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Source: Journal of Parasitology, 87(2):256-262.

Published By: American Society of Parasitologists

DOI: [http://dx.doi.org/10.1645/0022-3395\(2001\)087\[0256:HAVETO\]2.0.CO;2](http://dx.doi.org/10.1645/0022-3395(2001)087[0256:HAVETO]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1645/0022-3395%282001%29087%5B0256%3AHAVETO%5D2.0.CO%3B2>

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## HORIZONTAL AND VERTICAL ECTOPARASITE TRANSMISSION OF THREE SPECIES OF MALOPHAGA, AND INDIVIDUAL VARIATION IN EUROPEAN BEE-EATERS (*MEROPS APIASTER*)

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**ABSTRACT:** Dispersal of avian ectoparasites can occur through either vertical transmission from adult birds to their offspring in the nest or through horizontal transmission between adult birds or through phoresy. In this study, we investigated the importance of the 2 main transmission modes in the colonial European bee-eater and examined whether individual differences in ectoparasite intensity exist in relation to age, sex, and morphological features of the birds. The intensity of 3 chewing lice species was investigated. Almost all adult bee-eaters (98.3%,  $n = 176$ ) were infested with 1 of the 3 ectoparasite species, whereas only 10.8% ( $n = 167$ ) of all chicks were infested. *Meropoecus meropis* was the most frequent ectoparasite species on adult bee-eaters (prevalence 94.3%), whereas *Meromenopon meropis* was the most common species on chicks (prevalence 9.6%). Our results suggest that chewing lice are mainly horizontally transmitted among adult bee-eaters and mainly among pair members, whereas vertical transmission between parents and nestlings is less frequent. These conclusions were supported by a relation in ectoparasite intensity of pair members and a parasite removal experiment. Ectoparasite intensity was in general low in nestlings and did not correlate with ectoparasite intensity of their parents. Host age, sex, weight, and other morphological features did not explain variation in chewing lice infestation.

Studies of avian ectoparasite infestation usually examine the impact of parasites on their hosts. Adverse effects of ectoparasites on host condition have been demonstrated for adults and offspring (King et al., 1977; Loye and Carroll, 1991; Møller, 1993). Ectoparasites may also affect host behavior, especially social behavior and mate choice (Alexander, 1971, 1974; Hart, 1990; Keymer and Read, 1991; Loye and Zuk, 1991). Clayton and Tompkins (1994, 1995) pointed out that virulence of a parasite depends very much on the transmission mode. However, relatively little is known about the frequency and mechanisms of ectoparasite transmission. In general, dispersal of ectoparasites can occur through 2 routes, either through vertical transmission from adult birds to their offspring in the nest or through horizontal transmission between adult birds (Dubinin, 1947; Eichler, 1963; Marshall, 1981), with horizontal transmission being more virulent (Clayton and Tompkins, 1994). Chewing lice, for instance, are probably always transmitted vertically with a varying degree of horizontal transmission, because they depend very much on the environment provided by the host plumage for survival (Clayton and Tompkins, 1994). Ischnoceran chewing lice mainly feed on feathers, and hence vertical transmission occurs only when young grow feathers (Clayton and Tompkins, 1995). In contrast, ticks, mites, fleas, and bugs are less dependent on the host environment and on direct contacts between hosts (Clayton and Tompkins, 1995). A third possible transmission mode could be related to phoresy. In line with this, chewing lice might use other more mobile ectoparasites, especially hippoboscids, as a vehicle for reaching a new host.

Other determinants for the rate of ectoparasite transmission could be related to the probability that a parasite will encounter a new host, which may at least partly depend on host population density (Poiani, 1992; Côté and Poulin, 1995; Rózsa et al., 1996), or variation in susceptibility of host individuals, which may be due to differences in the ability to resist parasites (Ham-

ilton and Zuk, 1982), or to the length of host exposure to parasites, e.g., age-related effect (Bergstrand and Klimstra, 1964; Spellerberg, 1971; but see Foster, 1969; Everleigh and Threlfall, 1976). In addition to host density, transmission rate may depend on (1) the degree of active or passive dispersal of parasites (Dubinin, 1947; Marshall, 1981) and (2) host behavior, e.g. reuse of the same nest burrow or the use of communal sand bathing sites (Eichler, 1963).

