EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **120**: 129–136, 2023
doi: 10.14411/eje.2023.016
ORIGINAL ARTICLE

Bird nest boxes infested with *Carnus hemapterus* (Diptera: Carnidae): A perfect arena for the study of trophic interplays with a special focus on parasitoid Hymenoptera

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Key words. Interspecific interactions, food web, Aves, bird ectoparasite, wasp parasitoid, *Kleidotoma caledonica*, *Jynx torquilla*

Abstract. Birds' nests hold rich and diverse communities of invertebrates with complex interspecific interactions whose study could improve our understanding of food webs and resource dynamics. To reach this goal, identification of the participants of such interactions is basic but current knowledge on some key groups such as hymenopteran parasitoids is admittedly poor and unreliable. Here we describe the invertebrate fauna in nests of the Eurasian wryneck *Jynx torquilla* Linnaeus, 1758 (Piciformes: Picidae) and the relative importance of various trophic guilds. We found a rich community where ectoparasitic Diptera of birds, parasitoid wasps and scavenger Diptera had a prominent representation. We specifically studied the natural enemies of the most abundant bird ectoparasite *Carnus hemapterus* Nitzsch, 1818 (Diptera: Carnidae), which revealed that *Kleidotoma caledonica* Cameron, 1888 (Hymenoptera: Figitidae) is a specialized and frequent parasitoid of the ectoparasite. Information on the association between other parasitoid wasps, parasitoid flies and their hosts is also offered. Such associations could result in trophic cascades with remarkable consequences for the avian host.

INTRODUCTION

Species interactions are the basis of many of the properties and processes occurring in ecosystems, such as food webs (Lang & Benbow, 2013). Despite a remarkable effort in the study of interspecific interactions, our knowledge is hampered by factors such as overlooking high-order interactions (Møller, 2008) or, more fundamentally, ignorance of the organisms involved in the interactions (Johnson et al., 2010; Thieltges et al., 2013). This is particularly the case for interactions involving parasites and pathogens (Holt & Dobson, 2006). Parasites may feed on other parasites (Johnson et al., 2010), and thus, can determine to a large extent the food web structure and dynamics (MacNeil et al., 2003; Malmstrom et al., 2006). Parasitoids (organisms whose larval stages live as parasites and typically kill their hosts after completing development) are in fact keystone organisms in the majority of terrestrial ecosystems, being essential for the regulation of population densities of economic pests, and a valuable tool in testing many aspects of evolutionary theory (Godfray, 1994). Approximately 10% of the globally described species of insects are parasitoids (Eggleton & Belshaw, 1992). Most of them belong to the order Hymenoptera, namely to the superfamilies Chalcidoidea and Ichneumonoidea (Godfray, 1994), and play an important role, not fully assessed, in ecosystems (Peters & Abraham, 2010).

The nests of birds breeding in cavities provide a particular microhabitat and an abundance of food for both parasitic and nonparasitic invertebrates (Heeb et al., 2000; Tryjanowski et al., 2001; Roy et al., 2013), and, thus, diverse arthropod communities and complex trophic webs (many of them involving parasitoids) have been reported in such habitats (Peters & Abraham, 2010; Roy et al., 2013). They also offer a suitable scenario for exploring interspecific interactions, their participants and the ecological factors affecting the former (Baardsen et al., 2021; Salido et al., 2021). The hematophagous fly *Carnus hemapterus* Nitzsch, 1818 (Diptera: Carnidae) is a cosmopolitan nidicolous bird ectoparasite, widely distributed in the Palaearctic and Nearctic regions, parasitizing at least 64 host species belonging to 24 families of birds (Grimaldi, 1997; Brake, 2011), mainly cavity-nesting birds. It is a good study model since most of its life cycle occurs in the host's nest, which facilitates research on its involvement in trophic webs through the parasite's various life stages. Moreover, its ubiquity and abundance have made it a good subject for ecological and evolutionary studies (e.g. Hoi et al., 2018; Tomás et al., 2018; Václav & Valera, 2018). The Eurasian wryneck *Jynx torquilla* Linnaeus, 1758 (Piciformes: Picidae) is a secondary cavity breeding bird using both natural holes and nest boxes. Compared to other species of birds, there is little information on the nest parasites and nest-dwelling insects associated with this woodpecker. Moreover, it is known to be a common host of *Carnus hemapterus* (Grimaldi, 1997; Brake, 2011), which makes it a good object for determining the relationships of this ectoparasite with other insects. Recently, Salido et al. (2021) reported, for the first time, a parasitoid wasp *Chartocerus conjugalis* Mercet, 1916 (Hymenoptera: Signiphoridae) reared from *Carnus hemapterus* puparia in Spain. Thus, parasitic pressure on the avian host could be regulated by parasitoid wasps, but information on the participants in the various interactions and the factors influencing the players are poorly known (Salido et al., 2021).

