

Are parasite intensity and related costs of the milichiid fly *Carnus hemapterus* related to host sociality?

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Abstract Ectoparasites have often been shown to have detrimental effects on their host. Not much is known, however, about determinants of infestation, e.g. the question of which factors affect distribution and occurrence of parasites on different host species (degree of host specificity) and their infestation rates. In this study we examine possible effects of host determinants on parasite intensity of *Carnus hemapterus* (Carnidae), an ectoparasitic fly on nestling birds, in the European bee-eater (*Merops apiaster*), which is a common host of *C. hemapterus*. Our results show that European bee-eaters seem to be one of the most heavily infested host species of *C. hemapterus*. We found that brood size, nestling age, and colony size are the most important determinants of infestation by *C. hemapterus*. This parasite seems to prefer medium-sized bee-eater chicks and to select them according to their condition. Our results further suggest a negative effect of *C. hemapterus* on chick development.

Keywords *Carnus hemapterus* · Parasite intensity · Colony size · *Merops apiaster*

Introduction

Arthropods are a rather well studied group of bird ectoparasites (reviewed by Janovy 1997) and it has been shown that infestation of adult birds may result in anaemia, feather damage, decrease in clutch and brood size, increased nestling mortality, and nest desertion (Clayton and Tompkins 1995; De Lope and Møller 1993; Figuerola 2000; Lehmann 1993; Møller 1993, 1997; Poiani 1993).

In contrast with most other bird ectoparasites the 2 mm long bloodsucking milichiid fly *Carnus hemapterus* Nitzsch is nestling-specific (Kirkpatrick and Colvin 1989; Marshall 1981; Walter and Hudde 1987) and has been found on many bird species, even across different bird orders distributed over the Old and the New Worlds (Bequaert 1942; Canning 1986; Capelle and Whitworth 1973; Collin 1939; Grimaldi 1997; Guiguen et al. 1983; Janovy 1997; Matyukhin and Krivosheina 2008). *C. hemapterus* is a mobile ectoparasite species with a typical horizontal transmission mode among chicks within a nest and between nests even of different species (Valera et al. 2003). The winged flies actively search for the hosts (nest) and later lose their wings (Hennig 1937; Lloyd and Philip 1966; Marshall 1981). Even the dealated adults can move between nests by walking. Females deposit their eggs in the nest material (Marshall 1981; Walter and Hudde 1987). The egg and larvae stages are complete at the end of the summer. *C. hemapterus* overwinter as pupae in the nest of their bird host and adults usually emerge when host chicks hatch (Marshall 1981). There is evidence of a negative effect of *C. hemapterus* intensity on chick condition in the Northern Flicker *Colaptes auratus* (Wiebe 2009), Spotless Starlings *Sturnus unicolor* (Avilés et al. 2009), and our European bee-eaters *Merops apiaster* (unpublished data). Identification of factors affecting *C. hemapterus* intensity seems to be crucial.

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Even if a host seems suitable, *C. hemapterus* intensity varies substantially among and within host species. For example, variation in parasite resistance between individuals of a species is one factor responsible for variation in ectoparasite intensity (Roulin et al. 2001). Another likely determinant of parasite intensity could be transmissibility, which may depend on host density or distance between host nests. Walter and Hudde (1987) and Liker et al. (2001), for example, mentioned that in starlings (*Sturnus vulgaris*) the prevalence of *C. hemapterus* was much higher in a dense population.

In this study, we therefore address the importance of factors determining the extent of infestation of nestling European bee-eaters as host of *C. hemapterus*. Specifically, we examine factors related to the social environment of nestling, e.g. number and age of nest mates, host colony size, host nest density, and nearest distance between neighbouring nests. Furthermore, we investigate the importance of infestation intensity of *C. hemapterus* on nestling body condition. Most host species of *C. hemapterus* studied so far are solitary breeding species with considerable nest distances. Given their transmission mode, it seems likely that nest distance affects transmissibility of this ectoparasite. The European bee-eater is a colonial species with a varying colony size and inter-nest distance (Hoi et al. 1998) and hence it is an appropriate species for study of host density effects. Because *C. hemapterus* is exclusively found on nestlings, horizontal transmission of *C. hemapterus* between adult bee-eaters and vertical transmission between parents and offspring is less likely to be important. The colonial nesting situation with short inter-nest distances may be a crucial variable for transmissibility and intensity of *C. hemapterus* infestation.