In the present study, we attempted to investigate the relative importance of vertical and horizontal transmission of chewing lice in the colonial bee-eater *Merops apiaster*. Because both parents invest in offspring care, nestling period is rather long (27–30 days), and feather development of nestlings starts early (within about 6 days) (Koenig, 1951; Glutz von Blotzheim and Bauer, 1980), we expected vertical transmission to occur between parents and offspring. Because chewing lice feed mainly on feathers, one might expect that vertical transmission increases with the development of feathers in chicks (Clayton, 1991). The fact that ectoparasite intensity differs between colonies and increases with colony size of bee-eaters (Hoi et al., 1998), however, also suggests a role for horizontal transmission. In fact, high levels of horizontal transmission can be expected, because breeding density is high, i.e., bee-eaters are colonial breeders, and pairs spend most of their time together (Koenig, 1951; Glutz von Blotzheim and Bauer, 1980). Ectoparasites can quickly move between individual hosts during close contact of birds in communal perches and roosts, or between parents and offspring in the nest (Clayton, 1991; Hillgarth, 1996). In bee-eaters, transmission of ectoparasites can, therefore, occur between pairs during mating, copulation, pair preening, pair feeding, working in the nest chamber, and chick feeding (Koenig, 1951; Glutz von Blotzheim and Bauer, 1980). Horizontal transmission from other birds in the colony may occur at communal roost sites or perches, during fight, and during extrapair copulations (we observed several extrapair copulations during the study). The third transmission mode through phoresy can be neglected for bee-eaters, because no hippoboscids or any other more mobile ectoparasite could be detected during our investigation.

Received 10 May 2000; revised 5 September 2000; accepted 5 September 2000.

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## MATERIALS AND METHODS

### Study area and species

Bee-eaters nest in cavities at the end of deep, usually horizontal burrows (75 to 150 cm; Glutz von Blotzheim and Bauer, 1980) in mainly vertical sand or earth banks. Usually, bee-eaters dig new burrows for each breeding attempt (Glutz von Blotzheim and Bauer, 1980; Hudec, 1983). Bee-eaters are parasitized by several ectoparasite species (for details, see Kristofik et al., 1996; Hoi et al., 1998). Here, we focus on 3 species of chewing lice (Mallophaga), namely *Meropoecus meropis*, *Meromenopon meropis*, and *Brueelia apiastri* (Philopteridae), because they seem to have the greatest fitness impact on the birds (Kristofik et al., 1996) and occur on both adult and nestling birds (Eichler, 1963). For descriptions of the biology of chewing lice, see Blagoveschtschenskij (1959), Marshall (1981), and Hoi et al. (1998).

Bee-eaters were studied in southern and eastern Slovakia from 1995 to 1997. Data were obtained from different colony sites comprising single breeding pairs and colonies of up to 79 breeding pairs (see Hoi et al., 1998, for a detailed description of the colony sites). Investigation of horizontal transmission included 42 pairs, comprising 12 pairs from 3 colonies in 1995, 25 pairs from 9 colonies in 1996, and 5 pairs from 3 colonies in 1997. Adult breeding birds were caught during the feeding period (from 10 to 24 July). We used small claptraps attached to the entrance of the nest burrow. Birds were ringed with numbered metal bands using the Czech ringing scheme. Several morphological measures were taken: wing, tarsus, tail, and bill length according to Svensson (1992), and the length of the pintail. Measurements were taken with calipers to the nearest 0.1 mm. Additionally, birds were weighed to within 0.1 g with an electric balance and sexed on the basis of plumage characteristics and morphology (see Lessells and Ovendon, 1989). The age classes of the birds (1 yr or older) were determined on the basis of the brightness of coloration, specific color patterns, and the extension of the white forehead patch (Glutz von Blotzheim and Bauer, 1980; Cramp, 1985).

Investigation of vertical transmission includes only data from 1996 and comprises 167 chicks from 45 nests for 12 colonies. We accessed nestlings with the help of a bent spoon attached to a long stick. This method worked very well with nestlings of different ages. In the present study, chick age varied between 2 and 20 days. To examine chewing lice intensity in relation to feather development, we measured the length of the longest primary feather in each nestling.