In this study we: (i) examine the entomofauna of Eurasian wryneck nests and the relative importance of various trophic guilds, (ii) provide information on the life history of poorly known species, namely Diptera, Hymenoptera and Lepidoptera, (iii) describe the natural enemies of the most abundant ectoparasite *Carnus hemapterus* and the parasitoid pressure to which it is subjected. We finally discuss the consequences of such trophic interactions for each participant.

MATERIALS AND METHODS

Area and ecosystem studied

The area studied is located in the south of Sweden, where nest boxes specially designed for the Eurasian wryneck were previously placed in suitable habitats (sparsely wooded pasture-land) and maintained throughout this study. Data was collected during the period 2005–2013 to get a representative data set for the aims of this work.

The Eurasian wryneck is a cavity-nesting migratory bird arriving in central Sweden at the end of April. Nest box occupation occurs during the first and second week of May and laying starts around one week later (I. Struwe, pers. obs.). Wrynecks do not use any nest material. Their breeding period lasts until the end of June.

Carnus hemapterus (hereafter *C. hemapterus*) is a 2 mm-long, highly mobile, blood-sucking fly that infests nestling birds (Grimaldi, 1997). It has a wide geographical distribution and parasitizes a variety of host species, although it shows some preference for birds nesting in cavities (Dawson & Bortolotti, 1997; Grimaldi, 1997) and for Falconiformes, Strigiformes, Piciformes and Passeriformes (particularly Corvids) (Guiguen et al., 1983). Its life cycle encompasses an obligate host-dependent phase (the imago) and several off-host stages, namely three larval stages that are saprophagous in the detritus of the nest (Guiguen et al., 1983; Grimaldi, 1997) and a pupal stage that hibernates in the nest material. The imago emerges in apparent synchronization with the onset of reproduction of their hosts (Calero-Torralbo et al., 2013; I. Struwe, unpubl. data). *Carnus hemapterus* can be detrimental for nestlings (Whitworth, 1976; Cannings, 1986; Soler et al., 1999; Hoi et al., 2018, but see Kirkpatrick & Colvin, 1989; Dawson & Bortolotti, 1997).

Identification of the nidicolous entomofauna

The general procedure used to study the entomofauna of nests was as follows; in summer, after the fledglings had left, nest boxes were sealed with tape to prevent secondary colonization by hornets, an otherwise common event. At the beginning of October material was carefully collected from nest boxes and placed in wooden hibernation boxes that were kept in outdoor conditions during winter until insects started to emerge. In the following spring and summer, from the middle of April to the beginning of August, insects that emerged in each box were collected in emergence traps (500 ml transparent plastic jar attached to the exit hole by a 10 mm wide plastic tube), preserved in alcohol or dry mounted, counted and identified. This method is particularly suitable to trap arthropods whose pupae overwinter in nests but it can underestimate saprophagous calyptrate flies such as blow flies (Calliphoridae) and flesh flies (Sarcophagidae) as well as mites.

We used the keys of Tschorsnig & Herting (1994) and Anderssen (1996) for Tachinidae, Gorodkov (1969) for Heleomyzidae, Andersson (1971) for Chyromyidae, Andersson (1985) for Hippoboscidae, Shtakelberg (1969), Papp (1978), Grimaldi (1997) and Brake (2022) for Carnidae, Bengtsson & Johansson (2011) for Tineidae and Yponomeutidae, Quinlan (1978) and Forshage & Nordlander (2008) for Figitidae, Boucek & Rasplus (1991) and Graham (1969) for Pteromalidae, Broad et al. (2018) for Ichneumonidae, Shaw & Huddleston (1991) and Nixon (1973, 1976) for Braconidae, Nixon (1980) for Diapriidae, Pricop (2013) for Mymaridae.

