

Ectoparasitic aspects in Red-footed Falcon *Falco vespertinus* breeding colonies in the Po valley (Italy)

Devon CEVENINI¹, Marco GUSTIN² & Dino SCARAVELLI^{3*}



Received: April 13, 2023 – Revised: July 19, 2023 – Accepted: July 20, 2023

Cevenini, D., Gustin, M. & Scaravelli, D. 2023. Ectoparasitic aspects in Red-footed Falcon *Falco vespertinus* breeding colonies in the Po valley (Italy). – Ornis Hungarica 31(2): 138–150. DOI: 10.2478/orhu-2023-0025

Abstract Ectoparasite fauna of *Falco vespertinus* breeding colonies was investigated in a system of artificial nests in the Po valley (Parma province), Italy, during four subsequent breeding seasons (2019–2022). Conservation actions regarding *Falco vespertinus* led to a great increase in its presence in the area. This rise was believed to coincide with an increase in the prevalence of hematophagous ectoparasites breeding in the nests, with a potential negative impact on the attractiveness of the breeding site. Ectoparasites collected from the nestlings' bodies almost entirely belonged to a single species, Diptera *Carnus hemapterus*, with a quite variable prevalence in different years. Maximum ectoparasite load was consistently linked to younger than two weeks old chicks. *Carnus hemapterus* may pose a threat to less resilient specimens of *Falco vespertinus* because it feeds on live tissues, increases metabolic expenditure, and can introduce blood parasites. Nonetheless, this species is part of the ecosystem shared with the falcon and might have a conservational value itself. We propose that higher occurrence of this ectoparasite might be linked to diet parameters, especially the availability of small mammals and the lingering of prey remnants in the nests, as well as to the age of the parasitized nestlings. These findings might have important implications for the conservation of this rare *Falco* species.

Keywords: artificial nests, chicks, ectoparasites, *Carnus hemapterus*, age, diet

Összefoglalás A kék vércse (*Falco vespertinus*) telepek ektoparazita faunáját vizsgáltuk az olaszországi Pó-völgyben (Parma tartomány), mesterséges költőládákban, négy egymást követő költési időszakban (2019–2022). A természetvédelmi intézkedések nagymértékben növelték a kék vércsék jelenlétét a területen. Ez az emelkedés vélhetően egybeesik a fészkekben szaporodó vérszívó ektoparaziták mennyiségének növekedésével, ami potenciálisan negatív hatással lehet a kolónia vonzerejére. A fiókák testéről gyűjtött ektoparaziták szinte mindegyike a *Carnus hemapterus* (Diptera) fajba tartoznak, évente változó prevalenciával. A maximális ektoparazita fertőzés a kéthetesenél fiatalabb fiókákra volt jellemző. A *Carnus hemapterus* veszélyt jelenthet a kék vércsék kevésbé ellenálló példányaira. Mivel vérrrel táplálkozik, megterheli az anyagcserét, és egysejtű vérelősködőket terjeszthet. Mindazonáltal ez a faj a vércsével együtt része az ökoszisztémának, és maga is természetvédelmi értéket képviselhet. Feltételezzük, hogy ennek az ektoparazitának a gyakoribb előfordulása összefüggésbe hozható a táplálkozási paraméterekkel, különösen a kisemlősök elérhetőségével, a zsákmánymaradványok fészkekben való felhalmozódásával, valamint a fiókák életkorával. Ezek a megállapítások jelentős hatással lehetnek e ritka sólyomfaj megőrzésére.

Kulcsszavak: költőláda, fióka, ektoparazita, *Carnus hemapterus*, életkor, táplálék

¹ University of Bologna, Natural Sciences Department BiGeA, Via Selmi 3, 40126 Bologna, Italy

² Conservation Department LIPU-Birdlife Italia, Via Pasubio 3, 43122 Parma, Italy

³ University of Bologna, Natural Sciences Department BiGeA, Via Selmi 3, 40126 Bologna, Italy

* corresponding author; e-mail: dino.scaravelli@unibo.it

Introduction

The Red-footed Falcon (*Falco tinnunculus*) is classified as a near-threatened species on the IUCN Red List (IUCN 2022) and as a globally threatened Species of European Conservation Concern (SPEC 1) (BirdLife International 2017). Habitat degradation, soil sealing, pesticide spraying, loss of nesting sites, and the conversion of grasslands to agricultural fields are the main reasons behind the moderately rapid decline affecting its global population from the 1970s (Huber *et al.* 2008, BirdLife International 2018, Calabrese *et al.* 2020). The Red-footed Falcon usually exploits rookeries and solitary corvid nests (i.e. *Pica pica*, *Corvus cornix*) for breeding (Palatitz *et al.* 2009, Chavko & Krištín 2017), and has become a regular migrant and a breeding resident in the Italian rural landscapes since 1995 (Brichetti & Fracasso 2003, Sgorlon *et al.* 2013). As of 2015, over 90% of the Italian population bred in the alfalfa crops in the Parma province of the Emilia-Romagna region (Nardelli *et al.* 2015), two of the largest breeding colonies of this species in Italy (Ferrarini & Gustin 2022). Here the Red-footed Falcon can enjoy agricultural areas in a dry continental climate free of pesticides and rich in prey (Fior & Gustin 2012). To foster the presence of this rare raptor species in the area, many measures are implied, such as the regular monitoring of its occurrence patterns, the maintenance of artificial nests, and the nestlings' ringing for research purposes. The employment of nest-boxes is particularly useful, as they can be placed in accessible locations to better enable behavioural, ecological or conservation research (Bragin *et al.* 2017).

Nonetheless, crowded avian rookeries are often linked to the increase in ectoparasite abundance and infestation intensity (Liker *et al.* 2001). Moreover, nest-boxes are cleaned only once a year (prior to the beginning of the breeding season) (Calabrese *et al.* 2020) allowing organic matters to linger in the residual nest-material, providing an abundant food supply in an already micro-climatically suitable environment for ectoparasites (Fehérvári *et al.* 2015, Soltész *et al.* 2018, Castaño-Vázquez *et al.* 2022). Nest-dwelling ectoparasites are a community of species showing a plethora of eating and behavioural habits: most larvae are saprophagous or hematophagous and live in the nest substrate (Soltész *et al.* 2018).

