*Carnus*) in these mixed-species assemblages was explained by colony composition (number of nests of each host species), rather than by overall colony size or density.

Ectoparasite infracommunity in birds breeding in mixed-species colonies

The importance of host species identity for ectoparasite ecology has already been described in small mammals (Krasnov *et al.*, 2008; Lareschi and Krasnov, 2010). These results suggest that the four host species vary in their susceptibility (*sensu* Martin *et al.*, 2019) to different ectoparasite groups (Keesing *et al.*, 2006). Even the prevalence and intensity of *Carnus*, the most common and broadly considered generalist species (Veiga *et al.*, 2019), varied considerably between hosts. Nest- and host-related characteristics may account for some of the differences found, as suggested by our results on *Carnus*. Pigeons and starlings were the least attractive hosts. These bird species use vegetable material when building their nests, which was found to be avoided by *Carnus* (Valera *et al.*, 2006b, 2018). Pigeons also accumulate

Table 3. Results of model averaging on the effect of colony traits on *Carnus hemapterus* abundance in mixed-species colonies using nests from all four host species (lesser kestrels, rollers, pigeons, and starlings). Variables with a significant effect (P value < 0.05) are given in bold.

Parameter	Estimate	Adjusted s.e.	Z value	P value	Relative importance
Intercept	0.725	0.310	2.342	0.019	
N lesser kestrel nests	0.137	0.077	1.777	0.076	0.63
N starling nests	-0.200	0.089	2.237	0.025	0.74
Brood size	0.274	0.091	3.023	0.003	0.99
Host: roller	3.117	0.380	8.204	0.000	1.00
Host: lesser kestrel	2.185	0.316	6.921	0.000	
Host: starling	0.917	0.313	2.930	0.003	
Sampling date	-0.006	0.092	0.066	0.947	0.24
Artificial cavities	-0.128	0.268	0.477	0.633	0.19
Clay pots	-0.612	0.332	1.843	0.065	
Wooden nest-boxes	-0.177	0.265	0.667	0.505	
Medium density	-0.114	0.213	0.534	0.593	0.11
High density	-0.141	0.276	0.512	0.609	

Entry model: *Carnus* abundance ~ host species + brood size + sampling date + nest type + colony density (Cat) + number of lesser kestrel nests + number of starling nests + (1|colony ID); sample size = 230 nests (132 lesser kestrels, 28 rollers, 31 pigeons, 39 starlings). Values reported are conditional averages and adjusted s.e. *Carnus* abundance was studied using GLMMs following a negative binomial distribution of errors to account for its aggregated distribution among hosts. Colony ID was used as random factors. N, number of; Cat, categorical; ID, identity.

droppings inside the cavity that may limit the suitability of the detritus for the larval and pupal stages of this ectoparasite (Veiga *et al.*, 2019). Carnid flies seemingly also prefer rollers to lesser kestrels since the former bird species holds more than twice as many *Carnus* as lesser kestrels. Nestling kestrels are born with a down feather coat that may hinder the access to blood by ectoparasites, when compared to the naked body of roller nestlings.

Mites also infested all host species but were less prevalent and abundant on lesser kestrels. In a dry climate like the one in the study area, the humidity required by mites (Nordenfors *et al.*, 1999) may be secured by the vegetable material used in starling or pigeon nests, when compared to a mostly sandy substratum of lesser kestrel or roller nests. However, as rollers arrive later to the breeding grounds from their spring migration, they are likely to re-use a nest previously occupied by starlings or pigeons (hence more humid), potentially explaining why rollers had higher prevalence of mites compared to lesser kestrels (see below and Veiga *et al.*, 2020).