Voucher specimens of the Diptera and Hymenoptera are deposited in the Swedish Museum of Natural History, Stockholm.

The extracted arthropods from 19 clean nest boxes placed in the field at the beginning of the breeding season and subsequently occupied by Eurasian wrynecks in 2012 were counted and sorted into "Primary Taxonomic Groups" (PTGs), following Roy et al. (2013) and Baardsen et al. (2021). PTGs are a consensus between ecological and taxonomical knowledge. They are higher level identification groups based on taxonomy, ecological role and overall abundance that allow us to focus on trophic guilds (see Table 1). Species with parasitic and non-parasitic stages (e.g., *C. hemapterus*, fleas) were included in the guild ectoparasites. Mites (that can be haematophagous, predatory or detritivores) were not further identified and placed in the guild miscellaneous, which includes arthropods other than Hymenoptera, Diptera and Lepidoptera.

The occurrence of *C. hemapterus* in nest boxes occupied by Eurasian wrynecks was routinely checked during the ringing of the nestlings (about 12 days after the hatching of the first nestling) by scrutinizing all the nestlings in every nest (data from 2005–2012).

Parasitoids of *Carnus hemapterus*

The detritus from 79 nests boxes occupied by Eurasian wrynecks during the period 2005–2011 was hibernated after each breeding season in outdoor conditions in the Stockholm area (ca. 30–500 km away from the nesting habitats) and used to estimate the prevalence of *C. hemapterus* flies and of its parasitoids by collecting the emerging individuals.

In October 2010 all of the collected and overwintered nest material from 17 Eurasian wryneck nest boxes – all with previously verified presence of *C. hemapterus* on the nestlings – was put together, sieved in a 10 mm mesh and dissected selectively for puparia. This sampling was done on 2 June 2011 at a time when the main hatching of *C. hemapterus* flies had passed and the hatching of a uniform cohort of parasitic wasps was known to emerge

Table 1. Guilds and Primary Taxonomic Groups (PTGs) of arthropods found in nest boxes occupied by Eurasian wrynecks in 2012. Prevalence, mean and median intensity and their corresponding 95% confidence intervals (in parentheses) are shown (n = 19 nests). Species with parasitic and non-parasitic stages (e.g. *Carnus hemapterus*, fleas) were included in the guild ectoparasites. Mites were placed in the guild miscellaneous (see Methods).

Guild	PTGs	Prevalence	Mean intensity	Median intensity
Ectoparasites	Fleas	73.7 (48.7–90.8)	14.9 (8.2–25.4)	8.5 (3–17)
	Diptera	94.7 (73.9–99.8)	65.22 (41.2–103.3)	50.0 (10–70)
	Total	100.0 (82.3–100)	72.8 (49.7–107.2)	57 (22–82)
Parasitoids	Hymenoptera	89.5 (66.9–98.7)	48.4 (27.2–92.9)	25 (10–68)
	Diptera	21.1 (6.0–45.6)	4.25 (1.7–5.7)	4.5 –
	Total	89.5 (66.9–98.7)	49.4 (27.9–96.6)	29 (10–69)
Detritivores	Scavenger Diptera	52.6 (28.9–75.6)	53.0 (17.7–139.1)	9.5 (1–125)
	Saprophagous beetles	10.5 (1.3–33.1)	25.5 (1.0–25.5)	25.5 –
	Moths	78.9 (54.4–93.9)	16.8 (9.9–33.2)	10 (3–24)
	Total	78.9 (54.4–93.9)	55.5 (25.9–108.3)	15 (8–97)
Miscellaneous	Spiders	31.6 (12.5–56.5)	3 (1.3–4.0)	3 (1–5)
	Mites	21.1 (6.0–45.5)	80 (25.0–167.5)	55 –
	Total	47.4 (24.4–71.1)	37.6 (10.7–104.6)	5 (1–70)

(I. Struwe, pers. obs.). Isolated puparia were reared separately in glass dishes and hatched insects identified.