Materials and methods

Host species and study area

European bee-eaters raise their chicks in cavities at the end of deep, usually horizontal burrows (75–150 cm; Glutz von Blotzheim and Bauer 1980) which they dig into mainly vertical sand or earth banks. Adult bee-eaters are parasitised by several ectoparasite species (details are given by Hoi et al. 1998 and Krištofik et al. 1996). Nestlings are mainly infested by *C. hemapterus*; the extent of infestation by other ectoparasites (chewing lice) is, in comparison, fairly low (Hoi et al. 1998).

Bee-eaters and their parasites were studied in southern and eastern Slovakia in the breeding seasons of 1996–1998. All study sites were situated in abandoned sandpits of different size. We investigated eleven sites in 1996 and 1997 and fourteen in 1998 and collected data from 58

nests. Since some of the sites were sampled in more than one year, a total of 21 different sites, comprising single breeding pairs and colonies of up to 79 breeding pairs, were examined. The colony sites have been described in detail by Hoi et al. (2002). Although some of the sites were sampled two or three times over the years we treated each investigation as independent between years, because the variable investigated was colony size and:

1. the number of breeding pairs always varied for the same locality between successive years;
2. there were no recaptures of banded birds from year to year in any of these localities (Hoi et al. 2002); and
3. the nest cavities sampled for *C. hemapterus* between years were always different.

However, we cannot exclude the possibility that the intensity and prevalence of *C. hemapterus* in one year at a given colony site can, indeed, depend on the previous year. The winged morph may be able to actively move into a colony but, on the other hand, they winter in bee-eater burrows as pupae.

To represent the mean fate (e.g. ectoparasite intensity per colony site) of all colonies equally we increased sample size (varying from one to fifteen) depending on colony size (relationship between number of breeding pairs and sample size: $r_s = 0.83$, $P < 0.001$, $n = 36$). Mean (\pm SE) colony size was 7.1 ± 1.6 breeding pairs per locality ($n = 36$). On average about half ($41.2\% \pm 3.9$ SE) of all nests of a colony site were included in the analyses (details are given by Hoi et al. 2002).

We obtained nestlings with the help of a bent spoon attached to a long stick. This method worked very well with nestlings of every age (Hoi et al. 2002). For nestlings we measured wing length to the nearest 0.1 mm (following Svensson 1993) using callipers and weighed them to within 0.1 g with an electric balance.

C. hemapterus counts

To collect *C. hemapterus* from each nestling we blew them into a plastic bag and removed the remaining individuals with fingers or forceps. In 1997 and 1998 we also extracted the entire nest material (sand and detritus) with a spoon from the cavity and the burrow. This material (about 2 kg of sand) was immediately searched for *C. hemapterus*. To this end, the sand was spread in a thin layer (1 cm) on a white plate. After some minutes, all *C. hemapterus* moved to the surface and were collected with a teaspoon. Parasite collection was restricted to two weeks (the first two weeks in July) during the chick feeding period of 1996–1998.

Following Clayton and Moore (1997) we used the term “parasite intensity” for the number of parasites harboured by an individual host and “prevalence” as the proportion of

infested individuals (nests) of a population (colony) but also as the proportion of infested individuals per nest.

Statistical analysis

For statistical comparison parametric tests were used when requirements for normality were met. Means and SE are given throughout. *C. hemapterus* counts were $\log x + 1$ transformed to stabilise variances. When we were taking nestlings out of the nest, some parasites left the nestling, and therefore we also took the whole nest material (sand) to obtain an idea of the real parasite intensity/nest and nestling. Comparing the number of *C. hemapterus* on nestlings and in the nest material we found that, on average, 42.2 ± 7.7 *C. hemapterus* remained in the nest material, that is 47.5% of all *C. hemapterus* found in a nest. Comparing the number of *C. hemapterus* on the nestlings with the number left in the material, however, we found a significant positive relationship ($r = 0.83$, $P < 0.0001$, $n = 58$ nests). This suggests that even when only *C. hemapterus* found on nestlings are compared the results reflect very well the relative parasite intensity at each nest.

Nestling age was categorised into three groups according to wing length, with wing length less than 20 mm (chicks younger than nine days), wing length between 20 and 60 mm (chicks younger than eighteen days), and longer wings (chicks eighteen days and older) (details of age determination are given by Hoi et al. 2002).

