

## Life-history variation in three coexisting species of carnid flies (Diptera: Carnidae), *Carnus hemapterus*, *Hemeromyia anthracina* and *Hemeromyia longirostris*

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**Abstract.** Seasonal cycles constitute a major challenge for organisms since they may influence the genetic composition of a population, the species structure of a community and the interactions between organisms. Diapause is frequently used by insects to synchronize their life cycle with seasonal changes and is regarded as a key factor in the coexistence of competing species. Here the occurrence, abundance and emergence patterns of three poorly-known species of carnid flies (*Carnus hemapterus* Nitzsch, 1818, *Hemeromyia anthracina* Collin, 1949 and *Hemeromyia longirostris* Carles-Tolrá, 1992), which overwintered in the nests of several bird species at two localities, are reported and evidence of possible interspecific competition sought. Larvae of all three species were found in association with carrion and detritus. Both *Hemeromyia* species co-occurred in around 50% of the nests and *Carnus* with each of the *Hemeromyia* species at a lower rate (30–40% of the nests). Coexistence of all three carnid species was rare. We did not find any evidence of interspecific competition in the larval stage. Coexistence did not reduce the number of flies that emerged of any of the three species and the abundance of some species was even positively related. Species-specific emergence patterns and different habitat selection criteria (*Carnus hemapterus* seemed to avoid nests lined with vegetable material), which diminished the overlap between species were found. Such spatial and temporal segregation could facilitate the coexistence of these closely related species, which have similar ecological requirements, and might influence the seasonal dynamics of this poorly-known assemblage of insects inhabiting the nests of birds.

### INTRODUCTION

Seasonal changes in environmental variables (seasonal cycles) constitute a major challenge for organisms (Tauber & Tauber, 1981) and pose a universal problem for most insects, namely the timing and matching their life cycle to the appropriate season (Jones, 2001). Seasonal cycles also have the potential to influence both the genetic composition of a population and the species structure of a community (e.g., emergence from dormant eggs, Cáceres, 1998 and references therein), and can strongly affect interactions between organisms (e.g., coexistence of competing species, seasonal synchrony between host and parasites). In response to seasonal cycles insects commonly use diapause and quiescence to synchronize their life cycle with the moment when resources are abundant and available (Jones, 2001). Additionally, diapause has been hypothesised in both theoretical and empirical studies to be a key factor in maintaining the coexistence of competing species (Chesson, 1994; Hairston et al., 1996). Therefore, studying seasonal cycles and the related adaptations of a given species or population is basic for understanding how organisms exploit their environment, how they interact and how they evolve (Tauber & Tauber, 1981). Interspecific comparisons of seasonal cycles and life histories have been particularly fruitful, especially

when they involve closely related species that occur together or in adjacent geographic areas (Dearn, 1977; Dingle, 1978; Tauber & Tauber, 1981) since they can contribute to a better understanding of the evolution of life histories and the comprehension of stable coexistence (Tauber & Tauber, 1981, 1982). In this paper this approach is used to assess the interspecific relationships of coexisting species of the family Carnidae.

Carnidae is a poorly studied group of acalypterate flies found mainly in the Holarctic Region. It includes parasitic species (genus *Carnus* Nitzsch, 1818) as well as some non-parasitic ones belonging to the genera *Meoneura* Rondani, 1856 and *Hemeromyia* Coquillett, 1902 (Grimaldi, 1997). With the exception of *Carnus hemapterus*, which has been studied (see, for instance, Capelle & Whitworth, 1973; Guiguen et al., 1983; Dawson & Bor-tolotti, 1997; Roulin, 1998, 1999; Valera et al., 2003, 2004), there is little information on the ecology of *Hemeromyia* species and it consists mainly of reports on the geographical occurrence of the species (e.g., Papp, 1984, 1998; Carles-Tolrá Hjorth-Andersen, 2002). This is probably due to the fact that finding these species requires specialised sampling of birds nests (Merkl et al., 2004). Here we study the occurrence and seasonal cycle of *Carnus hemapterus* and two species of *Hemeromyia* (*H.*

