

INTERSPECIFIC PARASITE EXCHANGE IN A MIXED COLONY OF BIRDS

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ABSTRACT: Studies of avian host–parasite interactions rarely include consequences of relationships among hosts for either the host or parasite species. In this study, we examine the ectoparasitic burden of adult and nestling European bee-eaters (*Merops apiaster*) and rock sparrows (*Petronia petronia*) in a mixed colony. We found that (1) each bird species had its own species of lice; (2) hematophagous mites parasitized both adults and nestlings of both bird species; (3) *Carnus hemapterus*, a common parasite of nestling bee-eaters, also infested rock sparrow nestlings, a species not previously described as a host for this dipteran; and (4) whereas *C. hemapterus* did not show high host specificity within the colony, the emergence of adult flies was synchronized with the start of hatching in bee-eater nests. We suggest that coexistence of these 2 bird species results in parasite exchange, bee-eaters obtaining mites from sparrows and sparrows becoming infested by *C. hemapterus*. Differences in the detrimental effects of parasite transfer for each host species may result in a process of apparent competition mediated by shared parasites. Interspecific parasite exchange is an important aspect of host–parasite relationships in mixed colonies, which requires further attention.

Host sociality is an important factor in the study of host–parasite interactions (Ranta, 1992; Loye and Carroll, 1995). From the point of view of the parasite, host sociality increases the possibilities of finding a host and the opportunities of transmission for both contact-transmitted and mobile parasites (Anderson and May, 1979; Price, 1980; Proctor and Owens, 2000). For the host, the effects of parasites increase with the size of social aggregations. Specifically, it has been shown that colonial birds may suffer important fitness loss because of parasites (Brown and Brown, 1986; Loye and Carroll, 1991, 1995; Poiani, 1992). As a result, much work has been done on the relationship between birds' sociality and parasitism. However, some aspects of this relationship are still poorly understood. For instance, field data on parasite demography, including transmission rates and movement patterns from host to host and among sites, are extremely necessary (see, for instance, Burt et al., 1991; Pruett-Jones and Pruett-Jones, 1991; Bowers and Turner, 1997). Moreover, most of the studies on bird–parasite interactions have focused on the relationship between 1 parasite species and 1 host species and measuring the influence of the former on host behavior, survival, and fecundity (e.g., Moss and Camin, 1970; Brown and Brown, 1986; Møller, 1990; Loye and Carroll, 1991; but see, for instance, Burt et al., 1991). In contrast, the importance of ecological relationships among different potential host species on parasite transmission and its consequences has been frequently neglected (but see Hanley et al., 1995, 1998; Tompkins et al., 2000). This approach can be particularly fruitful in certain cases, like multispecific colonies (see Tella et al., 1998), where social contacts among hosts are frequent both at intraspecific and interspecific levels. Such studies are important from the point of view of both parasites and hosts. For instance, given that nests can be reused by different bird species, successive generations of a parasite may be exposed to different host species, which may have similar or very different breeding biology. This raises the question of whether the parasite is able to modify its breeding cycle in relation to host species, i.e., degree of host specificity (Roulin, 1998).

From the point of view of the host, it would be interesting to know the extent to which the occurrence of a second potential host species increases parasitism and its consequences.

The study of the effect of ecological relationships among several hosts on bird–parasite interactions is often hampered by the lack of suitable study systems. However, hole nesting, colonial breeding species provide an ideal opportunity because (1) dense aggregations of conspecifics favor transmission of parasites (Price, 1980); (2) multispecific colonies multiply the possibilities of transmission (Tella et al., 1998); and (3) reuse of previous breeding sites both by the same and different species enhance transmission (Burt et al., 1991).

European bee-eaters, *Merops apiaster*, and rock sparrows, *Petronia petronia*, frequently breed together in sandy cliffs in southern Spain, the sparrows using old nests of bee-eater. In this study, we report some aspects of host–parasite interactions resulting from the relationships between these 2 bird species. Specifically, we studied (1) the ectoparasitic burden of adult and nestling bee-eaters and rock sparrows; (2) the patterns of emergence of ectoparasites (the hematophagous fly *Carnus hemapterus* and hematophagous mites) affecting these bird species; and (3) the transmission of these ectoparasites between the 2 bird species.

MATERIALS AND METHODS

Species study

Rock sparrows are resident, secondary cavity nesters that usurp the nests of a variety of species. In our study area, they use nests of bee-eater from previous breeding seasons after adding abundant nest material including straw and feathers. Although not all individuals lay 2 clutches, second broods are not rare. In 2001, nest building started in our colony in mid-April, and the first nestlings appeared during the first week of May. The fledging period is about 16–20 days (Cramp, 1994).