The nest material collected in 2012 (see above) also yielded information on the parasitoids of *C. hemapterus*. Importantly, all our approaches were carried out under natural conditions.

Analysis of data

Prevalence (percentage of occurrence of species in nest boxes among all the nest boxes examined), as well as mean and median intensity (number of individuals recorded in the infested nest boxes) of species (and their respective 95% confidence intervals) were calculated. Two thousand replications were used for estimating the confidence intervals. Calculation of these parameters was done using the program Quantitative Parasitology 3.0 (Reiczigel & Rózsa, 2005).

RESULTS

Nidicolous entomofauna

Data from 19 nest boxes occupied by Eurasian wrynecks during the 2012 breeding season revealed a rich arthropod fauna (Table S1). We found at least 9 species of Hymenoptera and 10 species of Diptera, 8 species of Lepidoptera as well as Siphonaptera, spiders, mites and detritivorous Coleoptera. Overall, we collected 3396 individuals.

Diptera was the most abundant group (1721 individuals) and Lepidoptera the least abundant (254 individuals). Concerning trophic levels, the trophic guild with highest prevalence and intensity were ectoparasites whereas parasitoids and detritivores had a similar representation both in prevalence and intensity (Table 1).

We distinguished 9 PTGs, the most prevalent of which were ectoparasitic Diptera and parasitoid wasps and the ones with higher intensity were ectoparasitic Diptera, scavenger Diptera and mites. The number of PTGs per nest varied from 2 to 7 of the 9 PTGs found.

Among the ectoparasites, the most prevalent species was *C. hemapterus* (present in ca. 95% of all nests), that parasitized heavily (>200 individuals) some nests (Table S1). Fleas, some louse flies (*Ornithomyia avicularia*, Linnaeus, 1758) (Diptera: Hippoboscidae) in a single nest and, probably some mites (see below) were also parasites of the avian host.

Parasitoid wasps were well represented (at least 9 species, Table S1), with some species highly prevalent, namely *K. caledonica* and *Apanteles carpatus* Say, 1836 (Hymenoptera: Braconidae), or very abundant, viz. *Nasonia vitripennis* Walker, 1836 (Hymenoptera: Pteromalidae). Among the parasitoids, we also found two species of flies, *Actia pilipennis* Fallén, 1810 and *Actia infantula* Zetterstedt, 1844 (Diptera: Tachinidae).

The most relevant detritivorous PTGs were moths (7 species) and scavenger Diptera, most of them saprophagous during the larval stage: *Gymnochiromyia inermis* Collin, 1933 (Diptera: Chyromyidae), *Tephrochlamys flavipes* Zetterstedt, 1838 (Diptera: Heleomyzidae), *Megaselia* sp. (Diptera: Phoridae) and some gall midges (Diptera: Cecidomyiidae).

Other PTGs, such as spiders and saprophagous beetles were uncommon. The prevalence of mites was low but they reached high numbers in some nests (Table 1). *Ocnerostoma friesei* Svensson, 1966 (Lepidoptera: Yponomeutidae) was an unexpected visitor of wryneck nests since the larvae of this moth are miners of pine needles pupating on the ground. This species was not included in any PTG (see Table S1).

Parasitoids of *Carnus hemapterus*

Prevalence of *C. hemapterus* in the nests collected during the period 2005–2011 was 67% (n = 79 nests). *Kleidotoma caledonica* emerged from 18 out of 79 nests (22.8%), of which 15 were infested by *C. hemapterus* whereas we did not register emergence of carnid flies in 3 (which however does not exclude the occurrence of *C. hemapterus* infestation).

Data for 2012–2013 revealed the occurrence of *C. hemapterus* flies in 94% of nests whereas the prevalence of *K. caledonica* was 79% (i.e., just 3 nests – 16.7% – infested by *C. hemapterus* were seemingly free of the parasitoid).