*longirostris* and *H. anthracina*) in two separate geographic areas. Since all three species complete their life cycles within birds' nests, and in all cases their larvae feed on the organic material that accumulates in the bottom of the nests (Grimaldi, 1997; Papp, 1998), we hypothesise that coexistence can result in competition among the different species. Therefore, the effects of coexistence of the different species on their relative success were studied, and possible indications of interspecific competition looked for. Since subtle differences in habitat selection and/or differences in the timing of their life cycles may facilitate coexistence, the habitat selection criteria of the three species studied and their seasonal phenologies were studied to check for habitat and/or temporal segregation.

## MATERIALS AND METHODS

### Study species

The life cycle of the species comprise an adult stage, several larval phases and a puparium. Although there is no information on *Hemeromyia* species, *Carnus hemapterus* has three larval stages, then diapauses for several months (Guiguen et al., 1983), and adults emerge the following spring. Adult *Carnus* flies are parasites of nestlings of different bird species, whereas the scarce information on *Hemeromyia anthracina* and *H. longirostris* suggests that the adults of these species are saprophagous and feed on faeces and decaying vegetable material (Carles-Tolrá, 2001) although they have also been collected on Umbelliferous flowers (Carles-Tolrá, 2004). Therefore, they appear to coexist only in the larval and pupal stage.

### Collection of nest material

Occurrence and emergence time of carnid species was studied by collecting nest material with overwintering pupae from nests of several cavity-nesting bird species. During the second half of July 2002 27 bee-eater (*Merops apiaster*) nests from two colonies in central Spain (40°32'N, 03°27'W, Daganzo, Madrid) were sampled. During the period 17–28 January 2003 samples were also collected in southern Spain from 17 hoopoe (*Upupa epops*) nests (nine from Guadix, 37°18'N, 3°11'W, Granada, and eight from Doña María, 37°08'N, 02°43'W, Almería, 37 km from the first location), and five roller (*Coracias garrulus*) and four little owl (*Athene noctua*) nests in the Desert of Tabernas (Almería, 37°05'N, 2°21'W). On 3 March 2004 five additional roller nests and three little owl nests at Tabernas were sampled. Rollers, bee-eaters and little owls breed in holes dug in sandy cliffs, whereas hoopoes in our study area nest in natural holes in olive trees and piles of stones. Although bee-eaters seldom re-use their nests, rollers and little owls frequently breed in the same hole in successive years.

On 14 January 2004 26 nest boxes placed on electric masts in Cáceres (39°03'N, 5°14'W, Extremadura, Western Spain) were sampled. Several species (like the roller, European kestrel *Falco tinnunculus*, spotless starling *Sturnus unicolor* and house sparrow *Passer domesticus*) also breed in these boxes. Whereas it was possible to deduce which boxes were used the previous breeding season, it was not possible to presume by which species. Therefore the type of nest material (rotting material, detritus and faeces forming a solid substrate versus straw, sticks and vegetable material) was classified in a way that might indicate the previous occupant of the nest (rollers and kestrels versus starlings and sparrows, respectively).

Sampling consisted of removing part of the material from the bottom nest using a spoon attached to a stick long enough to

reach the nest chamber or by hand (nest boxes). In cases where the nest was composed of vegetable material, the whole structure (i.e., the nest cup) and the earth below the nest were taken. Samples were weighed after the flies had emerged, with the exception of five hoopoe samples that were lost. The amount of nest material collected varied among nests. Nevertheless, the number of flies that emerged from nests for which emergence was recorded was not correlated with the mass of material sampled for any of the species (Spearman rank correlations,  $P > 0.15$  in all three cases) or for all three species pooled ( $r_s = 0.09$ ,  $P = 0.63$ ,  $n = 28$ ). This is also the case both for those nests without vegetable material (Spearman rank correlations,  $P > 0.30$  in all four cases) and for those with vegetable material but for which only the weight of the earthy substratum was considered (Spearman rank correlations,  $P > 0.15$  in all cases).

