

# Ecology of parasitism of nestling American kestrels by *Carnus hemapterus* (Diptera: Carnidae)

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**Abstract:** Little is known about the basic biology of *Carnus hemapterus* (Diptera: Carnidae), a haematophagous parasite of nestling birds. We therefore explored the patterns of *C. hemapterus* infestations by repeatedly examining American kestrel (*Falco sparverius*) nestlings from 50 nests in north-central Saskatchewan. Most infestations occurred before chicks were 12 days old and were more frequent early in the breeding season. Nestlings from larger broods had higher prevalences of *C. hemapterus*, but we did not detect differences in intensity of infestations between broods of different sizes. Within broods up to 5 days old, the heaviest nestlings were preferentially infested by *C. hemapterus*. Although evidence suggests that ectoparasite infestations are harmful to hosts, we did not detect any mortality attributable to *C. hemapterus*. Similarly, we did not observe negative effects of *C. hemapterus* infestations on nestling mass, length of the tenth primary flight feather, haematocrit, or total plasma protein concentration at 24 days old.

**Résumé :** La biologie de *Carnus hemapterus* (Diptera: Carnidae), un parasite hématophage des oisillons au nid, est très mal connue. Nous avons donc étudié les infestations de *Carnus* par des examens répétés d'oisillons de la Crécerelle d'Amérique (*Falco sparverius*) dans 50 nids du centre nord de la Saskatchewan. La plupart des infestations commençaient avant que les oisillons n'atteignent l'âge de 12 jours et elles étaient plus fréquentes au début de la saison de la reproduction. La fréquence des infections était plus grande chez les oisillons des couvées plus nombreuses, mais la gravité des infections ne semblait pas varier en fonction du nombre d'oisillons dans la couvée. Au sein des couvées de 5 jours ou moins, ce sont les individus les plus lourds qui étaient le plus infectés. Bien que, de façon générale, les infections d'ectoparasites nuisent aux hôtes, aucune mortalité attribuable à *C. hemapterus* n'a été enregistrée chez les oisillons. Nous n'avons pas non plus constaté d'effets négatifs des parasites sur la masse des oisillons, sur la longueur de la dixième rémige primaire, sur l'hématocrite ou sur la concentration plasmatique totale des protéines à 24 jours. [Traduit par la Rédaction]

## Introduction

It is becoming increasingly apparent that ectoparasites can play a significant role in altering the behaviour and ecology of their avian hosts. For example, ectoparasites have been shown to decrease nestling body mass, body size, and haematocrit (Whitworth 1976; Brown and Brown 1986; Møller 1993; Richner et al. 1993; Merino and Potti 1995; Criste et al. 1996; Dufva and Allander 1996) and increase rates of nestling mortality (Brown and Brown 1986; Richner et al. 1993) and natal dispersal (Brown and Brown 1992). In addition, parent birds occupying infested nest sites may have reduced clutch or brood sizes (Møller 1993; Poiani 1993), fewer second clutches (Møller 1993), and longer intervals between successive clutches (de Lope and Møller 1993).

While most studies of avian ectoparasites have examined fleas (Siphonaptera: Ceratophyllidae) and fowl mites (Parasitiformes: Dermanyssidae) (e.g., see Møller et al. 1990), a common species of ectoparasite, *Carnus hemapterus* Nitzsch (Diptera: Carnidae), has been largely overlooked. Adults of this small (ca. 2 mm) fly have a Holarctic distribution

(Sabrosky 1987) and have been documented in bird nests throughout North America (Capelle and Whitworth 1973). Host records suggest that *C. hemapterus* do not exhibit host specificity but tend to occur on neonates of cavity-nesting birds or those species with nest sites protected from the elements (Capelle and Whitworth 1973), although infestations have been noted in species with relatively open nests (Lloyd and Philips 1966; Fitzner and Woodley 1983).

Little is known about the behaviour and life history of *C. hemapterus*. Adults are frequently found in the axillae of the wings of nestling birds and are haematophagous, while the larvae are believed to lead a saprophagous existence among nest debris (Whitworth 1976). After locating a suitable host, adult *C. hemapterus* frequently lose their wings and remain in the nest. Capelle and Whitworth (1973) noted that all adult female *C. hemapterus* were dealated, while one-third of males retained their wings, suggesting to the authors that males may move among local nests during mating.