Specific searching of *C. hemapterus* puparia in nest material from 2010 after the 2011 main emergence period of *C. hemapterus* yielded 11 pupae. Rearing of such puparia resulted in the emergence of 2 *C. hemapterus* flies and 9 individuals of the parasitoid hymenopteran *K. caledonica* (one individual per puparium). We also found 20 non-carnid puparia (superfamily Muscoidea) from which 80 individuals of the hymenopteran parasitoid *N. vitripennis* emerged.

DISCUSSION

Arthropod communities in nest boxes are often highly diverse in terms of species and trophic levels (Tomás et al., 2007; Roy et al., 2013; Masan et al., 2014). Yet, comparisons among studies are difficult to perform given the influence of meaningful factors such as method of extraction of arthropods (Roy et al., 2013), use of clean or previously used nest boxes or time elapsed from the abandonment of the nests to the sampling of the arthropods (Peters & Abraham, 2010; Krištofík et al., 2013). Our study is consistently based on nest material from just one breeding season and sampling was done several months after the nestlings left the nest. Admittedly, our sampling method might omit some species and underestimate the abundance of some taxa. For instance, mite populations are known to increase as the breeding season advances and many mite species emigrate from the nest soon after the nestlings depart (Burtt et al., 1991). Thus, sampling months after the fledging period could account for the low prevalence and abundance of mites recorded, which are otherwise common and abundant inhabitants of nest boxes occupied by birds (Krištofík et al., 2013).

Nidicolous insect community

Although such characteristics of our study led us to expect a not very diverse community, our results show a remarkable richness of species (e.g. at least 9 species of Hymenoptera, 10 species of Diptera, 8 species of Lepidoptera) and a good representation of trophic categories (9 PTGs, including ectoparasites, parasitoids and detritivores). In comparison, Roy et al. (2013) found 16 different insect and arachnid PTGs in a larger number of nest boxes available for Great tits *Parus major* Linnaeus, 1758 two years before. We found that ectoparasitic Diptera and parasitoid wasps were highly prevalent and that ectoparasitic Diptera and scavenger Diptera had the higher numerical representation.

The ectoparasitic Dipteran *C. hemapterus* was the most prevalent (prevalence range: 67–94%, data for 2005–2011 and 2012–2013) and abundant (>100 individuals in at least 20% of the nests) insect in our study, which agrees with results for other species of birds and populations [e.g. Eurasian kestrel *Falco tinnunculus* Linnaeus, 1758 (Fargallo et al., 2001); European roller *Coracias garrulus* Linnaeus, 1758 (Veiga et al., 2019)], which is to be expected given its remarkable colonization ability (Veiga et al., 2020).

The prevalence (89.5%) and richness of parasitoid wasps (at least 9 species, see Table S1) recorded in this study is particularly remarkable. For example, we found 5 species of parasitoid wasps attacking Diptera (*K. caledonica*, *N. vitripennis*, *Basalys* sp., *Phygadeuon* sp., *Dibrachys* sp.). In comparison, Peters & Abraham (2010) found 10 species of parasitoid wasps of Diptera in a much higher number of nest boxes occupied by various cavity-nesting songbirds. They found that only *N. vitripennis* was common whereas most of the remaining species were scarce and unspecialized. This wasp is a specific bird nest inhabitant attacking blow flies (Calliphoridae) and other cyclorrhaphous flies (Peters, 2010; Peters & Abraham, 2010; Garrido-Bautista et al., 2020). In our study, *N. vitripennis* was the most abundant wasp species whereas the most prevalent were *A. carpatus* and *K. caledonica*. *Apanteles carpatus* is a parasitoid of the lepidopteran family Tineidae (detritivorous moths), which was abundant in our nest rearings. Tineidae are also parasitized by parasitic flies (Tachinidae) such as *A. infantula* a specific parasite of the skin moth *Monopis laevigella* Denis & Schiffermüller, 1775 (Belshaw, 1993; Tschorsnig & Herting, 1994) and also reared from bird nests (Andersen, 1996). *Actia pilipennis,* which also hatched in a small number from the nests, is a parasitoid of a wide range of concealed microlepidoptera, mainly Tortricidae (Mesnil, 1965; Belshaw, 1993; Tschorsnig & Herting, 1994). No Tortricidae were reared from the nests but Tineidae obviously is an important host population in the nests and a possible host.