The goal of this study is to analyse, for the first time, the ectoparasite fauna of *Falco tinnunculus* in Italy, assessing prevalence, distribution, and role in the host species well-being during four subsequent breeding seasons.

Material and Methods

Study area

The sites where the colonies bred were labelled as: (a) Strada del Lazzaretto (Municipality of Treccasali, 44°88'82,64"N-10°28'22,64"E); (b) Bertinelli (Municipality of Treccasali, 44°89'91,99"N-10°27'73,29"E); (c) Calza (Municipality of Busseto, 44°97'55,44"N-10°11'72,58"E); (d) Crociletto (Municipality of Roccabianca, 44°97'89,22"N-10°17'68,22"E); (e) Boarini (Municipality of Roccabianca,

44°97'91,67"N-10°18'19,44"E); (f) Boni (Municipality of Trecasali, 44°53'33,22"N-10°17'45,20"E).

The study was conducted during the summers of 2019 to 2022 during the annual monitoring activities in a system of artificial nest-based *Falco vespertinus* colonies in Northern Italy. Examined clutches came from nest-boxes that have been routinely monitored to assess breeding success since the late 1990s, located on *Quercus robur*, *Platanus acerifolia*, and *Populus nigra* rows in the Po valley (Parma province) (30 m a.s.l.). The study area was identified dividing into three main sectors the 580 km² of farmed landscape, which also features six Natura 2000 sites and two natural reserves (Fior & Gustin 2012, Calabrese *et al.* 2020).

Field methods

On an annual basis, during the reproductive season (May-August), falcons were followed to their nests, stopping at previously known nesting sites to check for potential occupation, and their nestlings are ringed (Calabrese *et al.* 2020). Both the ringing activities and the ectoparasite collection are performed between the first week after hatching and just prior fledging, to have most nests occupied by chicks suitable for the study. Egg-laying period for this species is usually between the last ten days of April and mid-May, followed by approximately 23 days of incubation (Cramp & Simmons 1980). Nestlings from every nest-box are ringed using a metal ring with an alphanumeric code. For this study, ectoparasites were collected from every chick (even the ones too young to be ringed) through a visual examination of body and plumage, focusing on bald areas such as axillas, groin, goiter, and inner wings. All detectable ectoparasites were collected and then stored in 70% alcohol for later analytical purposes. Potential ectoparasites remaining in the nest were disregarded. Data coming from these activities were later organized in a dataset indicating: date and time, GI of the site, nest-box identification number, ring codes, age of the nestling, ectoparasite presence, weight, tarsus, and collected samples (e.g. unhatched eggs, pellets, prey remnants found in the nest-box). A specific age estimate was defined for each chick, being alternatively <7 days, 7–10 days, 10–12 days, 12–15 days, 15–20 days, 20–25 days old (i.e. between hatching and fledging ages). From the inside of some of the nest-boxes was collected unhatched eggs, pellets, and prey remnants (mainly *Microtus savii* specimens and the hardened forewing (*elytra*) of beetles (mainly *Pentodon bidens punctatus*). Stereomicroscopic observation was used to determine ectoparasite sex-ratio relying on sexual dimorphism cues. Male specimens showed easily detectable genitalia at the end of the abdomen while female specimens were characterized by a pronounced physogastry and the absence of abdominal sternites (Grimaldi 1997).

Ectoparasite abundance estimation

At a later stage, collected ectoparasites were individually examined by stereomicroscope for identification. Ectoparasites were counted as a comprehensive total and as the total number for each nest-box. Sex identification was based on anatomical differences between

female and male specimens as described in Grimaldi (1997). Mean values, standard deviation, minimum, and maximum for each clutch were then estimated. Resulting data were interpolated with the ringing datasets to obtain yearly ectoparasitic prevalence. To verify if the observed frequency distribution differs from sets arose by chance was used the Pearson's chi-squared test (χ^2). Data management was performed with R 4.2.1. (R Core Team 2022) with the packages *MASS* (Venables & Ripley 2002), *ggplot2* (Wickham 2016), *tidyr* (Wickham & Girlich 2022), and *dplyr* (Wickham *et al.* 2022).

Result

A total of 557 Red-footed Falcon nestlings coming from the artificial nests in the province of Parma were ringed between 2019 and 2022. Of these, 318 belonging to 112 clutches were also inspected to determine their ectoparasitic load. Among the 112 inspected clutches, 50 had parasitized nestlings (44.6%). Ectoparasites were stored per individual host in