The purpose of our study was twofold. First, we wished to gain further knowledge about the natural history of this dipteran, as relatively little is known despite its extensive geographical distribution and broad exploitation of host species. We investigated whether there were any effects of sampling date, brood size, or nestling age and gender on the prevalence of *C. hemapterus* in nests of the American kestrel (*Falco sparverius*), a small falcon. Within nests, we examined whether all members of a brood were susceptible to parasitism, or whether a brood would contain a mixture of infested and uninfested nestlings. If the latter occurred, we

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sought to test whether certain members of the brood were more likely to be parasitized. Second, given that ectoparasites have been implicated as having a wide range of detrimental effects on hosts, we wished to examine whether *C. hemapterus* caused significant deleterious effects on nestling American kestrels. We tested whether *C. hemapterus* infestations were associated with nestling mortality and whether infested nestlings fledged in poorer condition than those that were not infested.

## Materials and methods

We studied a wild population of American kestrels breeding in nest boxes near Besnard Lake (55°N, 106°W) in north-central Saskatchewan, Canada, during 1995. Old nesting material has been removed from our nest boxes after each breeding season, which may have reduced the prevalence and intensity of some ectoparasite infestations (Møller 1989). Kestrels arrived on our study area in mid to late April and egg laying commenced in mid-May. Nest boxes were visited every 3–5 days during May and early June until females began egg laying and then again after laying was complete so we could ascertain clutch size. We visited nests daily near the time of hatching to determine the day on which the first nestling of each brood emerged. Kestrels within a clutch generally hatch over a period of 1.5–3.5 days, therefore siblings can vary in age (Wiebe and Bortolotti 1994). Here we use "age" to refer to the age in days of the oldest nestling within a brood.

During each visit to a nest, we recorded the mass (to the nearest gram) and length of the tenth primary flight feather (to the nearest millimetre) of individually marked chicks. Because kestrels are sexually dichromatic as nestlings (Bird 1988), we also determined the sex of each individual. Each chick was carefully inspected and adult *C. hemapterus* were counted; however, because *C. hemapterus* are small and highly mobile within a nest, their prevalence is best determined from the presence or absence of feeding under the wings of birds (Whitworth 1976). Nestlings that have been fed upon are denuded of down feathers in their wing axillae and the area is covered by scabs and dried faecal material excreted by the flies (Kirkpatrick and Colvin 1989). Most of our analyses involve prevalence rather than intensity of infestation.

## Data analysis

We examined chicks repeatedly for the prevalence and intensity of *C. hemapterus* from the day of hatching to 25 days of age (292 chicks from 72 nests were examined a total of 1283 times). Nests were classified into four age categories (0–5, 6–12, 13–19, and 20–25 days old). For analyses of age, date, brood size, and sex effects, we included data from a nest if it was visited when chicks were in each age category and we had complete information on *C. hemapterus* infestations. Birds from this subset of data (50 nests) were also used to examine the effects of *C. hemapterus* on nestlings at fledging. For analyses of intensity of *C. hemapterus* infestations, we used all observations where individual *C. hemapterus* were detected (see below). Except where noted below, the nest is considered the unit of observation in all analyses.

To examine age effects, we used ratio estimators (Cochran 1977) where the percentage of infested nestlings in each brood was calculated, and we compared these percentages among the four age-classes using Friedman's analysis of variance for repeated measures (Siegel and Castellan 1988). We investigated date effects in two ways. First, we attempted to correlate the percentage of infested nestlings in each nest with the hatching date of the nest. Second, we categorized nests as "early-" or "late-" hatching and compared infestation rates using *t* tests (for details see Cochran 1977).

For analyses of brood-size effects, we restricted our sample to broods of 4 and 5 chicks, which are the most common sizes (Wiebe

and Bortolotti 1995a; Dawson and Bortolotti 1997). Percentages of infestations were compared between brood sizes with *t* tests. We examined whether the prevalence of *C. hemapterus* varied with sex at the population level (i.e., by comparing the prevalence of males to that of all females) using a *G* test. We also tested for sex-biased parasitism by comparing the ratio of infested males to total males with the ratio of infested females to total females in the same nest with a Wilcoxon matched-pairs signed-ranks test.