Bee-eaters are migrant, aerial insectivorous birds, which nest in cavities at the end of long burrows (von Blotzheim and Bauer, 1980) often in steep sandbanks. In our study area, spring arrival occurs at the end of April, and nest digging starts soon after. At our study site, a new burrow is usually dug for each reproductive attempt. Bee-eaters produce a single brood with the earliest nestlings hatching in the beginning of June. Hatching date was calculated based on direct observations, detection of food calls of nestlings (Cramp, 1985), and adult behavior (feeding). The fledging period of individual chicks is about 4 wk, but chicks hatch and fledge asynchronously so that the fledging period of the brood can be up to about a week more (Lessells and Avery, 1989). Most nests with nestlings occurred approximately 1 mo after the peak of rock sparrows.

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Chewing lice species found in this study are *Meropoeus meropis*, *Meromenopon meropis*, *Brueelia apiastri*, and *B. alexandrii* (Mallophaga). Chewing lice are relatively long-lived parasites, apparently feeding on the feathers and dead skin of adult and nestling birds. Different species are restricted to specific areas on the birds' body and spend their entire lives on the birds (Marshall, 1981). Although the mechanisms of dispersal are poorly understood, chewing lice can move among individual hosts in several ways: (1) through direct contact of birds; (2) by using the same nest burrow or resting place; and (3) phoresy (Marshall, 1981).

The ectoparasite *C. hemapterus* (Diptera: Carnidae) is a 2-mm-long blood-sucking fly that parasitizes nestling birds (Walter and Hudde, 1987; Kirkpatrick and Colvin, 1989; Dawson and Bortolotti, 1997; Roulin, 1998) and usually overwinters as pupae in nests. After its eclosion, adult is initially winged and capable of flying, but typically loses its wings once it locates a suitable host (Walter and Hudde, 1987; Dawson and Bortolotti, 1997; Grimaldi, 1997; Papp and Darvas, 1998). Because neither the adults nor the larvae have been found on adult birds, flies are assumed to colonize nest hosts actively during the winged phase of their life cycle (Grimaldi, 1997; Roulin, 1998, 1999).

Two hematophagous mite species have been found in our colony, i.e., the tropical fowl mite, *Ornithonyssus bursa* (Macronyssidae, Gamasida), and the chicken mite, *Dermanyssus gallinae* (Dermanyssidae, Acarina). The life cycle of these mites lasts for about 5–7 days, and each female produces several clutches (Sikes and Chamberlain, 1954). Both juvenile stages and adult mites need blood meals at intervals throughout their lives. Mite populations build up quickly during the reproduction of their hosts (Burt et al., 1991; Pacejka et al., 1996), reaching up to about 14,000 mites in a single swallow nest (see Møller, 1991). Mites overwinter in old nests (Burt et al., 1991; Møller, 1991).

Study area

A mixed colony of bee-eaters and rock sparrows was studied during 2000 and 2001 in a sandy cliff approximately 100 m long in Tabernas (Almería, southern Spain). Approximately the same number of rock sparrows (ca. 100 pairs) bred in the colony during both years, but bee-eaters decreased noticeably between 2000 (about 40 breeding pairs) and 2001 (25 breeding pairs). Other species nesting interspersed with the bee-eaters and sparrows include common jackdaws, *Corvus monedula* (minimum 5 nests), house sparrows, *Passer domesticus* (ca. 12 nests), and Spanish sparrows, *P. hispaniolensis* (1 nest). The distances between heterospecific nests can be very small (a few centimeters to a few meters).

Adult bee-eaters and rock sparrows were mist netted from establishment until the end of the breeding season. Adult birds were ringed with numbered aluminum bands, and rock sparrows were additionally provided with a unique combination of color plastic bands.

Both rock sparrow and bee-eater nestlings are difficult to remove from the nest. Removal of young rock sparrows usually requires disturbing nest material, and this can lead to desertion. Nestling bee-eaters can be removed if the burrow is straight. Nestling bee-eaters and rock sparrows were temporarily taken from nests where feasible. To avoid disturbance, we usually removed only 1 or 2 nestlings (see below).

Parasite monitoring and identification

Ectoparasites of adult bee-eaters were studied during both years, whereas those of adult rock sparrows were studied only in 2001. Parasites of bee-eater and rock sparrow nestlings were examined only during 2001.

We used the method described by Hoi et al. (1998) to monitor chewing lice. Two persons looked for lice on birds for about 10 min and used forceps to collect any chewing lice found. Chewing lice were collected from bee-eaters from the head, throat, and belly and from rock sparrows additionally from rump. Prevalence was calculated on the basis of the presence of adult or larval chewing lice (or both).