Data from three years were pooled, because we found no significant variation of *C. hemapterus* intensity in the three study years (Kruskal–Wallis test: $T = 0.1$, $df = 2$, $P > 0.9$). Testing the same null hypothesis repeatedly we used a Bonferroni correction to avoid type I error (Wright 1992), to ensure that significant results did not arise solely by chance. For statistical comparison of chick growth a *t*-test was applied for equal slopes (Kleinbaum and Kupper 1978).

Results

Parasite intensity per nest averaged 89.1 ± 11.7 *C. hemapterus*, ranging from zero to 515 ($n = 103$ nests) and average intensity/nestling was 18.6 ± 2.6 , ranging from zero to 302 ($n = 103$). Parasite intensity followed a left-tailed negative binomial distribution (Fig. 1) and depended on nestling age (ANCOVA: $F = 7.05$, $df = 2$, 103, $P < 0.002$; using colony size as the covariate) (Fig. 2) with the highest *C. hemapterus* intensity on medium age nestlings. *C. hemapterus* numbers were lower on very young nestlings (wing length < 20 mm) and on older nestlings (wing length > 80 mm).

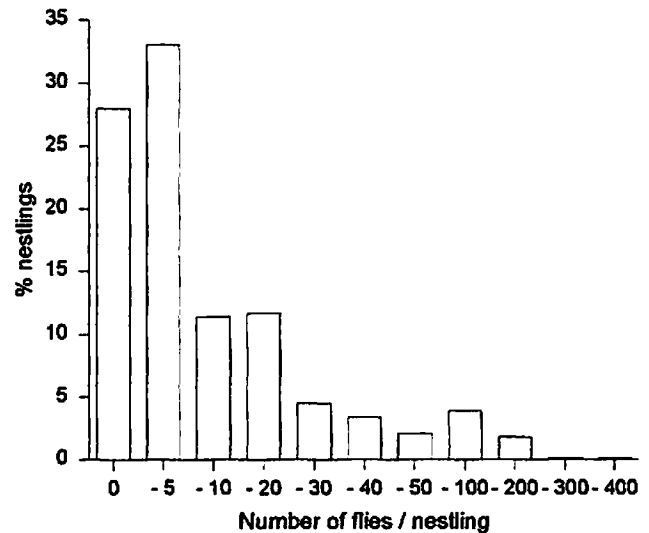


Fig. 1 The relative distribution of parasite intensity (number of flies) per nestling in our host population ($n = 58$ nests)

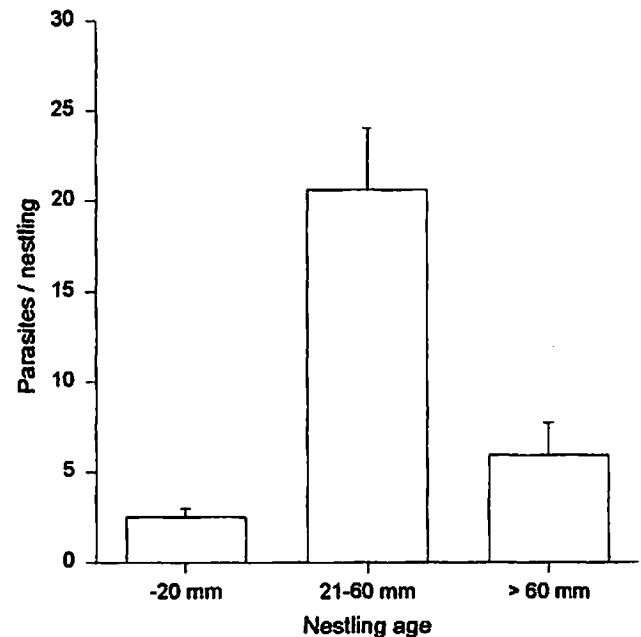


Fig. 2 Average (\pm SE) number of parasites per nestling in relation to three nestling sizes (age): nestlings with a wing length up to 20 mm (8 days) and up to 60 mm (17 days), and larger (older) nestlings

We also found a significant variation in *C. hemapterus* intensity/nestling with brood size (ANOVA: $F = 2.79$, $df = 6, 103$, $P = 0.01$) (Fig. 3). There was no linear increase or decrease; the intensity was highest for two nestlings.