Species of the genus *Kleidotoma* are generally parasitoids of different fly families living in concealed and decomposing material, including bird nests (Quinlan, 1986, 1988; van Noort, 2021). From a taxonomic point of view, this is a problematic genus since it is common and species-rich. The species diversity even in Europe is seriously underestimated with many undescribed taxa (Forshage & Nordlander, 2008; Buffington et al., 2020). The only modern revision of a regional European fauna is Quinlan's for the British Isles (Quinlan, 1967, 1974, 1978).

Concerning the other parasitoid wasps found in our study, *Bairamlia fuscipes* Waterston, 1929 (Hymenoptera: Pteromalidae) is a seldom recorded parasitoid of bird fleas (Siphonaptera: Ceratophyllidae) which were common in the nests. The genus *Basalys* (Hymenoptera: Diapriidae) has been reared from different families of small flies, such as Phoridae. A possible host for this species in our study might have been *G. inermis* Collin, 1933 (Diptera: Chyromyidae), but also *Megaselia* spp. (Diptera: Phoridae). *Camptoptera* spp. (Hymenoptera: Mymaridae) are egg parasitoids and difficult to link to any specific host found in this study. Wasps of the genus *Phygadeuon* (Hymenoptera: Ichneumonidae) (parasitoids of cyclorraphous flies) or the genus *Dibrachys* (Hymenoptera: Pteromalidae) are generalists with respect to both habitats and hosts and are natural members of the nest box ecosystem (McKay & Galloway, 1999; Peters, 2011). Most species of the genus *Pachyneuron* (Hymenoptera: Pteromalidae) are hyperparasitoids on primary parasitoid wasps of Braconidae, Aphelinidae and Encyrtidae (Gibson, 2001; van Noort, 2021).

Our results include some other taxa that could be mistakenly labelled as indifferent components of the nest fauna but that may in fact have important roles in the nest box mesocosm studied (as noted by Krištofík et al., 2013). For instance, spiders are cited as predators of carnid flies (Salido et al., 2021), carnivorous beetles may prey on fleas (Šustek & Jurik, 1980), and detritivores (such as fly larvae and beetles) may contribute to nest sanitation that, in turn, may improve the growth and health of nestlings (Krištofík et al., 2017).

Parasitoids of *Carnus hemapterus*

In Quinlan's (1978) key, the *Kleidotoma* species associated with *C. hemapterus* in this study (see below) runs to *K. caledonica* Cameron, 1888 (Hymenoptera: Figitidae), which is recognizable especially as the antennae of the female have short, subquadratic pre-club flagellar articles and a three-segmented antennal club where the first segment (F9) is clearly shorter and narrower than the second (F10), together with a combination of other character states (often more variable). Our specimens correspond well with Quinlan's neotype (Quinlan, 1974) of *K. caledonica*, so there is no uncertainty in applying this name here, though with the genus being understudied it is quite possible that future revisions may have to divide *K. caledonica* as currently conceived into more than one species or refine its boundaries in some other way. These issues reveal the importance of taxonomists, whose expertise is not always recognized by current scientific policies.

Our results presented indicate a close association between *C. hemapterus* and *K. caledonica* since: (i) this wasp emerged only from *C. hemapterus* pupae and not from other dipterous pupae, (ii) prevalence of infection in the study area is seemingly high. Nine (81%) out of 11 diapausing *C. hemapterus* pupae were parasitized and data suggest that a high percentage of the nests infested with *C. hemapterus* flies were also infested by *K. caledonica* (range: 83–100%); (iii) we observed a close match between the emergence period of *K. caledonica* (restricted to July) and the larval period of *C. hemapterus* (I. Struwe, unpubl. data). Such synchronization could account for the high parasitic pressure found (see Peters & Abraham, 2010 for the importance of host and parasite phenology), although other factors such as host density can also be important (Garrido-Bautista et al., 2020).