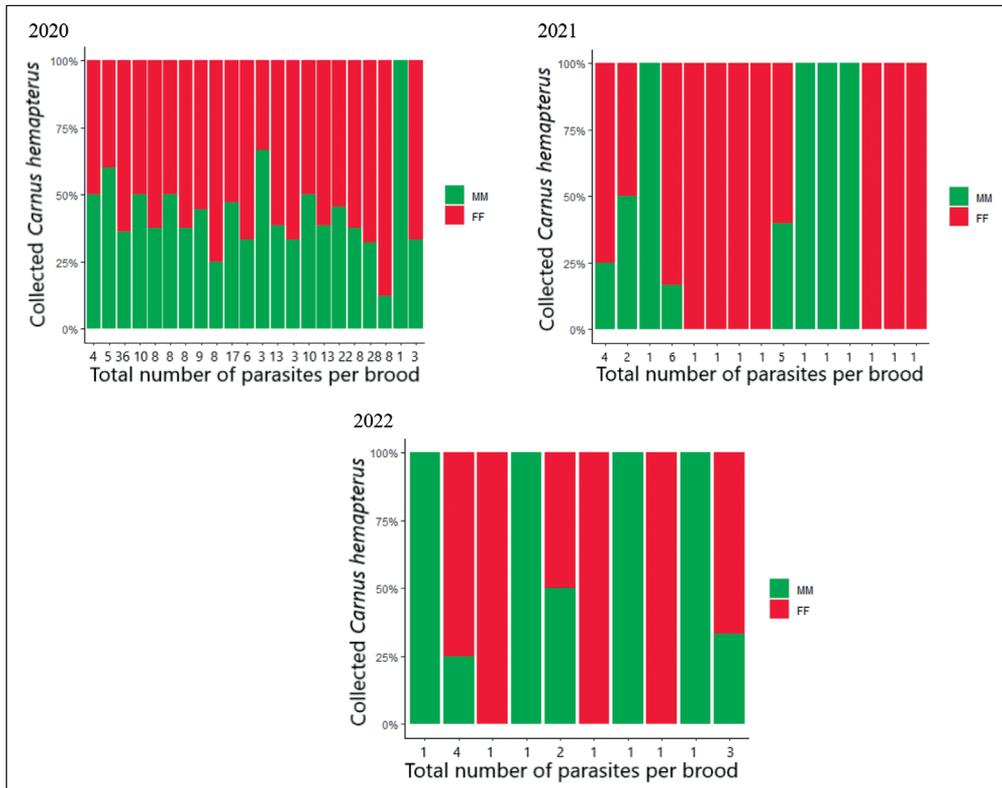


Figure 1. *Carnus hemapterus* sex-ratios per clutch (FF: females; MM: males). 100% FF or MM specimens means there was only one parasite in the whole clutch. Data for 2019 were not available

1. ábra *Carnus hemapterus* ivararányok az egyes fészekaljokban (FF: nőstények; MM: hímek). A 100% hím vagy nőstény ivararányok esetében csak egyetlen parazita volt a teljes fészekaljon. A 2019. évre az adatok nem elérhetőek

Table 1. Yearly ectoparasite prevalence from 2019 to 2022. Total number of inspected nestlings, per individual host, and per clutch prevalence are shown. Collected *Carnus hemapterus* specimens refer both to those collected from the overall inspected nestlings and to those coming from nestlings of known age only

1. táblázat Az ektoparaziták éves prevalenciája 2019 és 2022 között. A vizsgált fiókák teljes száma, valamint az egyedenként és fészekaljanként számított prevalencia. A begyűjtött *Carnus hemapterus* példányok száma az összes vizsgált fiókaról, illetve az ismert korú fiókákról

Year	Infested nestlings	Inspected nestlings	Per host prevalence (%)	Per brood prevalence (%)	Collected <i>Carnus hemapterus</i>	<i>Carnus hemapterus</i> collected from nestlings of known age
2019	3	50	6	19	3	/
2020	71	81	87.7	91.7	302	231
2021	23	107	21.5	37.5	28	28
2022	14	80	17.5	31.3	16	16

the years 2019 and 2021–2022 and per brood in 2020. Yearly ectoparasite prevalence and abundance details are available in *Table 1*. Collected ectoparasites belonged to the hematophagous Dipteran species *Carnus hemapterus* apart from the occasional finds of one specimen of *Laemobothrion* sp. and eight *Degeeriella rufa* (Phthiraptera) in two different nestlings in 2021.

Ectoparasites were mainly located on bald areas of the axilla and inner wing. Once disturbed, they scattered on the nestling's body moving towards the goiter and groin. Areas from which they were collected often exhibited skin lesions, bruises, and clotted blood related to their hematophagy. Disregarding potential ectoparasites left inside the nest, the range of *Carnus hemapterus* abundance was usually from 1 to 3 specimens for clutch, rarely from 4 to 8 (*Table 2, Figure 2*). The lowest percentage of parasitized nestlings and clutches was recorded for the 2019 breeding season, followed by a substantial increase in 2020 and a subsequent overall reduction for the years 2021 and 2022 (*Table 1*). The overall prevalence of ectoparasites in the year 2020 was highly significantly greater than the prevalence for the other three breeding seasons (Pearson's Chi-squared test, $\chi^2 = 28.053$, $df = 3$, $P < 0.001$). No significant difference among sexes could be detected for the overall number of collected ectoparasites (Pearson's Chi-squared test, $X^2 = 0.762$, $df = 2$, $P = 0.6835$), although the number of collected females was steadily higher than the number of collected males each year (*Table 3, Figure 1*).

Table 2. Frequency distribution of *F. vespertinus* broods across infestation intensity classes over the years

2. táblázat A kék vércse fészekaljak gyakorisági eloszlása a fertőzés intenzitási osztályok között az évek során

Year	Range of <i>C. hemapterus</i> abundance	Number of infested broods
2019	1–3	3
2020	1–3	4
	4–8	9
	9–12	3
	13–18	3
	20–40	3
2021	1–3	12
	4–8	3
2022	1–3	8
	4–8	2

In 2019, the collected sample was rather small if compared to the following breeding seasons and the inspected nestlings were all over 15 days old (i.e. already in the molting phase). Nestlings' age seems to be particularly important for *C. hemapterus* host choice, and these two variables turned out to be highly statistically significant dependent (Pearson's Chi-squared test, $P < 0.001$) for the overall four breeding seasons (Table 4, Figure 3). Figure 3 shows the yearly age-prevalence relationship for the clutches of known age. Results show that concentrations of *C. hemapterus* were highest for nestlings under 7 days of age and remained generally high for

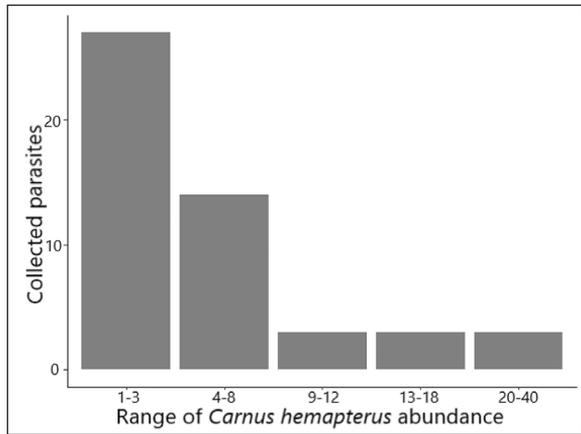


Figure 2. Frequency distribution of *Falco vespertinus* broods across infestation intensity classes during the 2019, 2020, 2021, and 2022 breeding seasons (N=50 broods)