The factors accounting for differences in the prevalence of lice and louse flies among host species are not so clear and their identification goes beyond the aims of our study. Nonetheless, it is worth reporting such differences in mixed colonies where the contact among species and individuals can facilitate transmission. Lice were mostly present on lesser kestrels and pigeons, with just a single louse found on one starling nestling and none on rollers. Although lice were not identified at the species level, these ectoparasites are considered species-specific and no studies were found reporting the same lice species infecting both pigeons and lesser kestrels (Rózsa, 1990; Ortego *et al.*, 2007; Calabuig *et al.*, 2010; Galloway and Lamb, 2015). Factors such as gregariousness can explain why species such as pigeons or lesser kestrels have many lice. In contrast, species usually breeding in low densities (e.g. rollers) could be less appropriate for lice. Because chewing lice are mostly found on feathers, they may be more common and abundant on post-fledging juveniles or adults, when compared to young nestlings (Liker *et al.*, 2001; Ortego *et al.*, 2007). Regarding louse flies, these were found almost exclusively on pigeons, with only three lesser kestrel and one roller nest infested

and no starling nest infested. Examination of six louse flies demonstrates that at least three different species occur in our study area: *Pseudolynchia canariensis* in pigeons and lesser kestrels, *Ornithophila gestroi* in lesser kestrels and *Hippobosca longipennis* in rollers. *Pseudolynchia canariensis* has a wide host range and is common in pigeons and in the *Falco* genus (Maa, 1966), although to the authors' knowledge this the first time *P. canariensis* has been reported in lesser kestrels. *Ornithophila gestroi* has already been reported in lesser kestrels, with similar abundances but at higher prevalence than the one found in this study (Tella *et al.*, 1997). *Hippobosca longipennis* is an ectoparasite typically found in carnivores (Maa, 1969; Mihalca *et al.*, 2019). Besides anecdotal references, there are no clear reports of *H. longipennis* on birds, so that this finding can be also considered circumstantial. Yet, the clear pattern found (preference of louse flies for pigeons) could be explained either by a higher abundance of the louse fly species typical of this particular host and/or interspecific differences in the suitability of each host species and their nests characteristics for the co-existing louse fly species (e.g. Veiga *et al.*, 2019). Understanding the pattern of occurrence of these parasites and what factors contribute to the interspecific differences found here requires detailed knowledge of the natural history and host choice criteria of these species and goes beyond the aims of this study. Nonetheless, it is important to remark that even in situations favouring intra- and interspecific parasite transmission, clear preference patterns are evident.

Ectoparasite abundance in mixed-species colonies is mostly driven by colony composition rather than colony size or density

It has been widely acknowledged that social breeding incurs in higher risk of parasite and pathogen transmission, with larger, denser colonies, having higher prevalence and intensity of ectoparasites, even in mobile, non-contact-transmitted species (Brown and Brown, 1986; Côté and Poulin, 1995; Hoi *et al.*, 1998; Kleindorfer and Dudaniec, 2009; Veiga *et al.*, 2020). Most of these studies have focused on mono-specific colonies or on single parasite species, overlooking the complex multi-species

associations that often occur in nature (Valera *et al.*, 2003). The results of this study on mixed-species colonies suggest that colony size, density or richness, common characteristics used to measure host sociality, do not affect the infracommunity of ectoparasites in each host, or the abundance of the generalist *Carnus*. Although the correlation among these variables prevented the identification of the isolated effect of each trait, none were selected using a model-averaging approach, suggesting a lack or weak effect of these variables in our study system. Instead, host species was the main predictor for *Carnus* abundance. Besides colony composition, which will be discussed below, *Carnus* abundance was found to increase with brood size. More nestlings in a nest translates to more food resources for ectoparasites and higher heat and CO₂ emissions that may facilitate nest detection. Thus, an increase in *Carnus* abundance with larger broods was expected (see also Veiga *et al.*, 2020). In contrast to previous results (Calero-Torrallbo *et al.*, 2013; Veiga *et al.*, 2020), the abundance of *Carnus* was not influenced by sampling date – a proxy of *Carnus* emergence patterns. But, contrary to these studies, the results reported here consider simultaneously different host species, so the lack of a global effect of date may be related to merging host species with different breeding phenologies, number of clutches and nestling development rates. There was also no influence of type of nest except for a marginally significant decrease in clay pots. Clay pots are shallower than cavities or nest-boxes, and some of them have low (sometimes almost inexistent) amounts of detritus, which may inhibit egg deposition or larvae development by *Carnus*.