### Emergence patterns of Carnidae

Emergence patterns are ideally studied in the field. Nevertheless this was not possible since this would necessitate the periodic sampling of nests occupied by birds during the breeding season, which would result in the disturbance of adults and nestlings. Therefore, the emergence of flies was recorded in the laboratory.

After collection, the samples were kept in plastic bags and stored in Almería under ambient conditions in semidarkness, which resembles natural conditions. Observational and experimental data (manipulating temperature during the pupal stage) suggest that, at least for *Carnus hemapterus*, emergence time is determined by an endogenous annual timing mechanism that can be modified, within certain limits, by temperature (Valera et al., in prep.), as is the case for many insects in temperate climates (Tauber & Tauber, 1981; Leather et al., 1993). Therefore, our method ensured homogeneous conditions (i.e., the same temperature) for the samples, which is not possible in the field, where the timing or length of use of nests by birds could influence emergence time. It is very unlikely that the three species studied would respond differently to these conditions.

Samples were monitored approximately every three-four days for fly emergence until insect emergence ceased. The study period lasted from 31 January until 8 July 2003 for the samples collected in 2002–2003, from 9 March until 13 July 2004 for those collected in 2004 in Tabernas and from 4 March until 13 July 2004 for samples collected in 2004 in Extremadura. Surveys of the samples collected in 2002–2003 (starting as early as the beginning of February) showed that the earliest emergence of any of the species studied occurred in the first week of March. Therefore, in 2004 (surveys starting on 4<sup>th</sup> March) only the very first flies to emerge could have been overlooked (see results).

Carnid species were detected in 20 of the 26 nest boxes sampled in western Spain. It was ignored whether the nest boxes sampled were occupied by any bird species. Given that the occurrence of flies may depend on the previous occupation of the nest (at least this is the case for *Carnus hemapterus*, Roulin, 1998; Valera et al., in prep.), the data is for those 20 nests where at least one species of carnid fly was recorded.

### Statistical methods

Parasite distributions are known to be aggregated, which makes their quantification and comparison difficult (Rózsa et al., 2000). Following Rózsa et al. (2000) prevalence (proportion of infected hosts among all the hosts examined) and mean intensity (number of individuals found in the infected nests) of flies (and the confidence intervals estimated after 4000 replications) were used for quantification purposes. Fisher's exact test was used to compare prevalences and mean intensities were com-

pared by using bootstrap t-tests (after 2000 replications). ANCOVAs were used to assess the effect of coexistence of the two species on the number of emerging flies of each species after controlling for confounding variables (the abundance of the third species). Logarithmic transformations were used to normalise the data. Nevertheless, since different measures of parasitism may yield different interpretations and answers (Rózsa et al., 2000), the consistency of our results was checked by calculating and comparing median intensities using Mood's median test. Tests are 2-tailed and 95% confidence intervals, CI, are provided unless otherwise stated.

Two parameters (total number of flies that emerged per nest at a given time and the moment in time when 50% of the flies had emerged) were used to describe the temporal overlap among species since each index has different biases. Whereas the number of individuals may overstate those nests with many flies, working with percentages may inflate the importance of early or late emergence of some flies in nests with few individuals.

Statistical tests were done using the program Quantitative Parasitology 2.0 (Reiczigel & Rózsa, 2001) and the STATISTICA 6.0 package (StatSoft, Inc. 2001).

## RESULTS

### Occurrence and abundance of carnid species

Three species of carnid flies emerged from the nests sampled: the ectoparasite *Carnus hemapterus*, and the non-parasitic *Hemeromyia anthracina* and *Hemeromyia longirostris*.

*Carnus hemapterus* was detected in 90.0% (9/10) of the roller nests, 85.7% (6/7) of the little owl nests, 70.6% (12/17) of the hoopoe nests and 37.0% (10/27) of the bee-eater nests. *Carnus* flies were also recorded in 8 out of 20 (40%) nest boxes sampled in Western Spain. In contrast, *Hemeromyia* flies were found only in hoopoe nests and nest boxes in western Spain.