### Parasite counts

To reduce sampling time and efficiency, chewing lice were collected from the head, throat, and belly of adult bee-eaters, because these areas are clearly separated by different coloration patterns and are the main infested areas (J. Kristofik, unpubl. obs.). In fact, *B. apiastri* is restricted to the belly and *M. meropis* to the head and throat of adult birds. For nestlings, we examined the whole body, because sampling was quicker because of the lack of fully developed feathers. To obtain comparative data for adult birds, 3 persons intensively searched each individual for 10 min. One person held the bird and all 3 persons carefully examined the 3 areas by gently blowing feathers apart and using forceps to collect chewing lice. Because the 3 louse species are about 2–5 mm in length and move slowly, it is unlikely that 3 people would overlook any of them. Nevertheless, we examined 10 birds repeatedly, but could not detect any additional parasites after the first 10 min. Nestlings were treated by 2 persons for 3 min. Chewing lice of each individual bird were then stored in tubes containing 75% alcohol and later identified to species. Parasite counts were restricted to the first 2 weeks in July 1996–1997, during the chick feeding period. To determine whether there was a seasonal change in chewing lice abundance, we additionally sampled 20 adult bee-eater individuals (4–6 June 1998, during egg laying), whereby chewing lice were not collected; during the first 2 wk in July 1998, we again examined for ectoparasite intensity. Adults and chicks were searched in the same time.

### Ectoparasite removal experiment

To examine whether chewing lice moved between individual bee-eaters during the fertile, incubation, and the chick-feeding period, we experimentally removed all ectoparasites from 1 individual of a pair (4–6 June 1998, the egg-laying period). Lice were collected by checking

every feather of an individual and removing all lice (adults and nymphs) with forceps. We additionally intensively sprayed birds with a Pyrethrum (0.04%) and piperonyl butoxide (0.1%) solution. We took about 45 min to clean 1 individual. We retrapped and rescanned the birds for ectoparasites 4 to 5 wk later (9 July to 18 July). In total, we manipulated 20 birds and retrapped 8 of them.

### Statistical analyses

Parametric tests were used when requirements for normality were met. To examine the effect of feather development on parasite intensity, we used an analysis of variance (ANOVA) using mean ectoparasite infestation of each nest as the dependent variable and mean length of the longest primary as the independent variable.

Parasite intensity was adjusted for between-year differences (mean adjustment of 1995 and 1997 to 1996 data), and these data were used in a partial regression model to examine the relation of ectoparasite intensities between pair members and between unmated colony members, controlling for colony size. A principal component analysis (PCA) was carried out separately for males and females to reduce the morphological variables to a smaller subset of independent morphological factors. Because differences in some morphological parameters exist between colonies, the PCA was done only for the largest (Somotor I) and additionally for 1 medium-sized colony (Sikenicka). In a multiple regression analysis, scores of each individual for each factor were then used as independent variables and parasite intensity as the dependent variable. Because louse numbers change seasonally (see *Results*), we compared ectoparasite intensities before and after manipulation by adjusting the number of parasites observed before (June) and after (July) manipulation for the mean number of parasites observed before and after manipulation of unmanipulated individuals.

## RESULTS

### Parasite transmission to chicks (vertical transmission)

Chewing lice parasitized 13.7% of all chicks, which were less frequently infested with lice than adults. *M. meropis*, the most common chewing louse in adults (94.3% of all adults infested, Hoi et al., 1998), occurred on only 1.2% of chicks ( $n = 167$ ). *M. meropis*, which was very infrequent on adults (13.1%,  $n = 176$ , Hoi et al., 1998), occurred on 9.6% of chicks. No *B. apiastri* were found on chicks (69.9% on adults, Hoi et al., 1998). Consequently, we found no correlation between parasite abundance (*M. meropis* and *M. meropis* pooled) on parents and on nestlings ( $r_s = -0.14$ ,  $P > 0.4$ ,  $n = 29$  nests). Only in 1 (8.3%) of 12 nests with *M. meropis* on chicks was the mother also infested, although only with 1 specimen of this species. Furthermore, only 2 chicks in 1 nest had more *M. meropis* than their parents. Ectoparasite intensity of only those nestlings having at least 1 chewing louse (mean intensity:  $2.25 \pm 0.4$ ,  $n = 16$  nestlings) was significantly lower than that of adults (mean intensity:  $18.1 \pm 1.3$ ,  $n = 86$ ) (Mann–Whitney  $U$ -test:  $z = 4.5$ ,  $P < 0.001$ ). Using the length of the longest primary as a measure for feather development of chicks, we found no significant relation between feather development and parasite intensity (ANOVA:  $F = 0.4$ ,  $P > 0.9$ ,  $df = 15$ ). Figure 1 shows that chewing lice occurred on small as well as on well developed chicks.