The main finding of this study is that in mixed-species assemblages, rather than colony size or density, it is the composition of the colony – the number of nests of the various host species – that influences the abundance of the most common ectoparasite. *Carnus* abundance decreased with increasing number of starling nests and increased with increasing numbers of lesser kestrels. Because *Carnus* mean intensity varied considerably between hosts, with lesser kestrels hosting more than three times more *Carnus* than starlings, starling-dominated colonies will have lower *Carnus* loads than lesser kestrel dominated ones. If the proportion of less competent hosts such as starlings increases in a mixed colony, then the total amount of ectoparasites will decrease. A dilution effect is occurring by ‘adding’ less competent host species, starlings (or pigeons), to the colony (Johnson and Thielges, 2010; Civitello *et al.*, 2015). Because most *Carnus*’ life stages occur in the nest (Valera *et al.*, 2006a), *Carnus* will produce less offspring in a colony dominated by less suitable hosts than in a colony with more suitable hosts. In parallel, the number of *Carnus* will increase in colonies with increasing number of preferred hosts such as lesser kestrels and rollers. This suggests that increasing colony diversity would only result in a dilution effect – decreasing parasitism – if the added host species are less suitable for a given parasite. For instance, pigeons are avoided by *Carnus* but are preferred by *P. canariensis* (Veiga *et al.*, 2019), so having pigeons in colonies may decrease *Carnus* abundance but increase *P. canariensis* in lesser kestrel nests.

The findings of this study must be considered in light of some limitations. Colony size, density, and host richness were correlated so that larger colonies also tended to have higher nest density and higher richness of hosts. This prevented the investigation of the effect of each colony trait, only allowing the comparison between smaller colonies (less dense and less rich) from larger ones (denser and richer). Increasing the sample size (which was not possible for this study due to logistics constraints) could potentially allow for the investigation of the correlation/interaction between colony traits and reveal other effects the authors were unable to detect. However, because large colonies had different host species composition – some dominated by lesser kestrels

and others by starlings – this study was able to untwine the effects of colony composition on ectoparasite infestation patterns. Also, as opposed to similar studies (Veiga *et al.*, 2019), nests in this study were not sanitized before sampling. As such, ectoparasites that spend most of their life cycle in the nest, such as carnid flies, were not removed, and so the prevalence and abundance (and their variability) found in this study may have been at least partially influenced by the outcome of previous breeding seasons (Valera *et al.*, 2006a). Nonetheless, results from this study suggest that the host species occupying the focal nest in the previous year had no effect (variable not selected) on the ectoparasite infracommunity or on *Carnus* abundance. The influence of the abundance of ectoparasites during the previous season may be diluted for several reasons. For instance, *C. hemapterus* – arguably the most nest-based ectoparasite from the ones addressed – was found to rapidly colonize new (and clean) nests and to discriminate between potential hosts, favouring some of them (Veiga *et al.*, 2019, 2020). Moreover, insect predation after the breeding season may decrease the abundance of carnid pupae (Salido *et al.*, 2021). These facts suggest that our approach may have had little impact on the results found for mobile ectoparasites (carnid flies and louse flies) and for parasites spending all their life cycle on the host’s body (e.g. lice). On the other hand, by examining uncleaned nests, this study reflects more closely the natural conditions than studies using sanitized nests, and thus our results are likely to apply to birds breeding in natural assemblages (Møller, 1989). Finally, this study examines ectoparasite groups instead of individual species. This limits our capacity to establish species-specific parasite–host relationships, but it does not preclude disentangling the effects of colony traits on the general patterns of ectoparasite infestations.