Mites on adult birds were readily detected because they rapidly moved onto our hands when birds were handled. The number of mites parasitizing adult bee-eaters was not estimated. However, mites found on adult rock sparrows were counted because they were very scarce.

The prevalence of *C. hemapterus* and mites on bee-eater nestlings was determined by examining chicks and nest material (sand). The occurrence of mites on rock sparrows was determined directly from nest-

lings taken from the nest or from nest material during the nestling phase or soon after (maximum 6 days) the nestlings deserted the nest. Prevalence of *C. hemapterus* on rock sparrows was determined by examining the chicks.

Overall, our data on prevalence are conservative for both bird species because (1) not all nestlings from a brood were examined; (2) we could not obtain sand from the breeding chamber of nests of some bee-eaters; and (3) mite populations seem to grow slowly during the early stages of the nesting period and only increase exponentially in the later stages (Burt et al., 1991; Pacejka et al., 1996). Most nestlings monitored were young.

The prevalence of *C. hemapterus* that we report may be more conservative than the one given for mites because the latter do not seem to choose specific individuals within a brood; they occupy nest material (Burt et al., 1991) and reach high numbers in every nest. In contrast, *C. hemapterus* shows intrabrood preferences (Dawson and Bortolotti, 1997; Roulin, 1998, 1999; Valera et al., unpubl.), usually avoiding very young nestlings and feathered nestlings, and is usually found on the host and not in the nest material. Thus, negative results when sampling only 1 individual or nest material do not mean that other nestlings or the nests are not infested.

Chewing lice from each bird were stored in 75% ethanol and were identified to the species level 1 mo later. Mites were collected and identified from a subsample of bee-eaters and rock sparrows (6 and 9 individuals, respectively). In this sample, only *O. bursa* was found parasitizing bee-eaters (all 6 individuals were parasitized), whereas both *O. bursa* (in 4 birds) and *D. gallinae* (in 5 birds) were found on rock sparrows. Given the low number of birds used for mite identification, we cannot exclude the possibility that some bee-eaters are parasitized by *D. gallinae*. Therefore, we will refer to hematophagous mites as a whole, i.e., pooling both species, rather than distinguishing parasitism by each mite species.

Determining the phenology of *Carnus hemapterus* emergence

The emergence of adult *C. hemapterus* flies in bee-eaters' nests was studied during 2001. Entomological chromatic traps (cardboard with glue on both sides and measuring 6 × 5 cm) were located at the entrance (ca. 10 cm inside the tunnel) of 13 nests of bee-eater used the previous season. Additionally, a 1.5- × 25-cm strip was placed approximately 15 cm inside the tunnel, fitting its perimeter to catch individuals leaving the nest on foot. We probably not only trapped most of the flies leaving the nest but also limited access of flies into the nest. A preliminary study in another mixed colony of bee-eaters and rock sparrows revealed that *C. hemapterus* emergence did not occur before the last week of May. Therefore, entomological traps were placed on 25 May, monitored, and changed weekly until 13 July. *Carnus hemapterus* emergence was detected in 10 out of 13 nests. Nonemergence in the 3 remaining nests could be because of early failure of the nests during the nestling phase of the previous year (therefore, precluding the completion of the life cycle of the fly), burrow collapse, or both. Only nests where *C. hemapterus* emergence was detected were used to calculate the phenology of emergence and mean number of immigrants and individuals emerged. For this, we counted the number of flies trapped on each side of the trap, thereby obtaining the number of individuals emerging from the nest (trapped on the side facing the incubation chamber) and the number entering the nest ("immigrants" trapped on the side facing outward). One nest where emergence was detected was occupied after the second week of monitoring by a rock sparrow, and therefore only 12 traps were active from 7 June onward. The first week's sample from 1 nest was lost because of human interference.

Statistical analyses

Prevalence (proportion of infected hosts among all the hosts examined) and mean intensity (mean number of parasites found in the infected hosts) of parasites (and their respective 95% confidence intervals) were calculated. Fisher's exact tests and bootstrap 2-sample *t*-tests were used for comparing prevalences and mean intensities, respectively; 2,000 replications were used for estimation of confidence intervals and bootstrap *t*-tests. Statistical tests were done with the program Quantitative Parasitology 2.0 (Reiczigel and Rózsa, 2001). Tests are 2-tailed unless otherwise stated.

TABLE I. Prevalence (proportion of infected individuals) (upper row) and mean intensity (mean number of parasites found in the infected hosts) (lower row) (with 95% confidence intervals in brackets) of ectoparasites found on adult breeding bee-eaters ($n = 18$ in 2000 and 29 in 2001) and rock sparrows ($n = 45$) in a mixed colony in southern Spain.