We tested whether all members of a brood were parasitized by *C. hemapterus* or the broods contained a mixture of infested and uninfested nestlings. Nests were categorized into one of three groups depending on whether all, some, or no chicks within a nest were infested with *C. hemapterus* during the brood-rearing period. Given our results (see below), we assessed whether certain chicks were more susceptible to *C. hemapterus* than others by comparing masses and tenth primary lengths of infested and uninfested nestlings in the same nest, using paired *t* tests.

We determined whether *C. hemapterus* infestations had detrimental effects on nestlings by comparing several parameters of birds at fledging that had no history of infestation with those in which infestations had been documented. When the first-hatched nestling was 24 days old (just prior to leaving the nest), all members of the brood were weighed and the length of their tenth primary feather was measured. In addition, a small sample of blood was collected from each chick and used to determine haematocrit and total plasma protein concentration (for details see Dawson and Bortolotti 1997). We compared the average mass, tenth primary length, haematocrit, and total plasma protein concentration of infested nestlings with those of uninfested nestlings in the same nest using paired *t* tests. We analyzed the data for each sex separately because mass, tenth primary length, and plasma protein concentration differ between males and females (Dawson and Bortolotti 1997).

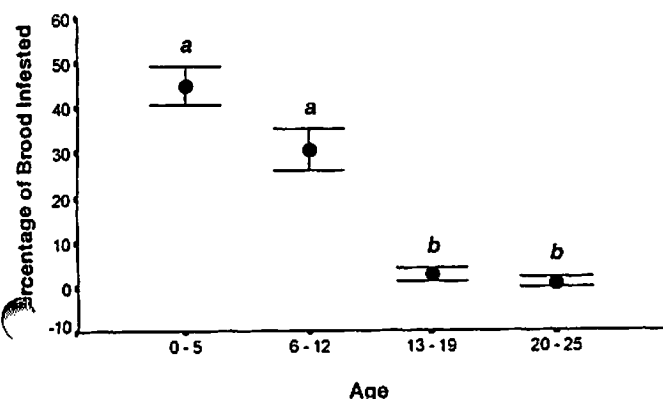
Finally, we examined whether the intensity of infestations varied with nestling age and date using correlation analyses, and whether intensity varied with brood size using a Mann–Whitney *U* test. Where the intensity of infestation was determined for more than one member of a brood, we used the average intensity for the brood.

## Results

The prevalence of *C. hemapterus* infestations declined as nestlings became older (Friedman ANOVA,  $\chi^2 = 98.40$ ,  $df = 3$ ,  $P < 0.0001$ ,  $n = 50$  broods; Fig. 1). Multiple comparisons made using a Bonferroni correction factor (Siegel and Castellan 1988) suggested that the prevalence of *C. hemapterus* did not differ between chicks aged 0–5 and 6–12 days, nor were differences detected between nestlings aged 13–19 and 20–25 days; however, prevalence when nestlings were both 0–5 and 6–12 days of age were significantly higher than when they were older (Fig. 1). The percentage of infested chicks in a nest tended to be lower the later in the season that the nest hatched, but this relationship was only marginally significant ( $r_s = -0.28$ ,  $P = 0.05$ ,  $n = 50$ ). When we compared infestations between early- and late-hatched nests, we did not detect higher infestations in early-hatched nests ( $t = 1.70$ ,  $df = 48$ ,  $P = 0.10$ ).

At the level of the entire population, there was no evidence that *C. hemapterus* preferentially infested either individual male (53 of 128) or female (50 of 103) nestlings ( $G = 2.32$ ,  $df = 1$ ,  $P = 0.13$ ); however, the ratio of infected males to total males within a nest was marginally higher than the ratio of infected females to total females (Wilcoxon's matched-pairs test,  $Z = -1.97$ ,  $P = 0.05$ ,  $n = 50$ ). Broods of 5 nestlings had higher infestation rates than broods of 4 nestlings ( $t = -11.71$ ,  $df = 48$ ,  $P < 0.001$ ).