Concerning hoopoe nests, both *Hemeromyia anthracina* and *H. longirostris* were detected in 7 (41.2%) out of 17 nests. Overall, 23 *H. anthracina* and 159 *H. longirostris* (115 flies emerged from a single nest) were collected. There were no differences in the mean number of *H. anthracina* (3.3, CI: 1.3–6.4) and *H. longirostris* flies (22.7, CI: 4.4–71.0) per infested nest (Bootstrap 2-sample t-test:  $t = 1.2$ ,  $P = 0.40$ ). Prevalence of *C. hemapterus* (70.6%) did not differ from that of either *H. anthracina* or *H. longirostris* (Fisher's exact test,  $P = 0.16$  in both comparisons). The mean number of *Carnus* flies per infested nest (17.0, CI: 5.33–39.2) was not significantly different from that of *H. anthracina* ( $t = 1.65$ ,  $P = 0.16$ ) or *H. longirostris* ( $t = 0.32$ ,  $P = 0.76$ ).

Regarding nest boxes, a total of 163 *Hemeromyia anthracina* flies were found in 16 (80.0%) out of 20 nest boxes and 237 *H. longirostris* flies emerged from 17 (85.0%) out of 20 boxes. The mean number of both *Hemeromyia* species in infected nests did not differ significantly (*H. anthracina*: 10.2, CI: 5.3–21.5; *H. longirostris*: 13.9, CI: 8.2–24.2,  $t = 0.67$ ,  $P = 0.50$ ). Prevalences of *H. anthracina* and *H. longirostris* were both significantly higher than that for *C. hemapterus* (40.0%) (Fisher's exact test,  $P = 0.02$  and 0.008 respectively) but the mean intensity of *Carnus* flies (18.2, CI: 7.4–34.2)

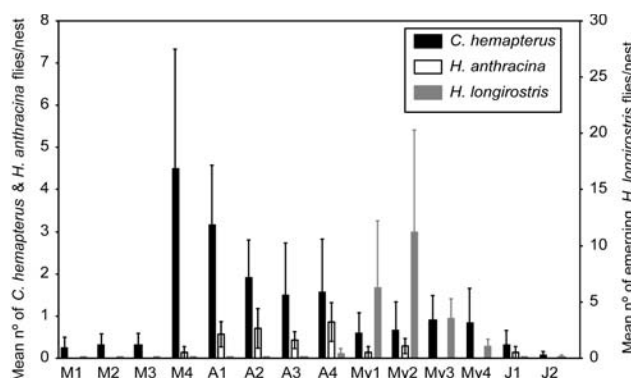


Fig. 1. Phenology of emergence of *Carnus hemapterus*, *Hemeromyia anthracina* and *H. longirostris* in 2003 from hoopoe nests located in southeastern Spain (see Methods for sample size). Mean values ( $\pm$  SEM) of flies per nest are shown.

did not differ from that for both *H. anthracina* and *H. longirostris* ( $t = 0.97$ ,  $P = 0.33$  and  $t = 0.51$ ,  $P = 0.62$ , respectively).

### Patterns of emergence and temporal segregation

Data from hoopoe nests as well as that from nest boxes show that the pattern of emergence of the three species of diptera differs (Figs 1 and 2).

*Carnus* flies from hoopoe nests had a long emergence period (Fig. 1) that started at the beginning of March, peaked at the end of this month and lasted until mid June. Emergence of *H. anthracina* flies started at the end of March, when 31.9% of the *Carnus hemapterus* flies had already emerged, and showed several peaks. The emergence period of *H. longirostris* lasts for only one month, with a clear peak around mid May and is delayed relative to the other species. The first *H. longirostris* flies emerged at the end of April, when 79.9% of the *Carnus* flies and 82.6% of the *H. anthracina* had already emerged (Fig. 1). The moment in time when 50% of the flies have emerged differs among the species (ANOVA:  $F_{2,23} = 14.7$ ,  $P < 0.001$ ).