### Parasite transmission to partner

Overall, only 3 (1.7%) of 176 adults were not infested with any of the 3 ectoparasite species encountered. We found a significant positive relation between overall parasite intensity (3 chewing lice species pooled) of pair members when controlling for colony size (partial regression model:  $r_{\text{part}} = 0.61$ ,  $P <$

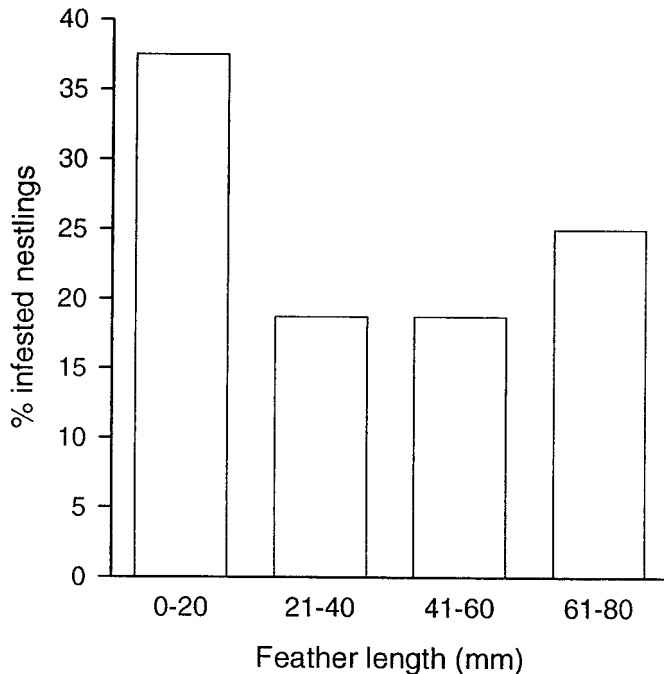


FIGURE 1. Percentage of nestlings with chewing lice in relation to length of longest primary feather ( $n = 39$  nestlings from 16 nests). Nestlings are categorized according to length of longest primary.

0.001,  $df = 1, 41$ ) (Fig. 2). In contrast, there was no relation in overall parasite intensity between unmated adults of the same colony (partial regression model:  $r_{\text{part}} = -0.05$ ,  $P > 0.6$ ,  $df = 1, 80$ ).

Examining only *M. meropis*, we found a nonsignificant tendency for parasite intensity to correlate between pair members (partial regression model:  $r_{\text{part}} = 0.23$ ,  $P > 0.2$ ,  $df = 1, 41$ ) and no relation between unmated colony members ( $r_{\text{part}} = -0.04$ ,  $P > 0.8$ ,  $df = 1, 80$ ). We could not test for horizontal transmission of *M. meropis* because this species occurred only in 3 bee-eater pairs and only in 1 pair were both partners infested. However, a significant relation was found for *B. apiastri* between pair members (partial regression model:  $r_{\text{part}} = 0.81$ ,  $P < 0.0001$ ,  $df = 1, 41$ ) (Fig. 2) and again no relation between unmated colony members ( $r_{\text{part}} = 0.14$ ,  $P > 0.3$ ,  $df = 1, 80$ ).

Except for weight ( $r_{\text{res}} = 0.42$ ,  $P = 0.02$ ,  $n = 32$ ) and bill length ( $r = 0.69$ ,  $P < 0.0001$ ,  $n = 32$ ), we found no relation in morphological parameters (including wing, tail, pintail:  $P > 0.3$  for all) between pair members. No correlation existed between the age of pair members either ( $r = 0.21$ ,  $P > 0.2$ ,  $n = 32$ ).