Final considerations

Previous studies on monospecific colonies have found a positive correlation between colony size and density and *C. hemapterus* infestations (Hoi *et al.*, 1998, 2010; Veiga *et al.*, 2020, but see Liker *et al.*, 2001). The current study in mixed-species colonies revealed that colony traits such as size, density, richness, or composition, had no effect on ectoparasite presence, with each avian host maintaining a distinct ectoparasite infracommunity. It also revealed that colony composition, rather than colony size or density, influenced the infestation of the most common ectoparasite in these assemblages. *Carnus* can be found from North America to Europe and Asia infesting a wide range of bird species, so the implications of this study go beyond our study area (Grimaldi, 1997; Brake, 2011; Ganbold *et al.*, 2020). The association between farmland buildings or artificial nests and secondary cavity nesters such as lesser kestrels and rollers is common in other European counties, such as Spain and Italy (Campobello *et al.*, 2012; Negro *et al.*, 2020). Similar natural species assemblages occur in sandstone cliffs and bridges (e.g. in south Spain), where many species, including the ones studied here (and others such as common kestrels, little owls, jackdaws, bee-eaters *Merops apiaster* and rock sparrows *Petronia petronia*) coexist and re-use the same natural and man-made cavities (Valera *et al.*, 2003; Veiga *et al.*, 2020). Lesser kestrel colonies throughout Europe that rely on man-made buildings are also likely comprised of other species (Blanco and Tella, 1997; Campobello *et al.*, 2012). Densities in these ‘natural scenarios’ are likely lower than those in artificial breeding towers, but it may depend on ecological circumstances such as availability of nest-sites. Our results that larger colonies do not necessarily translate into higher risk of ectoparasite transmission, and that this effect is influenced by the species composition of the colonies, are likely applicable to other mixed-species colonies of birds or even other non-bird mixed-species groups

(Goodale *et al.*, 2020). Yet, the exact outcome may vary depending on the specific parasites and hosts forming the assemblages. The interpretation of the ecological relationships between parasites and hosts should consider the interactions occurring among different hosts and their parasites and should be studied as they occur in nature, i.e. considering mixed-species assemblages, which are often overlooked despite being widespread. More studies on the natural history of ectoparasites and on host–parasite interactions in multi-species group living are clearly needed to fully understand the complex relationships between parasites and sociality.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182021000470>.

Acknowledgements. We would like to thank Liga para a Proteção da Natureza (LPN) for providing access to the colonies within the Castro Verde Special Protection Area, and to Instituto da Conservação da Natureza e Florestas (ICNF) for giving us the permission to sample birds' nests. We thank all contributors who helped during fieldwork and data collection. We would also like to thank the editor Helene Carabin and three anonymous reviewers for their valuable suggestions, which have greatly improved this manuscript.

Author contribution. All authors were responsible for conceiving and designing the study. J. G. and I. C. conducted data collection. J. G. and J. V. performed statistical analyses. J. G. wrote the manuscript. All authors reviewed and contributed to the final paper.

Financial support. This study was supported by cE3c (UIBD/00329/2020) and InBIO (UID/BIA/50027/2013), to FCT through national funds. I. C. was supported by a contract DL57/2016/CP1440/CT0023 and J. G. by a doctoral grant (PD/BD/128366/2017) from the Portuguese Foundation for Science and Technology (FCT). F. V. received financial support from the project PGC2018-097426-B-C22 (MCIU/AEI/FEDER, UE). J. V. was funded by a predoctoral grant (BES-2015-075951) of the Spanish Ministry of Economy, Industry and Competitiveness. The funding sources had no direct involvement in the study design or in the collection, analysis and interpretation of data.

Conflict of interest. The authors declare there are no conflicts of interest.

Ethical standards. Trapping and handling of birds during this study was approved by Instituto da Conservação da Natureza e Florestas (License 547/2018/CAPT).