	European bee-eater		Rock sparrow 2001
	2000	2001	
<i>Meromenopon meropis</i>	0.056 (0.0014 to 0.27) 1.0 (—)	0.034 (0.0008 to 0.18) 1.0 (—)	0.0 0.0
<i>Meropoecus meropis</i>	0.89 (0.65 to 0.99) 10.13 (7.7 to 12.6)	0.79 (0.60 to 0.92) 5.48 (3.6 to 7.2)	0.0 0.0
<i>Brueelia apiastri</i>	0.56 (0.31 to 0.78) 3.7 (1.3 to 6.7)	0.28 (0.13 to 0.47) 2.38 (1.6 to 3.0)	0.0 0.0
<i>B. alexandrii</i>	0.0 0.0	0.0 0.0	0.22 (0.11 to 0.37) 5.1 (2.4 to 7.5)
Hematophagous mites	0.33 (0.13 to 0.59) (—)	0.10 (0.022 to 0.27) (—)	0.089 (0.025 to 0.21) 1.25 (1 to 1.5)

RESULTS

Ectoparasites of adult and nestling bee-eaters

Three chewing lice species (*Meropoecus meropis*, *Meromenopon meropis*, and *B. apiastri*) were detected on adult bee-eaters during the 2-yr study (Table I). *Meropoecus meropis* was the most common species, whereas *Meromenopon meropis* was rare. Prevalence of *Meropoecus meropis* did not differ between years (Fisher's exact test, $P = 0.69$, $n = 18, 29$), but the mean intensity was significantly higher in 2000 than in 2001 (bootstrap t -test, $t = 2.89$, $P = 0.011$). The mean intensity of parasitism by *B. apiastri* did not differ between years (bootstrap t -test, $t = 0.84$, $P = 0.42$), but prevalence tended to be higher in 2000 than in 2001 (Fisher's exact test, $P = 0.07$, $n = 18, 29$).

Hematophagous mites parasitized adult bee-eaters during both study years (Table I). Prevalence tended to be higher in the first year (Fisher's exact test, $P = 0.068$, $n = 18, 29$). When analyzing the prevalence of mites in relation to the breeding cycle of bee-eaters, we found that in both years the percentage of adult bee-eaters with mites was lower before hatching than during the nestling phase: 0 out of 6 versus 6 (50%) out of 12 for 2000 (Fisher's exact test, $P = 0.054$) and 0 out of 18 versus 3 (27.3%) out of 11 for 2001 (Fisher's exact test, $P = 0.045$), (pooling both years: Fisher's exact test, $P = 0.001$). A higher proportion of individuals was trapped after hatching in 2000 than in 2001, and this apparently explains the higher prevalence of mites in the first year (see above). When considering only the individuals captured after hatching in both years, we found no interannual difference in prevalence (Fisher's exact test, $P = 0.40$). Although we did not estimate parasite load, most adult bee-eaters had more than 10 mites (some of them well above 50).

Concerning nestling bee-eaters, we found *C. hemapterus* in 10 (62%) out of 16 nests sampled (95% confidence interval = 0.35 to 0.85). Prevalence is very likely higher because only 1 chick was sampled in 2 nests and only material was sampled in the other nests where we did not find this parasitic fly. Hematophagous mites were also found parasitizing bee-eater nestlings with a very high prevalence (16–94% out of 17 nests, 95% confidence interval = 0.71 to 0.99). We did not find chewing lice, but most of the sampled nestlings were not feathered.

Ectoparasites of adult and nestling rock sparrows

Only 1 chewing louse species (*B. alexandrii*) was detected parasitizing adult rock sparrows (Table I), and prevalence was relatively low (22%, which increases to 31.1% when adult birds with parasite eggs are included).

Rock sparrows were also parasitized by mites. Prevalence did not differ from that on bee-eaters during the same study year (Fisher's exact test, $P = 1.0$). All 4 individuals with mites were trapped during the second half of the season.

Nestling rock sparrows were also parasitized by *C. hemapterus*, prevalence being at least 56% (9 out of 16 nests were infested, 95% confidence interval = 0.30 to 0.80). Most sampled nests come from second clutches, and the only first clutch monitored had no *C. hemapterus*. Two species of hematophagous mites were found parasitizing nestling rock sparrows (*O. bursa* and *D. gallinae*). Mites were recorded in 32 (78%) of 41 nests (95% confidence interval = 0.62 to 0.89).