In all of the 8 retrapped pair members from which we experimentally removed ectoparasites, we found lice again after a period of 4 to 5 wk (*M. meropis* in 7 [87.5%] of 8 and *B. apiastri* in 6 [75%] of 8 individuals). Parasite intensity of *M. meropis* was significantly lower for retrapped birds (Wilcoxon test:  $z = -2.5$ ,  $P = 0.011$ ,  $n = 8$ ) but not for *B. apiastri* ( $z = -1.68$ ,  $P = 0.093$ ,  $n = 8$ ) (Fig. 3a). However, overall parasite intensity declined from June to July (Fig. 4). The average intensity of *M. meropis* in unmanipulated birds was significantly lower in July than in June (Student's *t*-test:  $t = -5.3$ ,  $P < 0.0001$ ,  $n = 20, 26$ ). This decline was not evident in *B. apiastri*

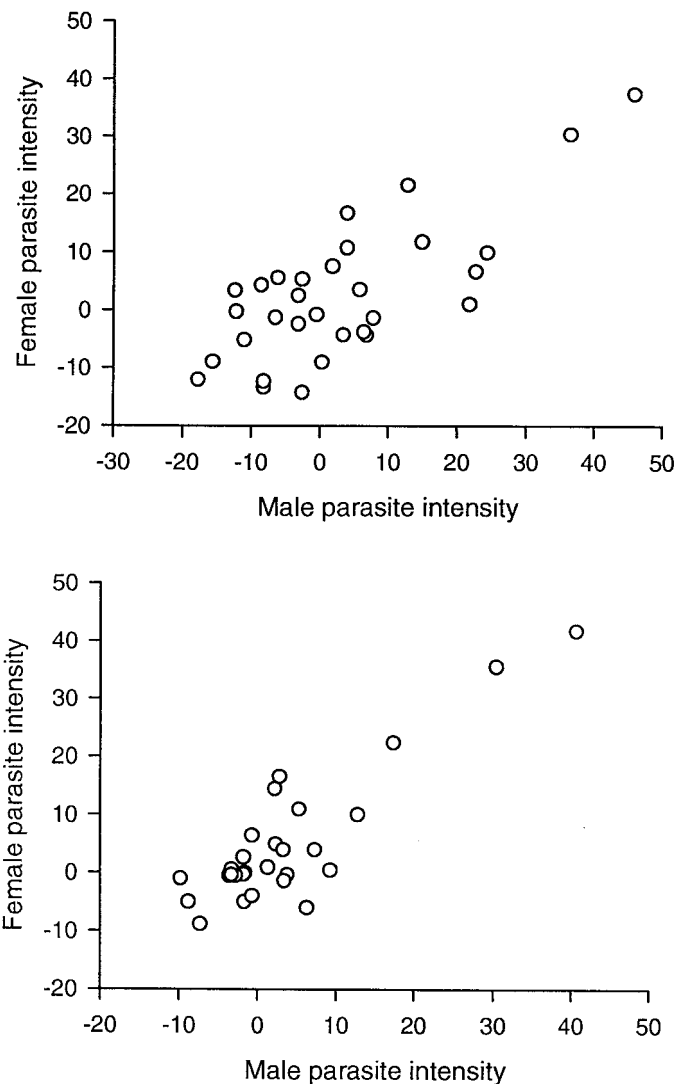


FIGURE 2. Relation between chewing lice intensity of pair members of bee-eaters (residual parasite intensity adjusted for colony size is given) for 3 chewing lice species (*Meropoeus meropis*, *Meromenopon meropis*, and *Bruelelia apiastri*) combined (upper graph) and *B. apiastri* only (lower graph).

( $t = 1.1$ ,  $P > 0.2$ ,  $n = 20, 26$ ). *M. meropis* occurred only on 3 of 20 adults of different pairs investigated in June, but could not be detected on any adult in July. The seasonal effect cannot be explained by vertical transmission to chicks because we found no *M. meropis* and no *B. apiastri* on the chicks of these nests ( $n = 20$ ). In 5 (25%) of these 20 nests, we found *M. meropis* on chicks in July, but we did not find *M. meropis* on adults in June and July. Examining relative intensity (adjusted for seasonal differences) revealed no significant effect of manipulation on ectoparasite abundance (Wilcoxon test: for *M. meropis*:  $z = 1.1$ ,  $P > 0.2$ ,  $n = 8$ ; for *B. apiastri*:  $z = 0.98$ ,  $P > 0.3$ ,  $n = 8$ ) (Fig. 3b). No correlation was found between ectoparasite intensity before and after manipulation (for *M. meropis*:  $r_s = 0.41$ ,  $P > 0.3$ ,  $n = 8$ ; for *B. apiastri*:  $r_s = -0.13$ ,  $P > 0.5$ ,  $n = 8$ ). *M. meropis* completely disappeared from June to July in unmanipulated individuals. Hence, the role of their removal in June cannot be evaluated.