References

- Arriero E and Møller AP (2008) Host ecology and life-history traits associated with blood parasite species richness in birds. *Journal of Evolutionary Biology* **21**, 1504–1513.
- Bartón K (2020) MuMIn: multi-model inference. Available at <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Scheipl F, Grothendieck G, Green P, Fox J, Bauer A and Krivitsky P (2020) lme4: linear mixed-effects models using 'Eigen' and S4. Available at <https://cran.r-project.org/web/packages/lme4/index.html>.
- Beldomenico PM and Begon M (2010) Disease spread, susceptibility and infection intensity: vicious circles? *Trends in Ecology and Evolution* **25**, 21–27.
- Blanco G and Tella JL (1997) Protective association and breeding advantages of coughs nesting in lesser kestrel colonies. *Animal Behaviour* **54**, 335–342.
- Borcard D, Gillet F and Legendre P (2011) *Numerical Ecology with R*. New York, USA: Springer Science and Business Media.
- Boyd E (1951) The external parasites of birds: a review. *Wilson Bulletin* **63**, 363–369.
- Brake I (2011) World catalog of the family Carnidae (Diptera, Schizophora). *Myia* **12**, 113–169.
- Brown CR and Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology* **67**, 1206–1218.
- Brown CR and Brown MB (2004) Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behavioural Ecology and Sociobiology* **56**, 498–511.
- Brown C, Roche EA and Brown MB (2017) Why come back home? Breeding-site fidelity varies with group size and parasite load in a colonial bird. *Animal Behaviour* **132**, 167–180.
- Burt EH, Chow W and Babbit GA (1991) Occurrence and demography of mites of tree swallow, house wren and eastern bluebird nests. In Loye JE and Zuk M (eds), *Bird-Parasite Interactions: Ecology, Evolution and Behaviour*. Oxford, UK: Oxford University Press, pp. 104–122.
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Calabuig G, Ortego J, Cordero PJ and Aparicio JM (2010) Colony foundation in the lesser kestrel: patterns and consequences of the occupation of empty habitat patches. *Animal Behaviour* **80**, 975–982.
- Calero-Torralbo MA and Valera F (2008) Synchronization of host-parasite cycles by means of diapause: host influence and parasite response to involuntary host shifting. *Parasitology* **135**, 1343–1352.
- Calero-Torralbo MA, Václav R and Valera F (2013) Intra-specific variability in life-cycle synchronization of an ectoparasitic fly to its avian host. *Oikos* **122**, 274–284.
- Campobello D, Sarà M and Hare JF (2012) Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. *Behavioural Ecology* **23**, 425–433.
- Catry T and Catry I (2019) Nest-site provisioning re-shapes species interactions within bird assemblages. *Ibis* **161**, 699–704.
- Catry I, Alcazar R, Franco AMA and Sutherland W (2009) Identifying the effectiveness and constraints of conservation interventions: a case study of the endangered lesser kestrel. *Biological Conservation* **142**, 2782–2791.
- Catry I, Catry T, Patto P, Franco AMA and Moreira F (2015) Differential heat tolerance in nestlings suggest sympatric species may face different climate change risks. *Climate Research* **66**, 13–24.
- Civitello DH, Choen J, Fatima H, Halstead NT, Liriano J, McMahon TA, Ortega CN, Sauer EL, Sehgal T, Young S and Rohr JR (2015) Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 8667–8671.
- Clayton DH and Tompkins DM (1995) Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). *Parasitology* **110**, 195–206.
- Clayton DH, Adams RJ and Bush SE (2008) Phthiraptera, the chewing lice. In Atkinson CT, Thomas NJ and Hunter DB (eds), *Parasitic Diseases of Wild Birds*. Iowa, USA: Wiley-Blackwell, pp. 515–526.
- Côté IM and Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. *Behavioural Ecology* **6**, 159–165.
- Davis JA and Brown CR (1999) Costs of coloniality and the effect of colony size on reproductive success in purple martins. *The Condor* **101**, 737–745.
- Gaglio D, Sherley RB, Cook TR, Ryan PG and Flower T (2018) The costs of kleptoparasitism: a study of mixed-species seabird breeding colonies. *Behavioural Ecology* **29**, 939–947.
- Galloway TD and Lamb RJ (2015) Seasonal population dynamics of four species of chewing lice (Phthiraptera: Menoponidae, Philopteridae) on feral pigeons (Aves: Columbiformes: Columbidae). *Canadian Entomologist* **147**, 712–722.
- Gameiro J, Franco AMA, Catry T, Palmeirim JM and Catry I (2020) Long-term persistence of conservation-reliant species: challenges and opportunities. *Biological Conservation* **243**, 1–10. <https://doi.org/10.1016/j.biocon.2020.108452>.
- Ganbold O, Azua J, Munkhbayar M, Khuderchuluun O, Paek WK, Purevee E, Chuluunbat S and Reading RP (2020) First records of the parasitic flies *Carnus hemapterus* and *Ornithophilina gestroi* on lesser kestrels (*Falco naumanni*) in Mongolia. *Journal of Raptor Research* **54**, 66–73.
- Goodale E, Sridhar H, Sieving KE, Bangal P, Colorado Z GJ, Farine DR, Heymann EW, Jones HH, Krams I, Martínez AE, Montaña-Centelles F, Muñoz J, Srinivasan U, Theo A and Shanker K (2020) Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews* **95**, 889–910.
- Grimaldi DA (1997) *The Bird Flies, Genus Carnus: Species Revision, Generic Relationships, and a fossil Meoneura in amber (Diptera, Carnidae)*. American Novitates. New York, USA: American Museum of Natural History.
- Grueber CE, Nakagawa S, Laws RJ and Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* **24**, 699–711.
- Halsey S (2018) Defuse the dilution effect debate. *Nature Ecology & Evolution* **3**, 145–146. <https://doi.org/10.1038/s41559-018-0764-3>.