Matching ectoparasite and host phenology

We detected the emergence of *C. hemapterus* in bee-eaters' nests from the fourth week of May until the first week of July, with a peak in the second week of June (Fig. 1). Emergence probably started a bit earlier, but the shape of the curve and the scarcity of immigrants in late May suggest that the number of flies emerging before the last week of May is low. Dispersal activity of *C. hemapterus* is higher in the first 3 wk of June, when 87.9% ($n = 664$) of emerging individuals and 78.9% ($n = 57$) of immigrants were trapped. This coincides with the phenology of the bee-eaters (Fig. 1); 93.7% of nests ($n = 16$) had chicks during that period, and only 9.0% of the captured flies emerged before any bee-eater nestlings hatched. In contrast, first broods of rock sparrows do not seem to be exposed to *C. hemapterus* from bee-eaters' nests, and only nests with nestlings from the end of May onward could be infected with this fly (Fig. 1).

Hematophagous mites were first detected during the second week of May, in the first nests of rock sparrows with nestlings (Fig. 1). Afterward, most nests of rock sparrows (first and second clutches) and bee-eaters were parasitized by mites. Prevalence of mites in rock sparrow nests did not differ significantly (Fisher's exact test, $P = 0.45$) before (83.3%, $n = 24$) and after

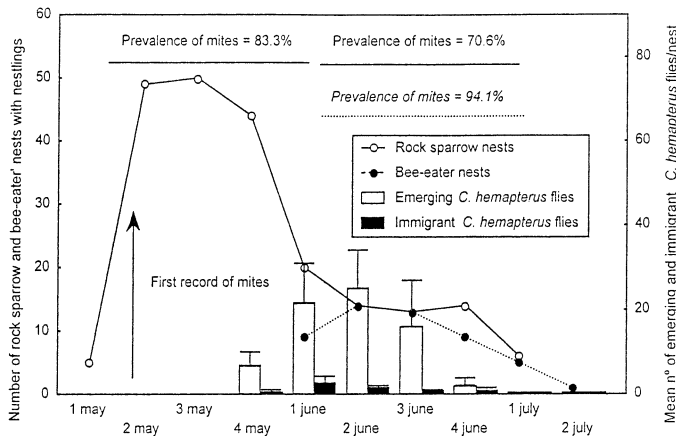


FIGURE 1. Breeding phenology of rock sparrows and bee-eaters in relation to phenology and prevalence of *Carnus hemapterus* and hematophagous mites. Open and filled bars show the mean values (\pm SE) of emergent and immigrant *C. hemapterus* flies in 1-yr-old bee-eater nests during 2001 (sample size is 9 nests for each week from end of May onward except for the first week of June, when 10 nests were sampled). Prevalence and phenology of mites are shown for bee-eater nests (in italics) and for early and late rock sparrow nests.

hatching of eggs of bee-eaters (70.6%, $n = 17$) (Fig. 1). Prevalence of mites on bee-eater nestlings did not differ from the one found on second clutches of rock sparrows (Fisher's exact test, $P = 0.17$).

DISCUSSION

Rock sparrows and bee-eaters carry different chewing lice species. The former has a single *Brueelia* species, whereas the latter are parasitized by *Meropocus meropis*, *Meromenopon meropis*, and *B. apiastris* (see Kristofik et al., 1996; Hoi et al., 1998; Darolova et al., 2001, for similar results). Mallophaga, particularly Ischnocera, are highly host specific (Marshall, 1981), and thus it is no surprise that there is no chewing lice exchange between both host species. In contrast, both bird species share several hematophagous parasites, namely *C. hemapterus* and mites.

Whereas it is well known that European bee-eater nestlings are hosts of *C. hemapterus* (Kristofik et al., 1996; Papp and Darvas, 1998), to date the rock sparrow has not been described as a host of this fly (Bequaert, 1942; Capelle and Whitworth, 1973; Walter and Hudde, 1987; Grimaldi, 1997). Rock sparrows occupy burrows used by bee-eaters in previous breeding seasons. The present results show that old nests of bee-eater are a source of *C. hemapterus* and that winged adult flies actively seek and colonize other nests (see also Roulin, 1998). It is, therefore, not surprising that sparrows breeding in such nests are parasitized by this fly, whose origin is probably the same nest (where the flies have been overwintering as pupae), as well as immigrants from neighboring nests (Roulin, 1998). Thus, in our colony, *C. hemapterus* could be transmitted among different host species through the occupation of a nest hole previously used by other species (see Burt et al., 1991; Tella et al., 1998). Host records suggest that this fly does not exhibit host specificity; it has an extensive geographical distribution and broad range of host species (Bequaert, 1942; Capelle and Whitworth, 1973; Dawson and Bortolotti, 1997; Grimaldi, 1997). We found

that the emergence of adult flies was synchronized with hatching of bee-eater (Fig. 1). *Carnus hemapterus*, therefore, seems to be specific in terms of the timing of eclosion of the resistance form (see Liker et al., 2001) but generalist in terms of the type of host that can be parasitized. This strategy maximizes the probability of synchrony with the most likely available species (those that were there the previous year) while not ruling out other hosts if the original host is unavailable.