These patterns parallel those found in nest boxes (Fig. 2). Although the earliest *Carnus* flies to emerge were probably missed, the shape of the curve of emergence suggests that *C. hemapterus* starts emerging earlier than *H. anthracina*. *Hemeromyia longirostris* is again the species with the shortest and most delayed emergence period (Fig. 2), as at least 86.3% of the *Carnus* flies and 46.6% of the *H. anthracina* flies had emerged by the end of March, when the first *H. longirostris* appeared. The absence of a significant difference in the time when 50% of each species had emerged (ANOVA:  $F_{2,38} = 0.95$ ,  $P = 0.39$ ) is probably partly due to the fact that the earliest *Carnus* flies to emerge were missed.

A comparison of Figs 1 and 2 suggests some degree of geographic variation in the emergence of the three species studied. All the *H. longirostris* had emerged in western Spain by the time they started emerging from hoopoe nests in southern Spain. Forty six percent of the *H. anthracina* had emerged in western Spain by the time the first fly of this species was recorded from hoopoe nests

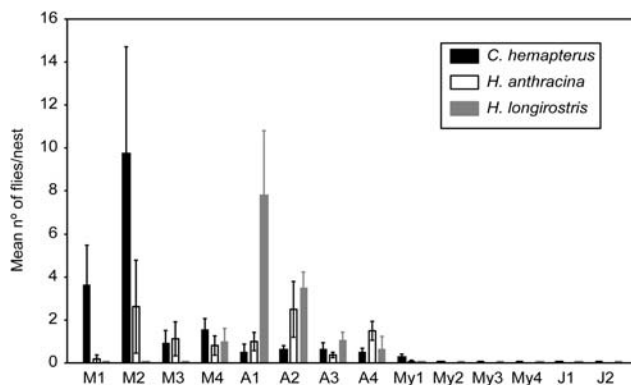


Fig. 2. Phenology of emergence of *Carnus hemapterus*, *Hemeromyia anthracina* and *H. longirostris* in 2004 from nest boxes in western Spain (see Methods for sample size). Mean values ( $\pm$  SEM) of flies per nest are shown.

and the peak of *C. hemapterus* emergence seemingly occurred 2 weeks earlier in western than in southern Spain.

### Coexistence and interspecific competition

Both *Hemeromyia* species co-occurred in four out of 17 hoopoe nests and in 13 out of 20 nest boxes. Coexistence of both species did not influence either of them, since the number of *H. anthracina* flies emerging when the species coexisted did not differ from that recorded for nests from which only this *Hemeromyia* species emerged (after controlling for the abundance of *Carnus* flies) (ANCOVA:  $F_{1,20} = 1.80$ ,  $P = 0.19$ , covariate:  $F_{1,20} = 2.73$ ,  $P = 0.11$ , Fig. 3a). The result was the same for *H. longirostris* (ANCOVA:  $F_{1,21} = 0.40$ ,  $P = 0.53$ , covariate:  $F_{1,21} = 0.98$ ,  $P = 0.33$ , Fig. 3a).

*Carnus hemapterus* and *H. anthracina* were both present in 13 nests (six out of 17 hoopoe nests and seven out of 20 nest boxes). There were no differences in the number of *Carnus* flies that emerged whether it coexisted or not with *H. anthracina* (controlling for the occurrence of *H. longirostris*, ANCOVA:  $F_{1,17} = 0.91$ ,  $P = 0.35$ , covariate:  $F_{1,17} = 8.63$ ,  $P = 0.009$ , Fig. 3b). In contrast, the mean number of *H. anthracina* that emerged was significantly higher when it coexisted with *Carnus* than when it did not ( $F_{1,19} = 11.96$ ,  $P = 0.003$ , Fig. 3b), although the abundance of *H. longirostris* was significantly correlated with the abundance of *Carnus* (covariate:  $F_{1,19} = 22.6$ ,  $P = 0.0001$ ). Nevertheless, the median value for *H. anthracina* flies did not differ in nests with and without *Carnus* flies (Mood's median test,  $P = 0.41$ , Fig. 3b).