- Hoi H, Darolová A, König C and Křištofik J (1998) The relation between colony size, breeding density and ectoparasite loads of adult European bee-eaters (*Merops apiaster*). *Ecoscience* 5, 156–163.
- Hoi H, Křištofik J, Darolová A and Hoi C (2010) Are parasite intensity and related costs of the milichiid fly *Carnus hemapterus* related to host sociality? *Journal of Ornithology* 151, 907–913.
- Hoi H, Darolová A, Křištofik J and Hoi C (2018) The effect of the ectoparasite *Carnus hemapterus* on immune defence, condition and health of nestling European bee-eaters. *Journal of Ornithology* 159, 291–302.
- Holt RD, Dobson AP, Begon M, Bowers RG and Schaub EM (2003) Parasite establishment in host communities. *Ecology Letters* 6, 837–842.
- Johnson PTJ and Thielges DW (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *Journal of Experimental Biology* 213, 961–970.
- Johnston R and Janiga M (1995) *Feral Pigeons*. New York, USA: Oxford University Press.
- Kappeler PM, Cremer S and Nunn CL (2015) Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. *Philosophical Transactions B* 370, 1–10. <https://doi.org/10.1098/rstb.2014.0116>.
- Keesing F, Holt RD and Ostfeld RS (2006) Effects of species diversity on disease risk. *Ecology Letters* 9, 485–498.
- Kleindorfer S and Dudanic RY (2009) Love thy neighbour? Social nesting pattern, host mass and nest size affect ectoparasite intensity in Darwin's tree finches. *Behavioral Ecology and Sociobiology* 63, 731–739.
- Krasnov BR, Korralo-Vinarskaya NP, Vinarski MV, Shenbrot GI, Mouillot D and Poulin R (2008) Searching for general patterns in parasite ecology: host identity versus environmental influence on gamasid mite assemblages in small mammals. *Parasitology* 135, 229–242.
- Lareschi M and Krasnov BR (2010) Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. *Medical and Veterinary Entomology* 24, 284–292.
- Liker A, Márkus M, Vozár A, Zemankovics E and Rózsa L (2001) Distribution of *Carnus hemapterus* in a starling colony. *Canadian Journal of Zoology* 79, 574–580.
- Maa TC (1966) On the genus *Pseudolynchia* Bequart. *Pacific Insects Monograph* 10, 125–138.
- Maa TC (1969) A revised checklist and concise host index of Hippoboscidae (Diptera). *Pacific Insects Monograph* 20, 261–299.
- Martin LB, Addison B, Bean AGD, Buchanan KL, Crino OL, Eastwood JR, Flies AS, Hamede R, Hill GE, Klaassen M, Koch RE, Martens JM, Napolitano C, Narayan EJ, Peacock L, Peel AJ, Peters A, Raven N, Risely A, Roast MJ, Rollins LA, Ruiz-Aravena M, Selechnik D, Stokes HS, Ujvari B and Grogan LF (2019) Extreme competence: keystone hosts of infections. *Trends in Ecology and Evolution* 34, 303–314.
- Merino S and Potti J (1995) Mites and blowflies decrease growth and survival in nestling pied flycatchers. *Oikos* 73, 95–103.
- Mihalca AD, Păstrav IR, Sándor AD, Deak G, Gherman CM, Sarmași A and Votýpka J (2019) First report of the dog louse fly *Hippobosca longipennis* in Romania. *Medical and Veterinary Entomology* 33, 530–535.