We found that rock sparrows are parasitized by *O. bursa* and *D. gallinae*. These data show that adult and nestling bee-eaters are also parasitized by hematophagous mites. Although only *O. bursa* was recorded, it is likely that some individuals could also be parasitized by *D. gallinae* (see Materials and Methods). Mites were first detected in the first broods of rock sparrows (Fig. 1). At that time, adult bee-eaters were incubating. Later in the season, most nests of bee-eaters were infested with mites, although bee-eaters in our study colony usually dig new (clean) holes every year. Moreover, adult bee-eaters trapped during the first half of the breeding season (before hatching) had no mite, whereas a considerable proportion of adults (ca. 39% pooling both years) trapped after hatching had started had mites. We presume that mites infested the first rock sparrow nestlings, and when bee-eater nestlings hatched, mites, whose populations increase as the season advances (Burt et al., 1991; Møller, 1991; Pacejka et al., 1996), moved to the latter. Mobile ectoparasites such as mites are able to move actively between both conspecific (Tella, 1996) and heterospecific (Poulin, 1991) hosts, and it is well known that many mite species emigrate from the nest soon after the nestlings depart (Burt et al., 1991). Thus, in our colony, mites could be transmitted by active walking. Population increases in the nests of the earliest breeders would provide large numbers of immigrants to the nests of individuals breeding later in the season or trying to raise a second brood (Burt et al., 1991). We found a very high prevalence of mites in bee-eater nests (higher than 90%) and, although we did not estimate mite load, parasitic burden was much higher for bee-eater than for rock sparrow nestlings (we found almost 500 mites on a single bee-eater nestling).

Our observational approach cannot prove that bee-eaters are infested with mites coming from neighboring breeding rock sparrows. Direct evidence for this could be obtained experimentally, e.g., precluding rock sparrow nesting in parts of the colony. However, in the absence of such experiments, some hints support our speculation of parasite transfer from rock sparrows to bee-eaters.

Hematophagous mites do not seem to be the common ectoparasites of bee-eaters, and their occurrence in bee-eater nests seems to be frequently associated with the presence of a second bird species. Kristofik et al. (1996) do not mention mites parasitizing adults but state that blood-sucking mites *D. hirundinis*, *D. gallinae*, and *O. sylvianum* were rare in bee-eater nests and that these 3 species also parasitized sand martins (*Riparia riparia*), whose small colonies were located in some cases close to the bee-eater nests. H. Hoi (pers. obs.) did not find mites parasitizing adult and nestling bee-eaters during a 6-yr study in Slovakia. Another long-term study on monospecific bee-eater colonies in southern France detected *C. hemapterus* parasitizing nestlings, but mites were not obvious either on adults or nestlings (C. M. Lessells, pers. comm.). I. H. Török (pers. comm.)

found that bee-eaters nesting in a mixed colony were more infested by mites than bee-eaters in monospecific colonies.

Species coexistence and reuse of previous breeding sites increase the probability of interspecific parasite exchange (Burt et al., 1991; Kristofik et al., 1996; Tompkins et al., 2000; Martin and Martin, 2001). Parasite transfer among host species raises 2 questions. The first is whether parasites can develop successfully in these “secondary” hosts? For instance, the length of the nestling period of the host may be an important factor for *C. hemapterus*. Rock sparrows begin pennaceous feather growth by 10 days of age (Cramp, 1994), whereas bee-eaters begin growing such feathers at about 20 days (Cramp, 1985). Therefore, rock sparrows become an inhospitable environment because of increased density and layering of feathers (Dawson and Bortolotti, 1997) sooner than bee-eaters. In turn, the long period that bee-eater nestlings stay in the nest (at least 4 wk) allows mites to produce several clutches, which may account for the vast numbers of mites found on the former.

The second question is what are the consequences for infestation of each host species from the other species? Although apparent competition mediated by shared parasites is potentially an important force influencing community structure, there is limited evidence to demonstrate its occurrence in the field (Hanley et al., 1995, 1998; Tompkins et al., 2000). In the interaction between the rock sparrow and the bee-eater, apparent competition, i.e., increased numbers of parasites of one species in the presence of a second one, may play a role because the costs and benefits of coexistence for each species seem to be very different. Rock sparrows get substantial benefits, i.e., nest sites, of breeding near bee-eaters and probably a low cost of parasitism by *C. hemapterus*, as most studies investigating parasitism by this fly have failed to identify detrimental effects on a variety of host species (Walter and Hudde, 1987; Kirkpatrick and Colvin, 1989; Dawson and Bortolotti, 1997; Liker et al., 2001; but see Cannings, 1986). In contrast, bee-eaters do not get obvious benefits of breeding near rock sparrows, but they may suffer from increased parasitism by detrimental blood-sucking mites. Blood-feeding nest mites, and specifically *Dermanyssus* and *Ornithonyssus* spp., have been frequently reported to severely influence the reproductive success of a variety of hosts (Møller, 1991; Proctor and Owens, 2000 and references therein). The ubiquity of mites in nests of bee-eaters and the size of their populations (seemingly higher than in rock sparrow nests) suggest that these parasites can affect the reproductive success of bee-eaters. This may explain why bee-eaters are very aggressive toward rock sparrows, particularly when the first ones are establishing their territories (data not shown). Nevertheless, removal experiments would be needed to understand the ecological consequences and fitness costs of coexistence for each species.