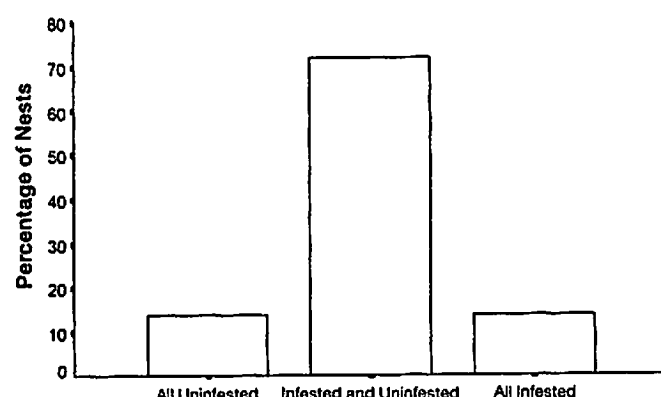
Fig. 1. The decline in infestations of American kestrel nestlings by *Carnus hemapterus* with age, using a sample of 50 nests examined when chicks were in four age periods (Friedman's analysis of variance,  $P < 0.0001$ ). The mean prevalence per nest is shown. Error bars indicate  $\pm 1$  standard error, calculated using the method of Cochran (1977). Groups with the same letter above error bars are not significantly different in multiple comparisons.



Most nests contained a mixture of infested and uninfested nestlings rather than all members being either infested or uninfested ( $\chi^2 = 33.64$ ,  $df = 2$ ,  $P < 0.0001$ ; Fig. 2). To examine whether certain members of a brood were more susceptible to parasitism, we compared the average mass and tenth primary length of infested birds with averages for those that were uninfested within nests that contained both infested and uninfested nestlings. For mass differences, we analyzed data from nests in the 0- to 5-day-old category, as this was the period with the highest infestation rates (Fig. 1). For tenth primary lengths, we analyzed data from nests in the 6- to 12-day-old category. Infestation rates were still high (Fig. 1), and we only included nests where feather growth had commenced, as remiges do not erupt until chicks are 7-10 days old (personal observation; Bird 1988). To control for differences in mass and tenth primary length attributable to age differences among nests within each age category, we calculated relative masses and tenth primary lengths by dividing average values for infested and uninfested birds in a nest by the average for all chicks in that nest. Within nests, the average relative mass of infested chicks was significantly greater than that of uninfested chicks (paired  $t = 5.18$ ,  $P < 0.0001$ ,  $n = 25$  nests); however, we could not detect differences in the relative length of the tenth primary between infested and uninfested birds within nests (paired  $t = 1.25$ ,  $P = 0.24$ ,  $n = 12$  nests), although the sample size was small.

At 24 days old, just prior to leaving the nest, male nestlings with a history of *C. hemapterus* infestations were marginally heavier than uninfested males (paired  $t = 2.04$ ,  $df = 20$ ,  $P = 0.05$ ), but there was no difference between infested and uninfested females within nests (paired  $t = 1.26$ ,  $df = 13$ ,  $P = 0.23$ ). Conversely, there was a trend for infested females to have longer tenth primaries than uninfested females (paired  $t = 2.04$ ,  $df = 13$ ,  $P = 0.06$ ), but there was no difference in male tenth primary lengths at 24 days old (paired  $t = 1.31$ ,  $df = 21$ ,  $P = 0.20$ ). We did not detect differences in either haematocrit (paired  $t$  test, males:  $t = -0.92$ ,  $df = 19$ ,  $P = 0.37$ ; females:  $t = -1.01$ ,

Fig. 2. Percentages of American kestrel broods ( $n = 50$ ) according to whether *Carnus hemapterus* infested all, a portion of, or no nestlings in a nest ( $P < 0.0001$ ).



$df = 13$ ,  $P = 0.33$ ) or total plasma protein concentration (paired  $t$  test, males:  $t = 0.28$ ,  $df = 19$ ,  $P = 0.78$ ; females:  $t = 1.78$ ,  $df = 13$ ,  $P = 0.10$ ) between infested and uninfested nestlings.