- Møller AP (1989) Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos* 56, 421–423.
- Møller AP, Dufva R and Allander K (1993) Parasites and the evolution of host social behaviour. *Advances in the Study of Behaviour* Vol. 22. London, UK: Academic Press, pp. 65–102.
- Muñoz AP, Pomarol M, Castella J, Gutierrez J and Galmes M (1993) *Ornithophilia gestroi* (Rodani, 1878) (Diptera: Hippoboscidae) on *Falco tinnunculus* and *Falco naumanni* in Monegros (Aragon, Spain). *Research and Reviews in Parasitology* 53, 71–72.
- Muriel J, Pérez-Rodríguez L, Puerta M and Gil D (2013) Differential effects of yolk testosterone and androstenedione in embryo development and nestling growth in the spotless starling (*Sturnus unicolor*). *General and Comparative Endocrinology* 194, 175–182.
- Negro JJ, Prenda J, Ferrero JJ, Rodríguez A and Reig-Ferrer A (2020) A timeline for the urbanization of wild birds: the case of the lesser kestrel. *Quaternary Science Reviews* 249, 1–11. <https://doi.org/10.1016/j.quascirev.2020.106638>.
- Nordenfors H, Höglund J and Uggla A (1999) Effects of temperature and humidity on oviposition, molting, and longevity of *Dermanyssus gallinae* (Acari: Dermanyssidae). *Journal of Medical Entomology* 36, 68–72.
- Oksanen, J (2020) Vegan: Community ecology package. R-package Vegan. Available at <https://cran.r-project.org/web/packages/vegan/index.html>.
- Ortego J, Aparicio JM, Calabuig G and Cordero PJ (2007) Risk of ectoparasitism and genetic diversity in a wild lesser kestrel population. *Molecular Ecology* 16, 3712–3720.
- Patterson JEH and Ruckstuhl KE (2013) Parasite infection and host group size: a meta-analytical review. *Parasitology* 140, 803–813.
- Pinheiro J, Bates D, DebRoy S and Sarkar D and R Core Team (2020). Nlme: linear and nonlinear mixed effects models. Available at <https://cran.r-project.org/web/packages/nlme/index.html>.
- Poulin R (1991) Group-living and infestation by ectoparasites in passerines. *The Condor* 2, 418–423.
- Poulin R (2007) Are there general laws in parasite ecology? *Parasitology* 134, 763–776.
- Randolph AE and Dobson ADM (2012) Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* 139, 847–863.
- R Core team (2016) A language and environment for statistical computing. Available at <https://www.r-project.org/>.
- Roulin A (1998) Cycle de reproduction et abondance du diptère parasite *Carnus hemapterus* dans les niches de chouettes effraies *Tyto alba*. *Alauda* 66, 265–272.
- Rózsa L (1990) The ectoparasite fauna of feral pigeon populations in Hungary. *Parasitology Hungarica* 23, 115–119.
- Rózsa L, Rékási J and Reiczigel J (1996). Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). *Journal of Animal Ecology* 65, 242–248.
- Rózsa L, Reiczigel J and Majoros G (2000) Quantifying parasites in samples of hosts. *Journal of parasitology* 86, 228–232.
- Salido A, Veiga J, Reyes-Lopez JL, Nieves-Aldrey JL and Valera F (2021) Insect predation reduces the abundance of a midicolous ectoparasite. *Ecological Entomology*. <https://doi.org/10.1111/een.13036>