*Carnus hemapterus* and *H. longirostris* coexisted in 11 nests (six out of 17 hoopoe nests and five out of 20 nest boxes). Emergence of *Carnus* flies from nests with and without *H. longirostris* did not vary (controlling for the occurrence of *H. anthracina*, ANCOVA:  $F_{1,17} = 1.26$ ,  $P = 0.27$ , covariate:  $F_{1,17} = 0.28$ ,  $P = 0.59$ , Fig. 3c). This was also the case for *H. longirostris* that coexisted or not with *Carnus* (ANCOVA:  $F_{1,21} = 1.19$ ,  $P = 0.28$ , covariate:  $F_{1,21} = 3.33$ ,  $P = 0.08$ , Fig. 3c).

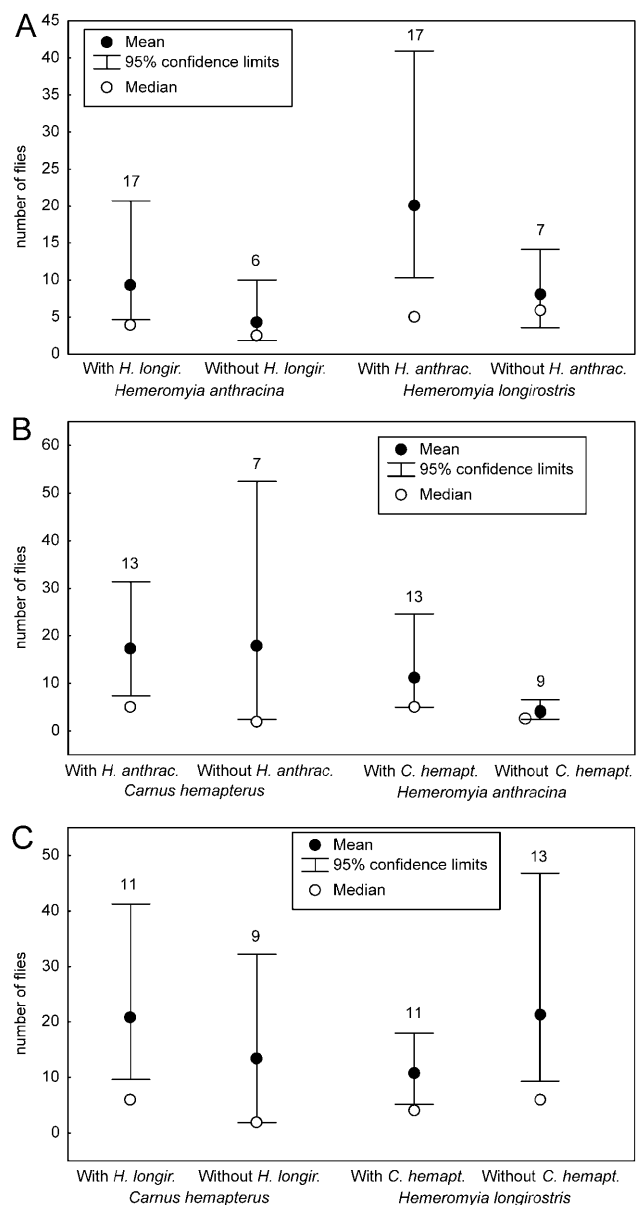


Fig. 3. Mean (and 95% confidence limits after 4000 replications) and median number of flies that emerged from nests where they did and did not coexist with one another: A – *Hemeromyia anthracina* and *H. longirostris*; B – *Carnus hemapterus* and *Hemeromyia anthracina*; C – *Carnus hemapterus* and *Hemeromyia longirostris*. Figures show the number of nests in each category.

Abundance of *H. anthracina* and *H. longirostris* in nests where they coexisted was marginally associated after controlling for the abundance of *Carnus* flies (partial correlation,  $r = 0.44$ ,  $P = 0.088$ ,  $n = 17$ ). Similarly, the number of *Carnus* flies correlated positively with the number of *H. longirostris* in the nests where they coexisted (partial correlation,  $r = 0.76$ ,  $P = 0.011$ ,  $n = 11$ ). In contrast, there was no association between the abundance of *Carnus* and *H. anthracina* flies in those nests where they coexisted (partial correlation,  $r = -0.20$ ,  $P = 0.52$ ,  $n = 13$ ).