In summary, parasite exchange among host species is an important aspect of host–parasite relationships in mixed colonies. Coexistence of several host and parasite species may have important ecological consequences and, therefore, requires further attention.

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LITERATURE CITED

- ANDERSON, R. M., AND R. M. MAY. 1979. Population biology of infectious diseases. *Nature* **280**: 361–367, 455–461.
- BEQUAERT, J. 1942. *Carnus hemapterus* Nitzsch, an ectoparasitic fly of birds, new to America (Diptera). *Bulletin of the Brooklyn Entomological Society* **37**: 140–149.
- BOWERS, R. G., AND J. TURNER. 1997. Community structure and the interplay between interspecific infection and competition. *Journal of Theoretical Biology* **187**: 95–109.
- BROWN, C. R., AND M. B. BROWN. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology* **67**: 1206–1218.
- BURTT, E. H., W. CHOW, AND G. A. BABBIT. 1991. Occurrence and demography of mites of tree swallow, house wren and eastern bluebird nests. *In* Bird–parasite interactions: Ecology, evolution and behaviour, J. E. Loye and M. Zuk (eds.). Oxford University Press, Oxford, U.K., p. 104–122.
- CANNINGS, R. J. 1986. Infestations of *Carnus hemapterus* Nitzsch (Diptera: Carnidae) in northern saw-whet owl nests. *Murrelet* **67**: 83–84.
- CAPELLE, K. J., AND T. L. WHITWORTH. 1973. The distribution and avian hosts of *Carnus hemapterus* (Diptera: Milichiidae) in North America. *Journal of Medical Entomology* **10**: 525–526.
- CRAMP, S. 1985. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. IV*. Oxford University Press, Oxford, U.K., 960 p.
- . 1994. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. VIII*. Oxford University Press, Oxford, U.K., 899 p.
- DAROLOVA, A., H. HOI, J. KRISTOFIK, AND C. HOI. 2001. Horizontal and vertical ectoparasite transmission of three species of malophaga, and individual variation in European bee-eaters (*Merops apiaster*). *Journal of Parasitology* **87**: 256–262.
- DAWSON, R. D., AND G. R. BORTOLOTTI. 1997. Ecology of parasitism of nestling American Kestrels by *Carnus hemapterus* (Diptera, Carnidae). *Canadian Journal of Zoology* **75**: 2021–2026.
- GRIMALDI, D. 1997. The bird flies, Genus *Carnus*: Species revision, generic relationships and a fossil *Meoneura* in amber (Diptera: Carnidae). *American Museum Novitates* No. 3190, American Museum of Natural History, New York, 30 p.
- HANLEY, K. A., K. PETREN, AND T. J. CASE. 1998. An experimental investigation of the competitive displacement of a native gecko by an invading gecko: No role for parasites. *Oecologia* **115**: 196–205.
- , D. M. VOLLMER, AND T. J. CASE. 1995. The distribution and prevalence of helminth and coccidial parasites of two competing species of gecko: Implications for apparent competition. *Oecologia* **102**: 220–229.
- HOI, H., A. DAROLOVA, C. KÖNIG, AND J. KRISTOFIK. 1998. The relation between colony size, breeding density and ectoparasite loads of adult European bee-eaters (*Merops apiaster*). *Ecoscience* **5**: 156–163.
- KIRKPATRICK, C. E., AND B. A. COLVIN. 1989. Ectoparasitic fly *Carnus hemapterus* (Diptera: Carnidae) in a nesting population of common barn-owls (Strigiformes: Tytonidae). *Journal of Medical Entomology* **26**: 109–112.
- KRISTOFIK, J., P. MASÁN, AND Z. SUSTEK. 1996. Ectoparasites of bee-eater (*Merops apiaster*) and arthropods in its nests. *Biologia* **51**: 557–570.
- LESSELLS, C. M., AND M. I. AVERY. 1989. Hatching asynchrony in European bee-eaters *Merops apiaster*. *Journal of Animal Ecology* **58**: 815–835.
- LIKER, A., M. MARKUS, A. VOZÁR, E. ZEMANKOVICS, AND L. RÓZSA. 2001. Distribution of *Carnus hemapterus* in a starling colony. *Canadian Journal of Zoology* **79**: 574–580.
- LOYE, J. E., AND S. CARROLL. 1991. Nest ectoparasite abundance and cliff swallow colony site selection, nestling development and departure time. *In* Bird–parasite interactions: Ecology, evolution and