2. ábra A kék vércse fészekaljok gyakorisági eloszlása fertőzöttség intenzitási osztályok között a 2019-es, 2020-as, 2021-es és 2022-es költési időszakban (N=50 fészekalj)

Table 3. *Carnus hemapterus* sex ratio (MM/[FF+MM]) and abundance per brood from 2020 to 2022 (sexing data from the year 2019 were not available). (FF: females; MM: males)

3. táblázat *Carnus hemapterus* ivararány (MM/[FF+MM]) és abundancia fészekaljanként 2020 és 2022 között (2019-es ivar adatok nem álltak rendelkezésre). (FF: nőstény; MM: hím)

Year	FF (per brood range)	MM (per brood range)	Sex ratio (MM/[FF+MM])	Mean abundance per brood (FF, MM)	St. deviation of mean abundance per brood (FF, MM)
2020	139 (0–23)	92 (1–13)	0.398	10.5 (6.3, 4.2)	8.4 (5.4, 3.1)
2021	19 (0–5)	9 (0–2)	0.321	1.9 (1.3, 0.6)	1.6 (1.3, 0.6)
2022	9 (0–3)	7 (0–1)	0.438	1.6 (0.9, 0.7)	1.0 (0.9, 0.5)

Table 4. Pearson's Chi-squared test results and rough data for the comparison between age ranges and the corresponding number of infested nestlings found in the four breeding seasons (from 2019 to 2022)

4. táblázat Pearson-féle Chi-négyzet teszt eredménye és a nyers adatok a korosztályok fertőzöttségének összehasonlítására a négy költési időszakban (2019-től 2022-ig)

Age range	Infested nestlings	Chi ²	df	P-value
< 7 days	19	23.845	5	0.0002325
7–10 days	23			
10–12 days	17			
12–15 days	14			
15–20 days	28			
20–25 days	10			

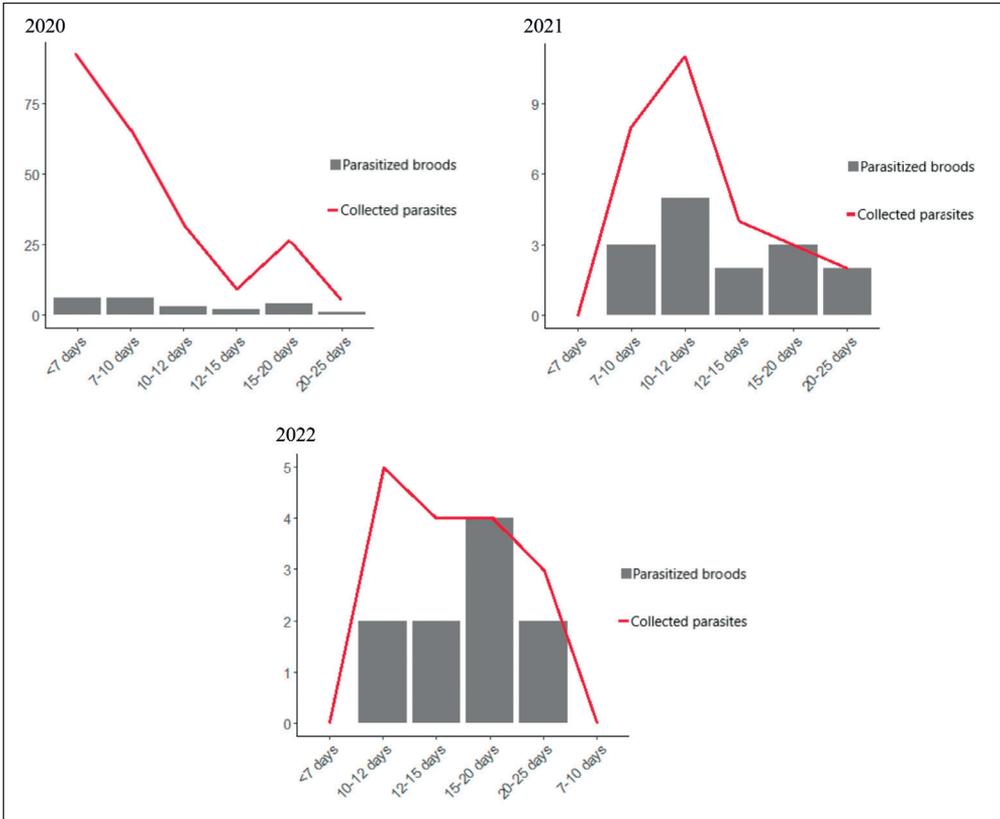


Figure 3. The number of infested broods and the number of *Carnus hemapterus* individuals per host-age categories. Year 2019 was disregarded due to the reduced sample size

3. ábra A fertőzött fészekaljok száma és a begyűjtött *Carnus hemapterus* legyek egyedszáma a három év során, a fiókák korosztálya szerint csoportosítva. A 2019-es évet a kis mintaelemzés miatt kihagytuk

individuals in the pre-molting phase (aged from 15 days under) tending to decrease in the following age groups, sharply in 2020 and 2021, gradually in 2022 (Figure 3). Maximum abundance was recorded in the <7 days old age group for the year 2020 and in the 10–12 days old age group for the years 2021 and 2022. Please note that in both seasons 2021 and 2022 average nestlings' age was a little higher if compared to 2020 (i.e. no <7 days old nestlings in 2021, and no <7 days old nor 7–10 days old nestlings in 2022).