TABLE 1. Relationship between occurrence of three species and type of substratum (vegetable – n = 6 nests; earthy – n = 14 nests) in nest boxes. Number of nests where *Carnus hemapterus*, *Hemeromyia anthracina* and *H. longirostris* were found and the percentages (in brackets) in which each species was recorded.

	Vegetable substratum	Earthy substratum
<i>Carnus hemapterus</i>	0 (0.0%)	8 (100.0%)
<i>Hemeromyia anthracina</i>	4 (25.0%)	12 (75.0%)
<i>Hemeromyia longirostris</i>	6 (35.3%)	11 (64.7%)

All three carnid species co-occurred in only 3 hoopoe nests and in 4 nest boxes.

### Habitat preferences and spatial segregation

*Hemeromyia* flies were found only in hoopoe nests and nest boxes, whereas *C. hemapterus* flies were recorded in natural nests of all the species studied as well as in eight out of 20 nest boxes. The occurrence of *C. hemapterus* is significantly associated with the type of substratum in the nest box (Fisher's exact test,  $P = 0.042$ ); all nests in which *C. hemapterus* was found had earthy rotting material and no *Carnus* fly emerged from nests lined with straw and vegetable matter (Table 1). In contrast, the occurrence of *H. anthracina* and *H. longirostris* was independent of the type of substratum in the nest box (Fisher's exact test,  $P > 0.1$  for both species).

### DISCUSSION

This study, to our knowledge, provides the first information on the ecology of two *Hemeromyia* species, shows that three closely related carnid species with ecologically similar larval and pupal stages can coexist and reveals clear differences in the life-history patterns of these species.

### Coexistence of carnid species and interspecific competition

Although the larval stages of all three diptera are found in association with carrion and the excrement of birds (Grimaldi, 1997), coexistence is infrequent. Despite both *Hemeromyia* species co-occurring relatively frequently (around 50% of nests), and *Carnus* co-occurring with each of the *Hemeromyia* species at only a slightly lower frequency (around 30–40% of nests), coexistence of all three carnid species was recorded for only seven out of 34 nests where any of the species was registered. Moreover, the differences in their seasonal cycles may facilitate coexistence by means of temporal segregation.

Coexistence here refers to the larval and pupal stages, therefore, interspecific competition for resources could occur in the larval phase. However, our results do not reveal any evidence of interspecific competition. For the two closely related *Hemeromyia* species, which showed the highest incidence of coexistence, the numbers of flies that emerged when they co-occurred and did not were similar. Assuming that the overlap in the emergence pattern of flies reflects a similar pattern of occurrence of larvae (this is likely if the species spend a similar time in

diapause), then a high degree of competition between *Carnus* and *H. anthracina* would be expected (the pair of species with the greatest degree of overlap in time of emergence). However, our results do not confirm this prediction. The number of *Carnus* flies that emerged is not affected by the presence of *H. anthracina* and the effect of the former on *H. anthracina* is, if anything, positive. In fact, the only associations found in this study are positive (a slight positive relationship between the numbers of *H. anthracina* and *H. longirostris* flies that emerged and a stronger one between those of *C. hemapterus* and *H. longirostris*). Thus, coexistence in this system did not seem to result in interspecific competition, but in neutral or slightly positive associations. Although, it is unlikely the positive associations were a result of differences in the amount of nest material (given the absence of a correlation between the number of flies that emerged per nest and amount of nest material – see methods), some qualitative factor, like the conditions for larval development, could account for the positive correlations found in this study. A better method would be to raise fly larvae and establish their growth rates in standardised media in the absence and presence of their putative competitors, but more basic knowledge about the biology of these species is needed before this can be successfully done.