Nest prevalence of *C. hemapterus* was 92.2% (94/102) and nestling prevalence was 71.7% (309/431). In half (48/94) of infested nests, however, we also found uninfested nestlings. *C. hemapterus* are very mobile and could, in principle, move between nestlings and, hence, could move from the nestling that is taken out to the next. From an

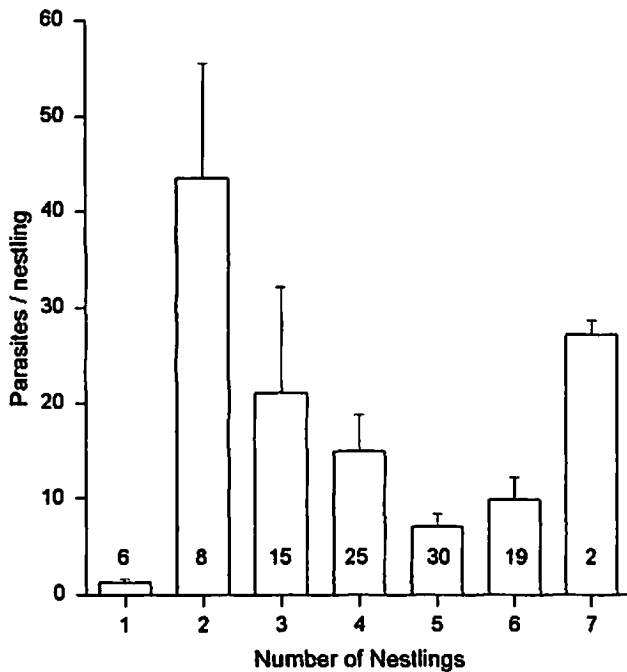


Fig. 3 Average (\pm SE) number of parasites per bee-eater nestling in relation to brood size. The number of nests sampled is given in the bars

earlier experiment with nestlings we know that they are reluctant to leave the host, especially when we bother the host (e.g. when we handle them) or the flies (e.g. when collecting them with forceps). In cases of disturbance, rather than move away from the host *C. hemapterus* try to escape and hide in body cavities (e.g. in the ears, in neck folds, under the wings, and between feather kills). In line with this our results for a subsample of 24 nests with five eggs actually did not reveal an order effect, which means that *C. hemapterus* intensity on nestlings is independent of the order of collection (repeated measures ANOVA. $F = 0.88, P > 0.49, df = 4, 24$). There was significant variation in parasite intensity/nestling with prevalence/nest (Fig. 4). Parasite prevalence/nest increased with intensity ($r = 0.45, P < 0.0005, n = 103$).

Comparing the sex ratio of *C. hemapterus* we found more males than females (1.28:1; 1775/1383, $\chi^2 = 49.1, P < 0.0001$) and 96.4% of *C. hemapterus* were dealated individuals (41.9% females and 58.1% males).

In 86 out of 103 (83.5%) nests we found infested and uninfested nestlings. A within-brood comparison of infested and uninfested nestlings (using averages for uninfested and infested nestlings of a nest) revealed a significant difference in wing length and growth. Infested chicks are significantly larger (difference between wing length: paired t -test: $t = -5.6, P < 0.0001, n = 86$ nests) and significantly heavier than expected for a given size in comparison with uninfested chicks of the same nest (residual weight,

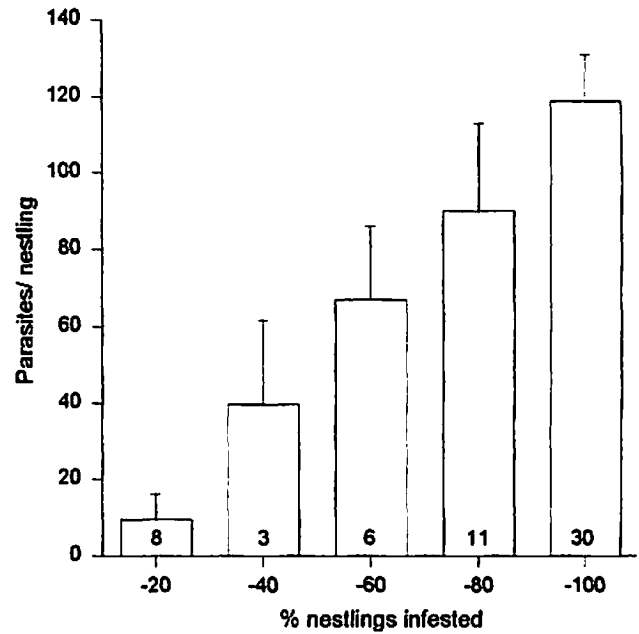


Fig. 4 Average (\pm SE) number of parasites per bee-eater nestling in relation to the number (%) of chicks harbouring parasites. The number of sampled nests is given in the bars