Discussion

In this study, we analyzed the prevalence and abundance of ectoparasites on *Falco vespertinus* nestlings in the Italian Po valley (Parma province). High ectoparasite loads on nestlings can impair their health condition and growth rate (Hoi *et al.* 2010, Cantarero *et al.* 2013, Romano *et al.* 2021), increase physiological stress by inducing costly immune

and inflammatory responses (Martínez-Padilla *et al.* 2004, Tomás *et al.* 2008, Cantarero *et al.* 2013), raise the mortality rate (Richner *et al.* 1994) or indirectly decrease their fitness through the transmission of blood parasites (Poiani 1993, Richner *et al.* 1994, Martínez-De La Puente *et al.* 2013). Given these negative impacts, ectoparasite abundance and spatial distribution might affect the attractiveness of a breeding site and the behavioural and social dynamics in the host population (Møller 1993, de Lope & Møller 1993, Møller & Erritzøe 1996, Cantarero *et al.* 2013, Veiga & Valera 2020). Therefore, parasitic drivers may be a key ecological variable for the reproductive success of a rare species such as the Red-footed Falcon, as already showed in colonies of this species in Hungary (Piross *et al.* 2015, Soltész *et al.* 2018).

Almost all specimens collected from *F. vespertinus* nestlings in the Italian Po valley belonged to a single species, *Carnus hemapterus*, an ectoparasite of the *Carnidae* family with Holarctic distribution (Sabrosky 1987, Grimaldi 1997), known to parasitize the nestlings of at least 45 bird species breeding in cavities or sheltered nests (Capelle & Whitworth 1973, Grimaldi 1997). *C. hemapterus* ecology is poorly known but it is believed that females lay their eggs in the debris of the nest where the saprophagous pupae winter in diapause, enjoying the humid microclimate and feeding on organic matter (Grimaldi 1997, Valera *et al.* 2006, Soltész *et al.* 2018). Hematophagous adults appear in the nest synchronizing with hatching and, once a suitable host is found, gather on bald skin areas, and lose their wings to move more easily between feathers (Grimaldi 1997). To feed, they tear the epidermis and suck the blood coming from the open wound (Bequaert 1942). Male adult flies remain in their winged phase longer than females, thus being able to colonize new hosts and new clutches for reproductive purposes (Capelle & Whitworth 1973, Grimaldi 1997, Roulin 1998).

C. hemapterus is the easiest-found ectoparasite in various raptor species breeding in nest-boxes (Dawson & Bortolotti 1997, Fargallo *et al.* 2001, Kal'avský & Pospíšilová 2010, Sumasgutner *et al.* 2014, Podofillini *et al.* 2018, Levesque-Beaudin *et al.* 2020) including the Red-footed Falcon (Fehérvári *et al.* 2015, Soltész *et al.* 2018).

Many studies on *Falco tinnunculus* show similar prevalence to the ones obtained here (Fargallo *et al.* 2001, Kal'avský & Pospíšilová 2010, Sumasgutner *et al.* 2014). *Carnus hemapterus* prevalence is expected to vary broadly both within and between years and is usually related to habitat parameters (e.g. vegetation structure, plant architecture) and date of inspection (Veiga *et al.* 2020). In accordance with our results (mean: 1.1) other studies on *Falco naumanni* show a usually low *Carnus hemapterus* load, frequently setting at 1–3 to around 6 parasites per nestling (Romano *et al.* 2021)

However, it is important to note that during the 2020 breeding season some individuals had up to 12 ectoparasites actively blood-feeding on their bodies during the inspection, setting at a higher load than expected (mean: 10.5). We consistently found female-biased sex ratios, regardless of the year of inspection and age of the host; however, no significant difference in collected amount could be detected among sexes for the overall four breeding seasons. The reason for this apparent sex-ratio unbalance could be that females in this species are wingless and bigger than males (Grimaldi 1997), so their detection tends to be easier. However, *Carnus hemapterus* sex-ratios per clutch were not significantly dissimilar in the

overall four breeding seasons Václav *et al.* (2016) suggest that *C. hemapterus* could be a threat not only for the damage caused to tissues (skin tearing) but may also be a vector for *Plasmodium* and *Haemoproteus* infestations. Despite this, however, *C. hemapterus* does not seem to have significant effects on nestlings' health, development, or mortality rate, proving that they easily survive significant blood losses (Dawson & Bortolotti 1997). Most studies likewise exclude a negative effect on parents' fitness, apparently being able to meet the energy needs of a parasitized offspring thanks to high food availability at the breeding site (Dawson & Bortolotti 1997, Fargallo *et al.* 2001, Kal'avský & Pospíšilová 2010, Soltész *et al.* 2018, Castaño-Vázquez *et al.* 2022).

Peaks of *C. hemapterus* abundance often coincide with the first two weeks of age of the nestling both in *Falco sparverius* (Dawson & Bortolotti 1997, Lesko & Smallwood 2012) and in *Falco tinnunculus* (Kal'avský & Pospíšilová 2010, Sumasgutner *et al.* 2014). Similar results have also been obtained for other bird species such as *Tyto alba* (Roulin 1998) and *Sturnus vulgaris* (Liker *et al.* 2001). The reasons behind this trend have been long debated but are most probably related to plumage molting (from downy to flight feathers) as an increased darker plumage density and layering may result in a less hospitable environment for the flies (Kirkpatrick & Colvin 1989). Moreover, nestlings tend to be more mobile as they grow and start spending most of their time standing up, thus making themselves less easily reachable for mostly wingless parasites (Dawson & Bortolotti 1997). Further, they physically eliminate most ectoparasites through preening (Piross *et al.* 2020) and have stronger immune defenses (Roulin 1998, 1999). Nest-box cleaning activities can be an unsustainable long-term cost, even though nestlings coming from clean nest-boxes are more likely to develop into a fledged offspring (Fehérvári *et al.* 2015, Romano *et al.* 2021). Difficult accessibility of the nests (i.e. fixed on trees several meters above the ground) and financial limitations (i.e. need for a self-propelled aerial platform) made it unfeasible to determine if more frequent cleaning activities in these colonies influence overall ectoparasitic prevalence. However, many studies analyzing the differences in ectoparasite loads in recently cleaned *Falco vespertinus* nest-boxes and in nest-boxes left intact for longer periods express conflicting opinions on the need for maintenance since some pupae can survive in the interstices of the nest (Dawson & Bortolotti 1997) and these ectoparasites easily re-colonize recently cleaned nest-boxes (Lesko & Smallwood 2012, Podofilini *et al.* 2018). Therefore, we hypothesized that increasing the frequency of these activities and/or the substitution of nest materials could be of no use, besides being highly expensive and time-consuming.