### Limitation of interspecific competition by spatial and temporal segregation

Several factors may limit competition and facilitate the coexistence of these closely related species, namely different habitat selection criteria resulting in spatial segregation, and different life cycles resulting in temporal segregation. Even though the larvae of all three species inhabit a specialised habitat there seems to be interspecific differences in habitat selection criteria. *Carnus hemapterus* seemed to avoid nests lined with vegetable matter and was common in nests with a sandy substratum (e.g., little owls, rollers and bee-eaters) in which *Hemeromyia* flies did not occur. Co-occurrence of *Carnus* flies with both *Hemeromyia* species was therefore restricted to hoopoe nests (that have an earthy substratum formed of wood shavings, excrement and prey remains), that seem to be good enough for *C. hemapterus*, and to artificial nest-boxes with a substratum suitable for both *Hemeromyia* species. Preference of *C. hemapterus* for specific hosts with particular types of nest has been already reported. Guiguen et al. (1983) described the preference of *Carnus* for a host species in a multispecific colony of birds and argued that such specificity could be determined by the type of nest although they could not ascertain the causal factor. Our data suggest that *C. hemapterus* rejects nests with abundance of vegetable matter since no flies emerged from these nests despite their probably being nests of bird species reported to be hosts of this parasitic fly (e.g., *Sturnus* and *Passer* spp., see Grimaldi, 1997). This agrees with the low prevalence and infestation intensity of *C. hemapterus* found by Westneat et al. (2004) in a colony of house sparrows (*Passer domesticus*). In contrast, Liker et al. (2001) found a high prevalence and abundance of these flies in a colony of

starlings (*Sturnus vulgaris*). Valera et al. (unpubl. data) found that the number of flies emerging from nests used the previous season by bee-eaters was significantly higher than from bee-eater nests re-used the previous season by rock sparrows (*Petronia petronia*). Thus, the type of nest could be more important for the larval-pupal stage than the adult stage. Concerning *Hemeromyia* spp., more information about their occurrence is needed before drawing any conclusions about their habitat preferences.

Our results also reveal distinctive and consistent temporal patterns in the emergence of each species at both study sites. The emergence of *C. hemapterus* precedes that of *H. anthracina*, whereas *H. longirostris* emerges last and overlaps little with the two other species. The occurrence of *Carnus* seems to be determined by its parasitic nature since several authors (Liker et al., 2001; Valera et al., 2003) report a synchronization between the emergence of *Carnus* flies and the hatching of their nestling hosts. Whereas the factors (i.e., resources) accounting for the emergence patterns of both *Hemeromyia* species are unknown, the limited temporal overlap in the emergence of *H. anthracina* and *H. longirostris* could have evolved as a way to reduce interspecific competition during the adult stage. Temporal segregation of adult emergence may also result in segregation at the larval stage, therefore diminishing competition between larvae. However, with our current knowledge, this cannot be assumed. In line with this it is remarkable that positive associations were found between all pairs of species except for the two that most overlapped in their emergence pattern (*Carnus hemapterus* and *H. anthracina*).

The variation in life-history patterns that allows closely related species to co-exist has been an important theme in ecology for decades. Diapause has been hypothesised, in both theoretical and empirical studies, to be important in the coexistence of competing species. Several studies show that differences in a key life-history trait like diapause among species that share the same spatial habitat facilitate coexistence (Santer et al., 2000; Frisch, 2001; Tomiuk et al., 2004). Thus, differences in diapause length and/or timing of diapause might have resulted in the different emergence patterns of the *Hemeromyia* species that, in turn, might diminish interspecific competition and facilitate coexistence. Unfortunately the lack of information on natural history, feeding habits and cues required to terminate dormancy for these species makes addressing the interspecific variance in the time of emergence of *Hemeromyia* adults pure speculation. Regardless of the mechanism involved, our results show an obvious seasonal succession of species with a marked increase and decrease in abundance that could play an important role in the seasonal dynamics of the assemblage of insects inhabiting nests of birds (see, for instance, Hairston et al., 2000 for a similar scenario).

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