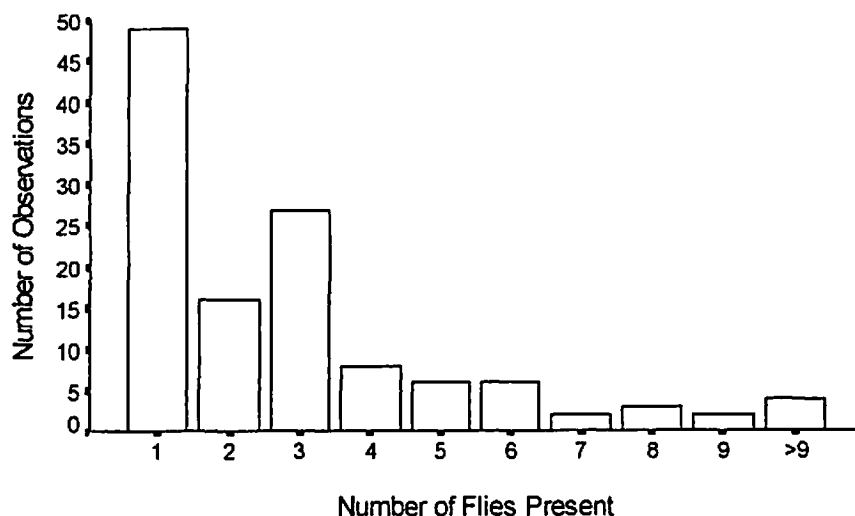
Fifteen chicks died before they were 24 days old. Chicks that died were no more likely to have been previously infested ( $n = 5$ ) as uninfested with *C. hemapterus* ( $\chi^2 = 1.67$ ,  $df = 1$ ,  $P = 0.20$ ;  $n = 10$ ). This result suggests that *C. hemapterus* is not associated with nestling mortality, although our test was weak, owing to the small sample size.

Although we documented the prevalence of *C. hemapterus* infestations using the presence of faeces and scabs, we also recorded the presence of 363 flies during 123 observations of 83 nestlings (Fig. 3). Intensity of infestations ranged from 1 to 17 flies (mean  $\pm$  SD =  $2.95 \pm 2.59$ , median = 2). Only 14 (3.9%) of *C. hemapterus* observed were winged, and 13 of these winged flies were noted during visits near the end of the breeding season (late July). Although the presence of the flies themselves should not be considered an accurate estimate of infestation intensity (Whitworth 1976), the probability of detecting individual flies should be a function of their density within a nest (see Brown and Brown 1996). These data can therefore be used to test factors affecting variability in the intensity of infestation. The number of individual adult *C. hemapterus* on a host was not related to the age of the host ( $r_s = 0.11$ ,  $P = 0.50$ ,  $n = 41$  nests) and did not vary with date ( $r_s = -0.11$ ,  $P = 0.50$ ,  $n = 41$  nests). The intensity of infestations did not vary with brood size, as we could not detect a difference in the numbers of individual adult *C. hemapterus* seen on chicks from broods of 4 and 5 ( $U = 86.5$ ,  $P = 0.18$ ,  $n = 33$ ).

## Discussion

It has been suggested that *C. hemapterus* is a widely distributed species (Capelle and Whitworth 1973; Kirkpatrick and Colvin 1989). To our knowledge, this is the first time it has been documented in the province of Saskatchewan, and also represents the highest latitude at which it has been recorded in North America. Although prevalence was high (Fig. 1), intensities of *C. hemapterus* infestations on our study area appeared moderate, as we found few flies on nestling kestrels (Fig. 3) compared with other studies

Fig. 3. Numbers of adult *Carnus hemapterus* present on nestling American kestrels (123 observations of 83 nestlings).