- Sanz-Aguilar A, Payo-Payo A, Rotger A, Yousfi L, Moutailler S, Beck C, Dumarest M, Igual JM, Miranda MÁ, Torres MV, Picorelli V, Gamble A and Boulinier T (2020) Infestation of small seabirds by *Ornithodoros maritimus* ticks: effects on chick body condition, reproduction and associated infectious agents. *Ticks and Tick-Borne Diseases* 11, 1–8. <https://doi.org/10.1016/j.ttbdis.2019.101281>.
- Tella JL (2002) The evolutionary transition to coloniality promotes higher blood parasitism in birds. *Journal of Evolutionary Biology* 15, 32–41.
- Tella JL, Forero MG, Donazar JÁ, Negro JJ and Hiraldo F (1997) Non-adaptive adoptions of nestlings in the colonial lesser kestrel: proximate causes and fitness consequences. *Behavioral Ecology and Sociobiology* 40, 253–260.
- Tella JL, Gajón A, Gortázar C and Osácar JJ (1998) High host specificity of *Crataerina melbae* (Diptera: Hippoboscidae) in a mixed colony of birds. *Journal of Parasitology* 84, 198–200.
- Václav R and Valera F (2018) Host preference of a haematophagous avian ectoparasite: a micronutrient supplementation experiment to test an evolutionary trade-off. *Biological Journal of the Linnean Society* 125, 171–183.
- Václav R, Calero-Torralbo MA and Valera F (2008) Ectoparasite load is linked to ontogeny and cell-mediated immunity in an avian host system with pronounced hatching asynchrony. *Biological Journal of the Linnean Society* 94, 463–473.
- Valera F, Casas-Crivillé A and Hoi H (2003) Interspecific parasite exchange in a mixed colony of birds. *Journal of Parasitology* 89, 245–250.
- Valera F, Casas-Crivillé A and Calero-Torralbo MA (2006a) Prolonged diapause in the ectoparasite *Carnus hemapterus* (Diptera: Cyclorrhapha, Acalypttratae) – How frequent is it in parasites? *Parasitology* 133, 179–186.
- Valera F, Martín-Vivaldi M and Carles-Tolrá M (2006b) Life-history variation in three coexisting species of carnid flies (Diptera: Carnidae), *Carnus hemapterus*, *Hemeromyia anthracina* and *Hemeromyia longirostris*. *European Journal of Entomology* 103, 347–353.
- Valera F, Veiga J, Sandoval A and Moreno E (2018) Coexistence, habitat associations and puparia description of three dipteran species of the family Carnidae. *Parasitology Open* 4, 1–9.
- Veiga J and Valera F (2020) Nest box location determines the exposure of the host to ectoparasites. *Avian Conservation and Ecology* 15, 1–13. <https://doi.org/10.5751/ace-01657-150211>.
- Veiga J, De Oña P, Salazar B and Valera F (2019) Defining host range: host-parasite compatibility during the non-infective phase of the parasite also matters. *Parasitology* 146, 1–7.
- Veiga J, Václav R and Valera F (2020) The effect of parasite density on host colonisation success by a mobile avian ectoparasite. *Ecological Entomology* 45, 867–875.
- Whiteman NK and Parker PG (2004) Effects of host sociality on ectoparasite population biology. *Journal of Parasitology* 90, 939–947.