Conclusion

Carnus hemapterus prevalence has significantly risen from the 2019 breeding season to 2020 in the *Falco vespertinus* colonies in the province of Parma. This increase was steadily reduced in the following two years. *C. hemapterus* has high transmissibility in avian colonies since winged adults are very mobile (Podofilini *et al.* 2018, Soltész *et al.* 2018). Given that *F. vespertinus* is mainly limited by the lack of suitable nesting sites, if

nest-boxes are available they are quickly occupied disregarding their state of cleanliness (Kotymán *et al.* 2015).

As a result, nest-box maintenance activities do not seem to have a direct effect on *F. vespertinus* nesting choices. Not having historical records on nestlings' growth parameters in the Parma colonies, although only in 2015 reproductive success was found to be lower than average (Calabrese *et al.* 2020), it is not possible to determine whether the 2020 increase in parasite load had direct negative effects nor whether it led to an increase in infestations or disease transmission. However, *C. hemapterus* feeds on live tissues, increases the metabolic expenditure of the host, and tends to be more prevalent in individuals with poor immune defenses, so it is conceivable that it may pose a threat to weaker and younger *F. vespertinus* individuals (Piross *et al.* 2020), especially if we consider that ectoparasite abundance was found to be significantly dependent on host age (higher the abundance the younger the host). In a context of a global ecological niche, these parasites still fall within the natural balance related to the Red-footed Falcon and could be elements to be preserved themselves. Still, reproductive success was consistently high in the 2019–2022 period, so it is conceivable that potential negative impacts remained limited. To understand the parasite-host relationship in these colonies it may be useful to determine if, as hypothesized, a higher parasite load is linked to a more mammal-based diet related to the overall abundance of micro-mammals in the foraging habitat. The 2020 breeding season was characterized by a higher-than-usual availability of *Microtus savii* and most inspected nest-boxes were rich in prey remnants infested by various fly species; this year was indeed the one when ectoparasite infestation was the highest and the difference in collection between this year and the other three was highly significant, hence a connection between diet and parasite load could be suggested. Indeed, the Red-footed Falcon is a short-grass specialist and can feed upon different food resources (e.g. *Amphibia*, *Hexapoda*, *Mammalia*, *Reptilia*), so differences in ectoparasite prevalence could result from different foraging behaviours in subsequent breeding seasons, adapted to the local abundance of prey in the available foraging patches (i.e. alfalfa crops and fallow land) during the chick-rearing season. It might be interesting to define the parameters affecting the variability in ectoparasite abundances such as host measurements and expression of begging traits (e.g. body mass, forearm length, size, and colour of the flange, cere, and cape) that are reported to change under higher ectoparasitic loads in Lesser Kestrels (*Falco naumanni*) (Romano *et al.* 2021); average concentrations of attractant stimuli (e.g. odour, heat, carbon dioxide emission) in bigger breeding colonies; food availability and foraging preferences; climatic conditions (e.g. humidity, rainfall patterns) before and during the breeding season (Castaño-Vázquez *et al.* 2022).

Acknowledgements

We wish to thank all the volunteers involved in the fieldwork, mainly from the Parma LIPU's Local Conservation Group, especially Andrea Zanichelli, for the extensive knowledge of the Red-footed Falcon colonies and the invaluable help.

References

- Bequaert, J. 1942. *Carnus hemapterus* Nitzsch, an ectoparasitic fly of birds, new to America (Diptera). – Bulletin of Brooklyn Entomological Society 37: 140–149.
- BirdLife International 2017. European birds of conservation concern: populations, trends and national responsibilities. – Cambridge, UK. BirdLife International
- BirdLife International 2018. BirdLife International and Handbook of the Birds of the World, *Falco vespertinus*. – Bird species distribution maps of the world. Version 2018.1. <http://datazone.birdlife.org/species/requestdis>
- Bragin, E. A., Bragin, A. E. & Katzner, T. E. 2017. Demographic consequences of nestbox use for Red-footed Falcons *Falco vespertinus* in Central Asia. – Ibis 159(4): 841–853. DOI: 10.1111/ibi.12503
- Brichetti, P. & Fracasso, G. 2003. Ornitologia Italiana, 1. Gaviidae – Falconidae. – Alberto Perdisa Editore, Bologna
- Calabrese, L., Mucciolo, A., Zanichelli, A. & Gustin, M. 2020. Effects of nest boxes on the most important population of Red-footed Falcon *Falco vespertinus* in Italy. – Conservation Evidence 20: 35–39. www.conservationevidence.com/actions/489
- Cantarero, A., López-Arrabé, J., Rodríguez-García, V., González-Braojos, S., Ruiz-De-Castañeda, R., Redondo, A. J. & Moreno, J. 2013. Factors affecting the presence and abundance of generalist ectoparasites in nests of three sympatric hole-nesting bird species. – Acta Ornithologica 48(1): 39–54. DOI: 10.3161/000164513X669982
- Capelle, K. J. & Whitworth, T. L. 1973. The distribution and avian hosts of *Carnus hemapterus* (Diptera: Milichiidae) in North America. – Journal of Medical Entomology 10(5): 525–526.
- Castaño-Vázquez, F., Merino, S., Valera, F. & Veiga, J. 2022. Experimental manipulation of humidity in a cavity-nesting bird influences ectoparasites' abundance. – Parasitology 149(4): 436–443. DOI: 10.1017/S0031182022000026
- Chavko, J. & Krištin, A. 2017. Foraging opportunism and feeding frequency in the Red-footed Falcon (*Falco vespertinus*) in Slovakia: case study from 2017. – Slovak Raptor Journal 11(1): 31–41. DOI: 10.1515/srj-2017-0009
- Cramp, S. & Simmons, K. E. L. 1980. The birds of the Western Palearctic. Hawks to Bustards, Vol. 2. – Oxford University Press, Royal Society for the Protection of Birds, London, UK.
- Dawson, R. D. & Bortolotti, G. R. 1997. Ecology of parasitism of nestling American Kestrels by *Carnus hemapterus* (Diptera: Carnidae). – Canadian Journal of Zoology 75(12): 2021–2026. www.nrcresearchpress.com
- de Lope, F. & Møller, A. P. 1993. Effects of ectoparasites on reproduction of their swallow hosts: A cost of being multi-brooded. – Oikos 67(3): 557–562. DOI: 10.2307/3545368
- Fargallo, J. A., Blanco, G., Potti, J. & Viñuela, J. 2001. Nestbox provisioning in a rural population of Eurasian Kestrels: Breeding performance, nest predation and parasitism. – Bird Study 48(2): 236–244. DOI: 10.1080/00063650109461223
- Fehérvári, P., Piross, I. S., Kotymán, L., Solt, S., Horváth, É. & Palatitz, P. 2015. Species specific effect of nest-box cleaning on settlement selection decisions in an artificial colony system. – Ornis Hungarica 23(1): 66–76. DOI: 10.1515/orhu-2015-0006
- Ferrarini, A. & Gustin, M. 2022. Introducing a new tool to derive animal behaviour from GPS data without ancillary data: The Red-footed Falcon in Italy as a case study. – Ecological Informatics 69: 101645. DOI: 10.1016/j.ecoinf.2022.101645
- Fior, E. & Gustin, M. 2012. Relazione monitoraggio faunistico [Wildlife monitoring report]. – Life 07 NAT/IT/000499 Pianura Parmense. – Azione E2. I risultati del monitoraggio e le prospettive, pp. 1–51. (in Italian)
- Grimaldi, D. 1997. The Bird Flies, Genus *Carnus*: Species Revision, Generic Relationships, and a Fossil *Meoneura* in Amber (Diptera: Carnidae). – American Museum Novitates 3190.
- Hoi, H., Krištofik, J., Darolová, A. & Hoi, C. 2010. Are parasite intensity and related costs of the milichiid fly *Carnus hemapterus* related to host sociality? – Journal of Ornithology 151(4): 907–913. DOI: 10.1007/s10336-010-0529-5
- Huber, S., Prokop, G., Arrouays, D., Banko, G., Bispo, A., Jones, R., Kibblewhite, M., Lexer, W., Möller, A., Rickson, J., Shishkov, T., Stephens, M., Van den Akker, J., Varallyay, G. & Verheijen, F. 2008. Indicators and Criteria report. ENVASSO Project (Contract 022713). Coordinated by Cranfield University, UK. – For Scientific Support to Policy, European Commission 6th Framework Research Programme