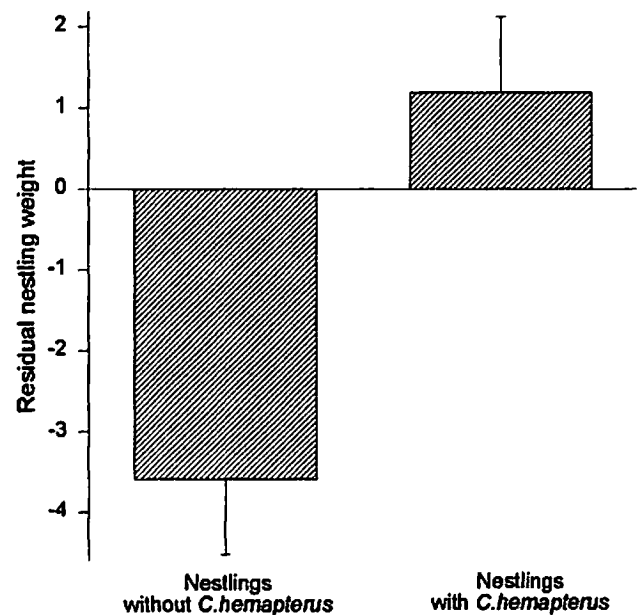


Fig. 5 Average (\pm SE) residual weight (adjusted for wing length) for bee-eater nestlings with and without *C. hemapterus*

adjusted for wing length: $t = -5.6, P < 0.0001, n = 86$) (Fig. 5). Examining the relationship between wing length and weight between infested and uninfested chicks we found a steeper slope for uninfested chicks, which suggests that nestlings without parasites grow faster (uninfested nestlings: $y = 0.66x + 10.3$, infested nestlings > 20 parasites: $y = 0.49x + 18.7, t$ -test: $t = 2.1, P = 0.034$).

Table 1 Relationship between different measures of colony size (number of breeding pairs, nest density, and distance between nests) and *C. hemapterus* intensity ($n = 37$)

	<i>R</i>	<i>P</i>
Number breeding pairs (log)	0.46	0.012
Nest density/m ² (log)	0.50	0.003
Inter-nest distance (log)	-0.58	0.0006

We used a Bonferroni correction to avoid type I errors

We found a significant variation in the *C. hemapterus* intensity/nest between colony sites (ANOVA: $F = 4.71$, $P < 0.03$, $df = 1, 36$). This variation may be due to variation in colony size because we found that all three measures describing colony size (colony size, nest density, and inter-nest distance) were significantly related to *C. hemapterus* intensity (Table 1). Only inter-nest distance entered into a stepwise multiple regression model suggests that inter-nest distance is the best predictor for *C. hemapterus* intensity ($F = 18.1$, $P < 0.0001$, $df = 1, 36$, $R^2 = 0.34$, $r_{part} = -0.58$).

Discussion

Parasite intensity among nestling bee-eaters seems to be much higher than for all other species we are aware of (Dawson and Bortolotti 1997; Guiguen et al. 1983; Walter and Hudde 1987). Liker et al. (2001) reported a maximum of 284 *Carnus hemapterus* for starling nests, whereas the largest number we found in a bee-eater nest (with five chicks) was 515 individuals. In many other bird species, even with larger body size, for example the Barn Owl *Tyto alba* (Kirkpatrick and Colvin 1989; Roulin et al. 2001), American Kestrel *Falco sparverius* (Dawson and Bortolotti 1997), or European Kestrel *Falco tinnunculus* (Fargallo et al. 2001, own unpublished data), parasite intensity is much lower. In comparison with most of these species the European bee-eater is a highly colonial species with probably the highest breeding densities. In fact, our results indicate an effect of breeding density on parasite intensity. We found a strong positive correlation between measures of nest density and colony size of bee-eaters and parasite intensity. Our results actually show that the best fit is between distance to the nearest neighbour and parasite intensity. Walter and Hudde (1987) also mentioned a density-dependent effect. They found that *Carnus hemapterus* prevalence on starlings increases with breeding density and varies between 25% and 100%. Our results seem reasonable because *C. hemapterus* is very mobile and can disperse over long distances via the alated morph (Marshall 1981), and *C. hemapterus* after arriving at a place and after losing its wings is still able to move to

neighbouring nests if not too far away (Marshall 1981). Another, not mutually exclusive, explanation of the particularly high intensity and prevalence of infection in European bee-eaters might be connected with the special conditions inside the burrow. For example, burrows more than one meter deep in the sand may protect them from frost and promote survival of the pupae.