The neotype of *K. caledonica* was collected from a heron's nest (but with no indication of the dipteran host). Quinlan (1978) also cited it being reared from *Spelobia manicata* (Richards, 1927) (Diptera: Sphaeroceridae) and this probably represents label data of other specimens in the Natural History Museum, London. *Spelobia manicata* has been recorded as a necrophagous species (Buck, 1997) although not specifically associated with bird nests. Host data on labels in collections are often not entirely reliable, frequently being anecdotal associations or guesswork rather than the result of controlled rearings. The need for caution is perhaps emphasised by the fact that Quinlan in the same work (1978) also cited another *Kleidotoma* species, *K. psiloides* Westwood, 1833 from *S. manicata* too, and thus presumably with the same origin of the specimens and the association – while *K. psiloides* is otherwise known as a parasitoid of Drosophilidae and not Sphaeroceridae. Thus, the association of *K. caledonica* with heron's nests may be regarded as more substantial than that with the named sphaerocerid. For that reason, it is notable that *C. hemapterus* is known to infest herons (Grimaldi, 1997).

Recently Salido et al. (2021) reported the emergence of *Chartocerus conjugalis* from isolated *C. hemapterus* pupae from nests of *C. garrulus* (Coraciiformes: Coraciidae) in Spain. They found lower prevalence (ca. 21%) and intensity (an average of ca. 11% pupae parasitized per infected nest), but unlike our study, these figures could be influenced by the fact that *C. hemapterus* pupae were kept in room conditions. It is important to note that *Chartocerus* spp. hitherto were known only as hyperparasitoids of primary parasitoid wasps (Woolley, 1988; Schimdt et al., 2019).

CONCLUSIONS

Our study reveals that bird nest boxes are the arena of complex interspecific interactions and food webs of whose components we know little, including the identity and specificity of their associations. This is particularly the case of parasitoids, for which available host records are notoriously unreliable, being anecdotal, often old, from uncontrolled circumstances, and frequently with uncertain identifications of host and/or parasitoid. This gap in our knowledge hampers further understanding of food web topologies, resource dynamics and the ecology of interspecific interactions. Here we contribute to fill such gap by offering information about occurrence, abundance and life history of poorly known species of different trophic guilds and their interactions. We specifically report the association between *K. caledonica* and *C. hemapterus*. The scarce information of this parasitoid associates it with birds' nests, and our results suggest that it may be a specialised parasitoid of the avian ectoparasite *C. hemapterus*, which could induce trophic cascades, releasing avian hosts from detrimental effects induced by the parasites.

ACKNOWLEDGEMENTS. E. Arbinger, Mariefred, Sweden, provided the nest material and data on Eurasian wryneck from his countless nest boxes. L. Carlsson, Eskilstuna, Sweden, was the ornithological expert and an inspiring companion during all field work. Several members of the Swedish Wryneck Project (a citizen science project) from different parts of Sweden kindly supplied us with nest box material. H. Hellberg, Stockholm, Sweden and Håkan Elmquist, Mariefred, Sweden generously identified the Lepidoptera. L. Struwe, New Brunswick, U.S.A., gave editorial assistance and comments on an earlier version of this manuscript. We are thankful to two anonymous referees for their constructive criticism. F. Valera was supported by grant PGC2018-097426-B-C22, funded by MCIN/AEI/10.13039/501100011033 and by "ERDF A way of making Europe". None of the authors has any conflict of interest to declare.

CONTRIBUTION OF AUTHORS. I. Struwe conceived and designed the study, performed the fieldwork and identified the Diptera. M. Forshage identified the Hymenoptera. All authors contributed to data analysis and writing. All authors accepted the final version of the manuscript.

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Received September 13, 2022; revised and accepted March 10, 2023
Published online April 17, 2023

Table S1. Arthropod fauna record in 19 nest boxes occupied by Eurasian wryneck, *Jynx torquilla*, in Sweden in 2012–2013. Primary Taxonomic Groups (PTGs), prevalence (95% Confidence Interval), mean and median intensity and range (maximum and minimum number of individuals per nest) are listed. N.c. – not classified within any PTG.