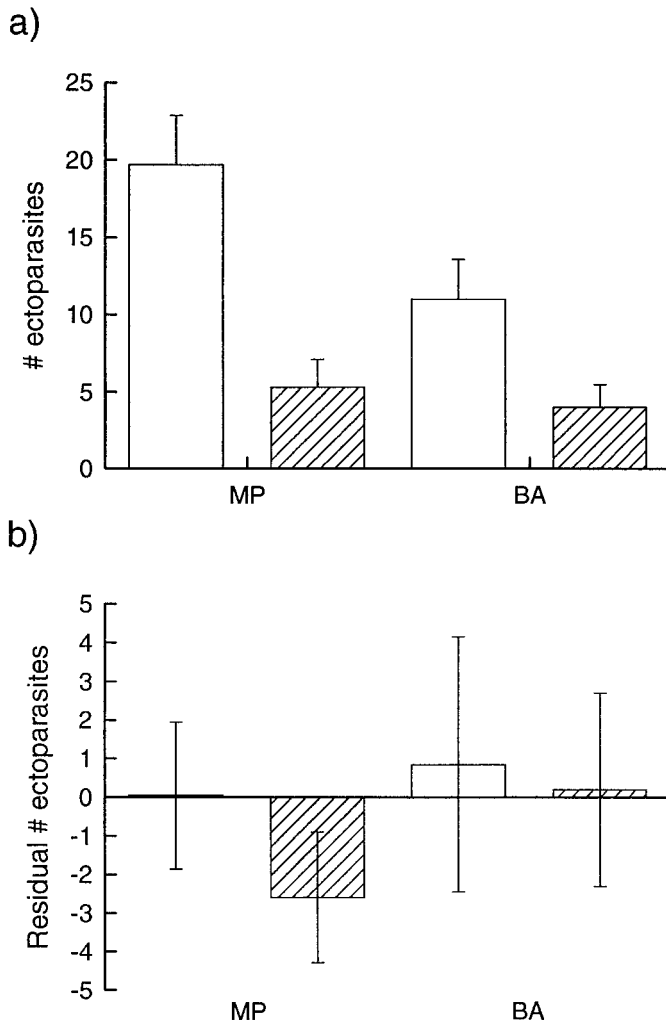


FIGURE 3. Absolute (a) and residual numbers (b) of *Meropoecus meropis* (MA) and *Brueelia apiastri* (BA) on 8 bee-eater individuals before parasite removal (filled bars) and 4 wk later (open bars). Residual number of parasites is the number of parasites on focal individuals in relation to average number of parasite on bee-eaters at the 2 time periods (for details see methods).

#### Parasite intensity and host age, morphology, and weight

We found no difference between the age classes (1 yr against older birds) and the parasite intensity of the chewing lice species separately and the overall ectoparasite intensity when controlling for colony size (analysis of covariance: for males,  $P > 0.4$ ; for females,  $P > 0.3$ ).

To examine the relation between morphology, bird weight, and parasite intensity, a PCA was performed to describe a smaller subset of independent morphological factors. Only the largest and 1 medium-sized colony were considered for this analysis.

In the largest colony (Somotor I), the PCA resulted in 2 factors for males and 3 for females (Table I). The high factor loadings for wing length, tail length, and weight for both sexes suggest that factor I is a size and condition factor. In males, factor II and in females, factor III have high loadings for bill length and length of the pintail. Because both traits seem vul-

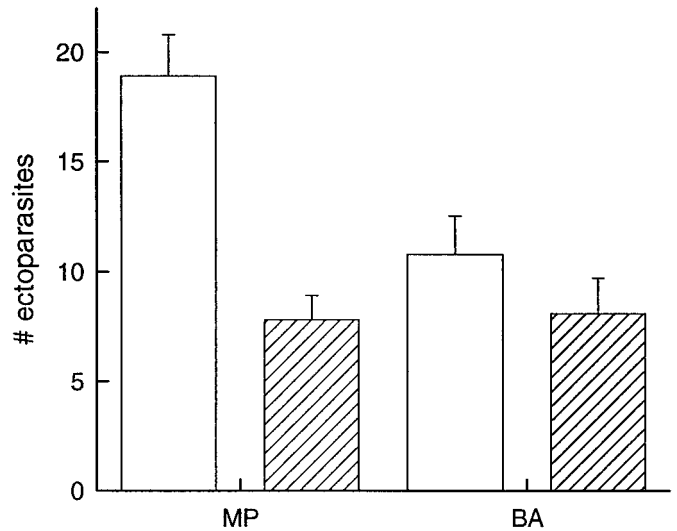


FIGURE 4. Average number of *Meropoecus meropis* (MA) and *Brueelia apiastri* (BA) per individual bee-eater during the mating (4–6 June,  $n = 19$ ) (open bars) and chick feeding period (9–18 July,  $n = 26$ ) (filled bars).