Prevalence and intensity of *Carnus hemapterus* is also related to the age of the nestlings. Nestling birds seem to become a hostile environment, owing to increased density and layering of feathers (Dawson and Bortolotti 1997). Dawson and Bortolotti (1997) reported a significant decrease in *C. hemapterus* prevalence with nestling age in American kestrels. In contrast with that study, in our bee-eater population parasite intensity increased with age, was highest for medium age, and decreased for older nestlings. Walter and Hudde (1987) and Liker et al. (2001) found a similar pattern for starlings (their highest parasite intensity was on nestlings six to eight days old). Alternatively, however, the parasite may be forced to synchronize their life cycle with the development of the host and this selective pressure could similarly explain the coincidence between the peak of infection intensity with a given nestling age.

Several results indicated that *C. hemapterus* moves between host individuals within a brood and that it is highly selective when choosing a host (Valera et al. 2004). We found that parasite prevalence per nest depends on their intensity. This, in contrast, suggests competition between parasites increases with intensity and that they try to disperse more evenly in a nest when their abundance increases. However, in 50% of all infested nests we found host individuals without any flies, which indicates that *C. hemapterus* prefer some chicks to others. Within a brood, chicks with flies are significantly larger than chicks without flies, but the individual hosts used as a habitat are also heavier than expected for their body size. This does not allow any assumptions about the effect (positive or negative) of the parasite on the host but indicates that *C. hemapterus* prefers individual hosts in better condition (Valera et al. 2004). Differences in developmental patterns, in contrast, suggest that *C. hemapterus* may have a negative effect on chick growth. Thus experimental manipulation of parasite intensity would be necessary to determine whether a negative effect of *C. hemapterus* really exists. Under natural conditions, however, a negative effect might not be that strong, because *C. hemapterus* quickly moves between hosts and may therefore change its habitat as soon as the chick's condition worsens. On the other hand, host nest site selection may also affect parasite intensity. Preliminary results suggest that *C. hemapterus* intensity varies with colony size but also between centre and edge nests of a colony (unpublished results). Hence host individuals may

trade parasite intensity against other negative impacts, for example nest predation. They may prefer to breed in a big colony with a higher parasite intensity or a smaller colony with potentially higher nest predation.

Zusammenfassung

Hängen Intensität und Kosten des Befalls Durch die Gefiederfliege *Carnus hemapterus* von der Geselligkeit des Wirtes ab?

Obwohl Ektoparasiten meist negative Auswirkungen auf ihren Wirt haben, weiß man generell sehr wenig darüber, welche Faktoren für den Parasitenbefall verantwortlich sind. Im Speziellen ist kaum bekannt, welche Faktoren z. B. die Verbreitung von Ektoparasiten und ihr Auftreten an bestimmten Wirtsarten (Wirtsspezifität) ermöglichen und welche die Befallsstärke beeinflussen.

In dieser Studie untersuchen wir, welche Faktoren die Befallsintensität durch *Carnus hemapterus* (*Carnidae*) auf Nestlingen des Europäischen Bienenfressers (*Merops apiaster*) regulieren. *C. hemapterus* ist eine Fliegenart, die auf Nestlingen vieler Vogelarten parasitiert, wobei der Europäische Bienenfresser ein äußerst häufiger Wirt sein dürfte. Unsere Ergebnisse zeigen, dass Europäische Bienenfresser zu einer der am stärksten von *C. hemapterus* befallenen Vogelarten zählen. Die Größe der Brut, das Alter der Nestlinge und die Größe der Brutkolonie scheinen bei der Wirtswahl eine Rolle zu spielen. Die Befallsintensität innerhalb der Brut deutet darauf hin, dass *C. hemapterus* mittelgroße Bienenfressernestlinge und solche in guter physischer Kondition bevorzugt. Unsere Ergebnisse lassen zudem darauf schließen, dass sich *C. hemapterus* Befall negativ auf die Entwicklung der Jungen auswirkt.

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