(Capelle and Whitworth 1973; Cannings 1986a; Kirkpatrick and Colvin 1989). Some ectoparasites (e.g., fleas and mites) require old nesting material to survive between host breeding seasons (Sikes and Chamberlain 1954; Marshall 1981), and removing old nests may reduce these ectoparasite populations (Møller 1989; Rendell and Verbeek 1996; but see Mappes et al. 1994). That Capelle and Whitworth (1973) recovered pupae of *C. hemapterus* from nest material and Cannings (1986b) found high-level infestations on northern saw-whet owls (*Aegolius acadicus*) inhabiting cavities containing old starling (*Sturnus vulgaris*) nests suggests that old nest material may be required for high-intensity infestations to occur. In our study, the removal of old nests may account for the moderate levels we observed. However, heavy infestations have been found when old nest material had been removed (Cannings 1986a; Kirkpatrick and Colvin 1989), and are frequently noted in nests of bird species that construct new nests each breeding season (Capelle and Whitworth 1973). It is possible that *C. hemapterus* eggs and (or) pupae remain in crevices in the nest even after old nesting material is removed.

Despite the routine removal of old nest material from our kestrel nest boxes after the breeding season (Bortolotti 1994), a large proportion of nestlings on our study area were infested (Fig. 1), suggesting that *C. hemapterus* have considerable ability to locate hosts. Capelle and Whitworth (1973) found that one-third of male *C. hemapterus* in Utah retained their wings, implying that males may move between host nests during the breeding season. In contrast, we found very few winged specimens on kestrels, a situation similar to that found in red-tailed hawks (*Buteo jamaicensis*) in Utah (Lloyd and Philips 1966). Moreover, all but one winged specimen on kestrels were observed at the conclusion of the kestrel breeding season, suggesting temporal and (or) geographical differences in breeding movements of *C. hemapterus*. Although Marshall (1981) states that dealated adult *C. hemapterus* can move between nests by walking, this does not seem to be a plausible mechanism for dispersal during breeding. We suggest that after hosts are initially located, subsequent breeding dispersal by *C. hemapterus* on our study area is limited. The preponderance of winged forms at the

conclusion of the kestrel breeding season may represent movements by a second generation of *C. hemapterus*.

Most infestations of kestrel nestlings occurred during the first 12 days of the nestling period (Fig. 1). Similarly, in previous studies it has been found that nestlings infested early in the brood-rearing period were uninfested when they were older (e.g., Cannings 1986b), although it appears that some bird species maintain infestations for a longer period than our kestrels. For example, *C. hemapterus* were commonly observed on barn owls (*Tyto alba*) in New Jersey up to 4 weeks of age, but rarely thereafter (Kirkpatrick and Colvin 1989). The reduction in infestations as birds age may be the result of several factors. Kirkpatrick and Colvin (1989) suggested that a reduction in infestation levels coincides with the moult from downy to contour feathers. Kestrels begin pennaceous feather growth by 2 weeks of age (Bird 1988), while barn owls begin growing such feathers at 3–5 weeks (Cramp 1985). Therefore, kestrels become an inhospitable environment, owing to increased density and layering of feathers, sooner than barn owls. Infestations of both species would also decline as maturing nestlings become increasingly mobile. Kestrels spend most of the day on their feet by the age of 16 days (Bird 1988), perhaps making them less available to *C. hemapterus*, especially once the flies become dealated. Similarly, more time is spent preening as chicks mature, making the physical removal of *C. hemapterus* by infested chicks a possibility.

Whitworth (1976) suggested that within nests, the smallest chicks were more susceptible to feeding by larval *Protonotaria calliphora* spp. (Diptera: Calliphoridae) and *C. hemapterus* (see also Kirkpatrick and Colvin 1989). In contrast, we found that *C. hemapterus* were more likely to infest the largest chicks in a nest. Kestrels on our study area hatch asynchronously (Wiebe and Bortolotti 1994), resulting in size hierarchy within broods. Larger chicks may be more prone to infestations simply because they are physically larger, and *C. hemapterus* would have a higher probability of encountering these chicks. The above explanation suggests that parasitism is random; however, *C. hemapterus* may actively choose the largest nestlings within a brood. The largest kestrel nestlings in a brood have a competitive advantage

tage, and generally receive proportionately more food than their smaller nestmates (Anderson et al. 1993; Wiebe and Bortolotti 1995b), which suggests that they will generally be the healthiest. As *C. hemapterus* procure resources from their hosts, it would seem wise for them to choose the healthiest host; however, further investigation is required to elucidate the mechanisms of host selection within nests.