nerable to time-dependent deterioration, these factors may be interpreted as a factor of “wear plus tear”. Additionally, in females, factor II describes tarsus length only. The relation between individual parasite intensity and these morphological factors was tested. However, multiple correlation between parasite intensity of males and females as the dependent variable and individual factor scores on each factor as the independent variables revealed no relation between morphology and parasite intensity for males ( $R^2 = 0.02$ ,  $F = 0.16$ ,  $P > 0.8$ ,  $df = 2, 14$ ) or females ( $R^2 = 0.35$ ,  $F = 1.11$ ,  $P > 0.4$ ,  $df = 2, 9$ ).

For the medium-sized colony (Sikenicka), we identified 2 factors for males and females with similar factor loadings (Table I). Again, multiple correlation revealed no relation between these factors and parasite intensity of males ( $R^2 = 0.45$ ,  $F = 1.7$ ,  $P > 0.2$ ,  $df = 2, 6$ ) or females ( $R^2 = 0.13$ ,  $F = 0.38$ ,  $P > 0.7$ ,  $df = 2, 7$ ).

#### DISCUSSION

The fact that there is a relation in parasite intensity between pair members, quick recolonization by ectoparasites on individuals after cleaning them, and our earlier finding (Hoi et al., 1998) that ectoparasite intensity significantly varied between colony sites and increased with colony size all suggest that horizontal rather than vertical transmission is the main route of dispersal for chewing lice on European bee-eaters. This is different from the general pattern found in other studies (see Clayton, 1991; Clayton and Tompkins, 1995), where the main route reported for chewing lice transmission was vertical because of the close contact between parents and offspring in the nest. Louse abundance usually increases quickly on juveniles, often exceeding numbers found on adults (Clayton, 1991). This is not the case in bee-eaters. Nestlings acquire some chewing lice from their parents, but the number is surprisingly low and not related to their feather growth. The transmission pattern we found for chewing lice on European bee-eaters more closely resembles other ectoparasite taxa, e.g., hematophagous mites,

TABLE I. The extracted factors and accompanying factor loadings from a Varimax rotated *R*-type orthogonal principal component analysis using morphological parameters for males and females separately for (a) the largest (79 breeding pairs) and (b) a medium-sized colony (15 breeding pairs).

	Males		Females		
	FI	FII	FI	FII	FIII
(a)					
Wing	0.69		0.76		
Bill		-0.81			-0.76
Tarsus		-0.57		0.97	
Tail	0.78		0.83		
Pintail		-0.73			-0.90
Weight	0.70		0.81		
Variance explained	34.1%	23.9%	43.5%	25.1%	18.6%
(b)					
Wing	-0.92		0.77		
Bill		0.85	-0.91		
Tarsus	-0.75			-0.85	
Tail	0.87			0.93	
Pintail		0.69	0.89		
Weight	0.93			0.74	
Variance explained	53%	23.4%	44.1%	33.3%	

Zero factor loading was 0.5 throughout and values below are not listed in the table.

which are mainly horizontally transmitted or transmitted by moving between nests (Clayton and Tompkins, 1994). Møller (1991) found such a pattern with respect to mites in barn swallows (*Hirundo rustica*) but did not find a strong tendency with respect to chewing lice (only in 1 of 4 yr). However, male barn swallows were caught before arrival of their mates, and females before choosing their mates. Thus, assortative mating rather than horizontal transmission may account for the relation between mite numbers on mates. The role of assortative mating as a factor responsible for similar mite numbers on mates cannot be completely excluded for our bee-eaters. In fact, Lessells and Krebs (1989) found assortative mating according to age in their study population of the European bee-eater. We found no age-related assortative mating in our population, but even if this was the case, our results do not indicate any age-related variation in ectoparasite infestation. Furthermore, we found no relation between chewing lice and any morphological feature investigated for our birds, and no correspondence in morphological parameters between pair members, except in bill length and weight. These similarities between pair members are likely due to the fact that both partners participate in digging the nest hole and the effort may vary in relation to nest site characteristics. For example, local variation in the degree of soil hardness may produce a higher variance between, than within, pairs in digging effort reflected in body weight and the use of the bill reflected in bill length.