- IUCN 2022. The IUCN Red List of Threatened Species. Version 2022-1. – <https://www.iucnredlist.org>.
- Kal'avský, M. & Pospíšilová, B. 2010. The ecology of ectoparasitic species *Carnus hemapterus* on nestlings of Common Kestrel (*Falco tinnunculus*) in Bratislava. – Slovak Raptor Journal 4(1): 45–48. DOI: 10.2478/v10262-012-0045-z
- Kirkpatrick, C. E. & Colvin, B. A. 1989. Ectoparasitic Fly *Camus hemapterus* (Diptera: Carnidae) in a nesting population of Common Barn-owls (Strigiformes: Tytonidae). – Journal of Medical Entomology 26(2): 109–112. DOI: 10.1093/jmedent/26.2.109
- Kotymán, L., Solt, S., Horváth, É., Palatitz, P. & Fehérvári, P. 2015. Demography, breeding success and effects of nest type in artificial colonies of Red-footed Falcons and allies. – Ornis Hungarica 23(1): 1–21. DOI: 10.1515/orhu-2015-0001
- Lesko, M. J. & Smallwood, J. A. 2012. Ectoparasites of American Kestrels in northwestern new jersey and their relationship to nestling growth and survival. – Journal of Raptor Research 46(3): 304–313. DOI: 10.3356/JRR-11-56.1
- Levesque-Beaudin, V., Sinclair, B. J., Marshall, S. A. & Lauff, R. F. 2020. Diptera communities of raptor (Aves) nests in Nova Scotia, Canada. – Canadian Entomologist 152(3): 342–354. DOI: 10.4039/tce.2020.26
- Liker, A., Márkus, M., Vozár, A., Zemankovics, E. & Rózsa, L. 2001. Distribution of *Carnus hemapterus* in a Starling colony. – Canadian Journal of Zoology 79(4): 574–580. DOI: 10.1139/cjz-79-4-574
- Martínez-De La Puente, J., Martínez, J., Rivero-De-Aguilar, J., del Cerro, S. & Merino, S. 2013. Vector abundance determines *Trypanosoma* prevalence in nestling Blue Tits. – Parasitology 140(8): 1009–1015. DOI: 10.1017/S0031182013000371
- Martínez-Padilla, J., Martínez, J., Dávila, J. A., Merino, S., Moreno, J. & Millán, J. 2004. Within-brood size differences, sex and parasites determine blood stress protein levels in Eurasian Kestrel nestlings. – Functional Ecology 18(3): 426–434. DOI: 10.1111/j.0269-8463.2004.00874.x
- Møller, A. P. 1993. Ectoparasites increase the cost of reproduction in their hosts. – Journal of Animal Ecology 62(2): 309–322. DOI: 10.2307/5362
- Møller, A. P. & Erritzøe, J. 1996. Parasite virulence and host immune defense: Host immune response is related to nest reuse in birds. – Evolution 50(5): 2066–2072. DOI: 10.1111/j.1558-5646.1996.tb03592.x
- Nardelli, R., Andreotti, A., Bianchi, E., Brambilla, M., Brecciaroli, B., Celada, C., Dupré, E., Gustin, M., Longoni, V., Pirrello, S., Spina, F., Volponi, S. & Serra, L. 2015. Rapporto sull'applicazione della Direttiva 147/2009/CE in Italia: dimensione, distribuzione e trend delle popolazioni di uccelli (2008–2012) [Report on the application of Directive 147/2009/EC in Italy: size, distribution and trend of bird populations (2008–2012)]. – ISPRA. Serie Rapporti, 219/2015 (in Italian)
- Palatitz, P., Fehérvári, P., Solt, S. & Barov, B. 2009. European Species Action Plan for the Red-footed Falcon *Falco vespertinus* Linnaeus, 1766. – Szarvas: BirdLife International Environment, Nature Conservation, Wild Birds Action Plans Per Species. – <https://www.researchgate.net/publication/267271581>
- Piross, I. S., Fehérvári, P., Vas, Z., Solt, S., Horváth, É., Palatitz, P., Giosele, C., Gustin, M., Pedrelli, M., Kumar, R. S., Williams, N. P., Pretorius, R., Bernitz, Z., Bernitz, H. & Harnos, A. 2015. Louse (Insecta: Phthiraptera) infestations of the Amur Falcon (*Falco amurensis*) and the Red-footed Falcon. – Ornis Hungarica 23(1): 58–65. DOI: 10.1515/orhu-2015-0005
- Piross, I. S., Siliwal, M., Kumar, R. S., Palatitz, P., Solt, S., Borbáth, P., Vili, N., Magonyi, N., Vas, Z., Rózsa, L., Harnos, A. & Fehérvári, P. 2020. Sex interacts with age-dependent change in the abundance of lice-infesting Amur Falcons (*Falco amurensis*). – Parasitology Research 119(8): 2579–2585. DOI: 10.1007/s00436-020-06753-w
- Podofillini, S., Cecere, J. G., Griggio, M., Curcio, A., de Capua, E. L., Fulco, E., Pirrello, S., Saino, N., Serra, L., Visciglia, M. & Rubolini, D. 2018. Home, dirty home: effect of old nest material on nest-site selection and breeding performance in a cavity-nesting raptor. – Current Zoology 64(6): 693–702. DOI: 10.1093/cz/zoy012/4835146
- Poiani, A. 1993. Small clutch sizes as a possible adaptation against ectoparasitism: A comparative analysis. – Oikos 68(3): 455–462. DOI: 10.2307/3544913
- R Core Team 2022. R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Richner, H., Oppliger, A. & Christe, P. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the Great Tit (*Parus major*). – Journal of Animal Ecology 62(4): 703–710. <http://beheco.oxfordjournals.org/>