Kestrels show sexual size dimorphism (Bird 1988): females can be larger than males of the same age when they are as young as 6 days old (Anderson et al. 1993). Although we did not expect differences in infestation based on gender per se, we expected that females might be more susceptible because of their larger size (see above); however, we could only demonstrate a slight sex bias in infestation rates, and contrary to expectation, males seemed to be more susceptible. Despite sex differences in the sizes of chicks of comparable ages, hatching asynchrony is more important than sex differences in determining size hierarchy early in the brood-rearing period, when *C. hemapterus* infestations are most common (Fig. 1).

The exact nature of the resources procured from hosts by *C. hemapterus* was a contentious issue in earlier literature (Lloyd and Philips 1966; Whitworth 1976). Microscopic examination of gut contents has revealed that *C. hemapterus* is haematophagous (Kirkpatrick and Colvin 1989). Uptake of blood from hosts has also been directly observed (T. Schulz, personal communication; T. Whitworth, personal communication). Although these observations suggest that *C. hemapterus* is capable of having detrimental effects on nestlings, published evidence has been equivocal. Kirkpatrick and Colvin (1989) could find no evidence that infestations adversely affected barn owls. In contrast, Cannings (1986b) implicated *C. hemapterus* in the deaths of nestling northern saw-whet owls in British Columbia. We were unable to attribute mortality of the nestling kestrels to *C. hemapterus*. In fact, there was a trend for kestrels that had a history of *C. hemapterus* infestations to be slightly heavier (males) and to have longer tenth primaries (females) at 24 days old than nestlings in which *C. hemapterus* infestations were never observed. We do not suggest that *C. hemapterus* infestations are beneficial to kestrels (but see Blanco et al. 1997); rather, differences in mass and feather length at 24 days of age are more likely the result of preferential infestations of larger chicks earlier in the nestling period (above), as hierarchies in size among brood members in the wild tend to be maintained throughout the nestling period (unpublished data).

A reduced haematocrit is often associated with ectoparasitism (e.g., Richner et al. 1993; but see Johnson and Albrecht 1993). Schulz (1986, 1990) cites unpublished data suggesting that barn owls heavily infested with *C. hemapterus* had lower haematocrits. Whitworth (1976) found that nestling magpies (*Pica pica*) had reduced haematocrits and haemoglobin concentrations when infested with *C. hemapterus*. We could find no effect of *C. hemapterus* infestations on haematocrit or plasma protein concentrations of kestrels at 24 days old. The disparity between the results of our study and Whitworth's may be due to several factors. First, Whitworth took blood samples from his birds while they were actively being fed upon, whereas we sampled kestrels exclusively at 24 days old, about 12 days after most feeding ceased (Fig. 1). Given the ability of nestling birds to with-

stand large blood losses (see Roby et al. 1992; Whitworth and Bennett 1992), it is likely that if *C. hemapterus* affected the blood parameters of kestrels, there was sufficient time between *C. hemapterus* feeding and blood sampling for nestlings to recover. Second, some of Whitworth's birds had concurrent *Protocalliphora* spp. infestations, and it is not known whether *C. hemapterus* and *Protocalliphora* spp. might act in a synergistic fashion in affecting their hosts. *Protocalliphora* spp. infestations of kestrel nests on our study area were rare, and none were detected in any nests used for this study (R.D. Dawson, T.L. Whitworth, and G.R. Bortolotti, unpublished data).

Kestrel nestlings from 5-chick broods were more likely to be infested than those from 4-chick broods. We are unaware of any other study on *C. hemapterus* that has examined brood-size effects, nor do studies exist that document mechanisms by which *C. hemapterus* locates host nests. We expect that there would be subtle differences in emission rates of certain chemical substances, such as CO<sub>2</sub>, between nests containing broods of different sizes, potentially making nests with larger broods more attractive to *C. hemapterus*. However, we could not detect differences in the intensity of infestations between broods of 4 and 5 chicks, although it was examined only in an indirect fashion. This suggests that there may be limits to the density of *C. hemapterus* which an individual nest can support, regardless of nestling biomass. Intraspecific competition among adult flies may prevent immigration to certain nests, thus limiting population densities within nests. However, without further knowledge of the basic biology of *C. hemapterus*, this is speculation at best.

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