The fact that lice appeared again on bee-eaters 4 to 5 wk after they had been removed does not only suggest horizontal transmission. Because all individuals were infested again with parasite numbers equivalent to those on unmanipulated individuals, our field experiment indicated that transmission was rather high for this period (incubation and chick feeding) where less contacts between pair partners can be expected. According to our results, we assume that most of these "new" parasites originated from the other partner rather than from other adults in

the colony, although the relation between colony size and average ectoparasite infestation (Hoi et al., 1998) indicates some transmission by the latter method. Transmission from nestlings is very infrequent.

Although intensive parental care is combined with a very long nestling period in bee-eaters, vertical transmission from parents to nestlings does not seem to play a role in this species. Nestlings may not be adequate "vehicles" for the louse species investigated in the present study because they mainly forage on feathers (Marshall, 1981). However, Eichler (1963) pointed out that chewing lice do infest small nestlings. Furthermore, no increase in chewing lice numbers with chick age was evident, even though in some of the nestlings feathers were fully developed. Transmission may increase once juveniles are outside the nest burrow and colonize the communal roost sites. We found a decrease in louse numbers on adults from June to July, which may be related to parasite phenology, or a change in the grooming behavior of the birds, but one could also argue that this is due to the fact that some of the lice move from the parents to their offspring. This is likely not the case because we found no increase in ectoparasite numbers on nestlings with respect to season. Overall parasite intensity on nestlings (for those that had lice at all) was more than 9 times less than on adults. Including all nestlings, overall ectoparasite intensity of nestlings was 1.1% (mean  $0.2 \pm 0.18$ ,  $n = 167$ ) of adult intensity. Thus, summing lice for parents and offspring did not influence the results.

From the parasite's perspective, dispersal to nestlings might be less advantageous than dispersal to fully fledged juveniles, because mortality in nestlings is generally higher than in adults (Ricklefs, 1969). Habitat choice experiments suggest that *B. apiastri* and *M. meropis* are quite selective in their choice of a suitable environment and possibly discriminate between nestlings and older birds.

Our data do not suggest variation in individual susceptibility

to parasites. Because older birds are usually fitter because of their ability to survive (Weatherhead, 1984), one would expect a decrease in parasite intensity with host age (see Baum, 1968; Everleigh and Threlfall, 1976); however, we found no such relation (see also Foster, 1969). Bergstrand and Klimstra (1964) and Spellerberg (1971) found an increase in chewing lice infestation with age and explain this result as a cumulative increase in parasite numbers with time. Variation in body size with age (Marshall, 1981) may also contribute to an increase in parasite intensity. Grooming efficiency may increase with age and, in contrast, acts against ectoparasite intensity (Clayton, 1991). Therefore, the effect of host age on chewing lice infestation is inconclusive and host age is not necessarily a predictor for host fitness. Experiments would be the only way to disentangle these different factors.

We also found no relation between the body size/weight factor, the bill/pintail factor (a kind of wear plus tear factor), and parasite intensity of males and females. Such a relation would either suggest variation in the ability to resist parasites, or an effect of parasites on bird condition. Hamilton and Zuk (1982) proposed that external characters should be reliable predictors of parasite intensities, especially when they are involved in sexual selection (mate choice). For instance, Møller (1992) showed that the size of tail ornaments in male barn swallows is negatively related to parasite intensities and female choice is actually related to the length of the outermost tail feathers (Møller, 1988). Similarly, Darolova et al. (1997) showed that male mask width in penduline tits reflects nest ectoparasite load and female choice is related to mask width (Grubbauer, 1995; Schleicher et al., 1996). However, we know of no obvious sexual dimorphic trait in bee-eaters that could be important as a reliable predictor of parasite load or resistance. To conclude, quality differences of the host do not seem to be important determinants for ectoparasite intensity in the European bee-eater.

#### ACKNOWLEDGMENTS

We thank D. Clayton, T. Pizzari, S. Kleindorfer, B. Walther, and two anonymous referees for fruitful comments on earlier drafts of this paper. We thank M. Romero Pujante for assistance in the field. The study was supported by the grant 95/5305/360 of the Slovakian Ministry of Education.

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