- Roulin, A. 1998. Cycle de reproduction et abondance du diptère parasite *Carnus hemapterus* dans les nichées de chouettes effraies *Tyto alba* [Reproductive cycle and abundance of the parasitic dipteran in the nests of Barn Owl *Tyto alba*]. – *Alauda* 66(4): 265–272. (in French)
- Roulin, A. 1999. Fécondité de la mouche *Carnus hemapterus*, ectoparasite des jeunes chouettes effraies *Tyto alba* [Fecundity of the fly *Carnus hemapterus* ectoparasite of young Barn Owl *Tyto alba*]. – *Alauda* 67(3): 205–212. (in French)
- Romano, A., Corti, M., Soravia, C., Cecere, J. G. & Rubolini, D. 2021. Ectoparasites exposure affects early growth and mouth colour in nestlings of a cavity-nesting raptor. – *Behavioral Ecology and Sociobiology* 75(11): DOI: 10.1007/s00265-021-03098-x
- Sabrosky, C. W. 1987. Carnidae. – In: McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R. & Wood, D. (eds.) *Manual of Nearctic Diptera*. Vol. 2. – Ottawa: Agriculture Canada Monograph 28., pp. 909–912.
- Sgorlon, G., Panzarin, L. & Veneti, A. F. 2013. Biologia riproduttiva del *Falco cuculo* (*Falco vespertinus*) in provincia di Venezia [Reproductive biology of Red-footed Falcon *Falco vespertinus* in Venetia province]. – *Atti Secondo Convegno Italiano Rapaci Diurni e Notturni*. Ministero dell’Ambiente 2012, pp. 12–13. (in Italian)
- Soltész, Z., Seres, N. & Kovács-Hostyánszki, A. 2018. Dipteran Assemblages in Red-footed Falcon (*Falco vespertinus*) nest boxes. – *Acta Zoologica Academiae Scientiarum Hungaricae* 64(1): 91–102. DOI: 10.17109/AZH.64.1.91-2018
- Sumasgutner, P., Vasko, V., Varjonen, R. & Korpimäki, E. 2014. Public information revealed by pellets in nest sites is more important than ecto-parasite avoidance in the settlement decisions of Eurasian Kestrels. – *Behavioral Ecology and Sociobiology* 68(12): 2023–2034. DOI: 10.1007/s00265-014-1808-6
- Tomás, G., Merino, S., Martínez-De La Puente, J., Moreno, J., Morales, J. & Lobato, E. 2008. Determinants of abundance and effects of blood-sucking flying insects in the nest of a hole-nesting bird. – *Oecologia* 156(2): 305–312. DOI: 10.1007/s00442-008-1001-6
- Václav, R., Betáková, T., Švančarová, P., Pérez-Serrano, J., Criado-Fornelio, Á., Škorvanová, L. & Valera, F. 2016. Nest ecology of blood parasites in the European Roller and its ectoparasitic carnid fly. – *Experimental Parasitology* 165: 71–80. DOI: 10.1016/j.exppara.2016.03.014
- Valera, F., Vivaldi, M. M. & Tolrá, M. C. 2006. 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.
- Veiga, J., Václav, R. & Valera, F. 2020. The effect of parasite density on host colonisation success by a mobile avian ectoparasite. – *Ecological Entomology* 45(4): 867–875. DOI: 10.1111/een.12864
- Veiga, J. & Valera, F. 2020. Nest box location determines the exposure of the host to ectoparasites. – *Avian Conservation and Ecology* 15(2): 1–13. DOI: 10.5751/ACE-01657-150211
- Venables, W. N. & Ripley, B. D. 2002. *Modern Applied Statistics with S*. 4th ed. – Springer, New York
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. – Springer-Verlag New York
- Wickham, H. & Girlich, M. 2022. *tidyr: Tidy Messy Data*. R package version 1.2.0. – <https://CRAN.R-project.org/package=tidyr>
- Wickham, H., François, R., Henry, L. & Müller, K. 2022. *dplyr: A Grammar of Data Manipulation*. R package version 1.0.9. – <https://CRAN.R-project.org/package=dplyr>