TAXON	PTG	Prevalence (95% CI)	Mean intensity	Median intensity	Range
HYMENOPTERA					
Apanteles carpatus (Say, 1836), Braconidae	Parasitoid wasp	78.9 (54.4–93.9)	13.7	5.0	1–109
Basalys sp., Diapriidae	Parasitoid wasp	5.3 (0.1–26.0)	3.0	3.0	–
Kleidotoma caledonica (Cameron, 1888), Figitidae	Parasitoid wasp	78.9 (54.4–93.9)	20.33	13.0	1–64
Phygadeuon sp., Ichneumonidae	Parasitoid wasp	5.3 (0.1–26.0)	1.0	1.0	–
Camptoptera sp, Mymaridae	Parasitoid wasp	5.3 (0.1–26.0)	1.0	1.0	–
Bairamlia fuscipes (Waterston, 1929), Pteromalidae	Parasitoid wasp	5.3 (0.1–26.0)	1.0	1.0	–
Dibrachys sp., Pteromalidae	Parasitoid wasp	26.3 (9.1–51.2)	1.4	1.0	1–2
Nasonia vitripennis (Walker, 1836), Pteromalidae	Parasitoid wasp	26.3 (9.1–51.2)	59.6	28.0	3–221
Pachyneuron sp., Pteromalidae	Parasitoid wasp	5.3 (0.1–26.0)	2.0	2.0	–
DIPTERA					
Pegomya sp., Anthomyiidae	Scavenger fly	26.3 (9.1–51.2)	4.6	5.0	1–10
Calyptrata spp.	Scavenger fly	10.5 (1.3–33.1)	87.5	87.5	50–125
Carnus hemapterus (Nitzsch, 1818), Carnidae	Ectoparasitic fly	94.7 (73.9–99.8)	65.1	50.0	2–250
Cecidomyiidae spp.	Scavenger fly	5.3 (0.1–26.0)	8.0	8.0	–
Gymnochiromyia inermis (Collin,1933), Chyromyidae	Scavenger fly	26.3 (9.1–51.2)	58.6	2.0	1–250
Tephrochlamys flavipes (Zetterstedt,1838), Heleomyzidae	Scavenger fly	10.5 (1.3–33.1)	15.0	15.0	1–29
Ornithomyia avicularia (Linnaeus,1758), Hippoboscidae	Ectoparasitic fly	5.3 (0.1–26.0)	2.0	2.0	–
Megaselia sp., Phoridae	Scavenger fly	5.3 (0.1–26.0)	1.0	1.0	–
Actia infantula (Zetterstedt,1844), Tachinidae	Parasitoid fly	21.1 (6.0–45.5)	4.0	4.0	1–7
Actia pilipennis (Fallén,1810), Tachinidae	Parasitoid fly	5.3 (0.1–26.0)	1.0	1.0	–
LEPIDOPTERA					
Monopis fenestratella (Heyden,1863), Tineidae	Moth	15.8 (3.3–39.5)	8.0	9.0	5–10
Monopis laevigella (Denis & Schiffermüller, 1774), Tineidae	Moth	26.3 (9.1–51.2)	12.8	5.0	1–29
Monopis weaverella (Scott, 1858), Tineidae	Moth	10.5 (1.3–33.1)	4.5	4.5	1–8
Niditinea striolella (Matsumura, 1931), Tineidae	Moth	21.1 (6.0–45.5)	10.0	8.5	2–21
Tinea pellionella (Linnaeus, 1758), Tineidae	Moth	15.8 (3.3–39.5)	2.0	2.0	1–3
Tinea svenssoni (Opheim, 1966), Tineidae	Moth	15.8 (3.3–39.5)	7.33	5.0	4–13
Tinea trinotella (Thunberg, 1794), Tineidae	Moth	15.8 (3.3–39.5)	34	15	1–86
Ocnerostoma friesei (Svensson, 1966), Yponomeutidae	N.c.	5.3 (0.1–26.0)	2.0	2.0	–
ARTHROPODS OTHER THAN HYMENOPTERA, DIPTERA AND LEPIDOPTERA					
Acari spp.	Mites	21.1 (6.0–45.5)	80	55	10–200
Araneae spp.	Spiders	31.6 (12.5–56.5)	3	3	1–5
Coleoptera, Dermestidae spp.	Saprophagous beetles	10.5 (1.3–33.1)	25.5	25.5	1–50
Siphonaptera spp.	Fleas	73.7 (40.7–90.8)	14.9	8.5	1–50