- behaviour, J. E. Loye and M. Zuk (eds.). Oxford University Press, Oxford, U.K., p. 222–241.
- , AND ———. 1995. Birds, bugs and blood: Avian parasitism and conservation. *Trends in Ecology and Evolution* **10**: 232–235.
- MARSHALL, A. G. 1981. The ecology of ectoparasitic insects. Academic Press, London, U.K., 459 p.
- MARTIN, P. R., AND T. E. MARTIN. 2001. Ecological and fitness consequences of species coexistence: A removal experiment with wood warblers. *Ecology* **82**: 189–206.
- MØLLER, A. P. 1990. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* **71**: 2345–2357.
- . 1991. Parasite load reduces song output in a passerine bird. *Animal Behaviour* **41**: 723–730.
- MOSS, W. W., AND J. H. CAMIN. 1970. Nest parasitism, productivity and clutch size in Purple Martins. *Science* **168**: 1000–1003.
- PACEJKA, A. J., E. SANTANA, R. G. HARPER, AND C. F. THOMPSON. 1996. House wrens *Troglodytes aedon* and nest-dwelling ectoparasites: Mite population growth and feeding patterns. *Journal of Avian Biology* **27**: 273–278.
- PAPP, L., AND B. DARVAS. 1998. Contributions to a manual of Palaearctic Diptera, Vol. 3. Science Herald, Budapest, Hungary, 880 p.
- POIANI, A. 1992. Ectoparasitism as a possible cost of social life: A comparative analysis using Australian passerines (Passeriformes). *Oecologia* **92**: 429–441.
- POULIN, R. 1991. Group living and infestation by ectoparasites in passerines. *Condor* **93**: 418–423.
- PRICE, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey, 256 p.
- PROCTOR, H., AND I. OWENS. 2000. Mites and birds: Diversity, parasitism and coevolution. *Trends in Ecology and Evolution* **15**: 358–364.
- PRUETT-JONES, M., AND S. PRUETT-JONES. 1991. Analysis of ecological correlates of tick burdens in a New Guinea avifauna. In Bird–parasite interactions: Ecology, evolution and behaviour, J. E. Loye and M. Zuk (eds.). Oxford University Press, Oxford, U.K., p. 154–178.
- RANTA, E. 1992. Gregariousness vs. solitude—Another look at parasite faunal richness in Canadian fresh-water fishes. *Oecologia* **89**: 150–152.
- REICZIGEL, J., AND L. RÓZSA. 2001. Quantitative parasitology 2.0. Budapest, Hungary.
- ROULIN, A. 1998. Cycle de reproduction et abondance du diptère parasite *Carnus hemapterus* dans les nichées de chouettes effraies *Tyto alba*. *Alauda* **66**: 265–272.
- . 1999. Fécondité de la mouche *Carnus hemapterus*, ectoparasite des jeunes chouettes effraies *Tyto alba*. *Alauda* **67**: 205–212.
- SIKES, R. K., AND R. W. CHAMBERLAIN. 1954. Laboratory observations on three species of bird mites. *Journal of Parasitology* **40**: 691–697.
- TELLA, J. L. 1996. Condicionantes ecológicos, costes y beneficios asociados a la colonialidad en el cernícalo primilla. Ph.D. Thesis. University of Barcelona, Barcelona, Spain, 251 p.
- , A. GAJÓN, C. GORTÁZAR, AND J. J. OSÁCAR. 1998. High host specificity of *Crataerina melbae* (Diptera: Hippoboscidae) in a mixed colony of birds. *Journal of Parasitology* **84**: 198–200.
- TOMPKINS, D. M., R. A. H. DRAYCOTT, AND P. J. HUDSON. 2000. Field evidence for apparent competition mediated via the shared parasites of two gamebird species. *Ecology Letters* **3**: 10–14.
- VON BLOTZHEIM, G., AND K. M. BAUER. 1980. Handbuch der Vögel Mitteleuropas. Band 9 Akademische Verlagsgesellschaft, Wiesbaden, Germany. 1148 p.
- WALTER, G., AND H. HUDDE. 1987. Die Gefiederfliege *Carnus hemapterus* (Milichiidae, Diptera), ein Ektoparasit der Nestlinge. *Journal für Ornithologie* **128**: 251–255.