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The biology of the Alpine Accentor *Prunella collaris.* V. The sex ratio and transmission of lice *Philopterus emiliae*

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Abstract. Of the 105 inspected accentors, 52 birds yielded lice. Species *Philopterus emiliae* highly prevailed to *Ricinus subpallidus*. Only four birds were infested by both species. There was an apparent decrease in the number of lice *Ph. emiliae* in August and late autumn (October - November) but 85 per cent of the accentors caught in September yielded *Philopterus* lice. In total, we collected 221 specimen of lice, 89 % (196) of all individuals were *Ph. emiliae* and only 11 % were *R. subpallidus*. The ratio males: females of *Ph. emiliae* was biased towards females from summer to winter. The average number of louse individuals was the lowest in summer, 1.8 on individual alpine accentors.

Among adult birds, the female accentors were more often infested by females than males of *Ph. emiliae*. The female-biased sex ratios of lice and female louse loads of the females of accentors clearly signalize that there is the vertical transmission in lice in summer and autumn. The same sex ratio of lice, approximately 2:1 towards the lice females, was also found in wintering males of accentors. We hypothesize that these findings may result from the increased frequency of horizontal transmission via increased body-to body contacts among nighting accentors in winter.

Key words: Prunella collaris, Philopterus emiliae, Ricinus subpallidus, Mallophaga, vertical and horizontal transmission, biased sex ratio

Introduction

Louse populations tend to be highly structured, with each host individual being effectively an „island“ colonised by small numbers of lice. Two forms of transmission may reduce the level of isolation among subpopulations of lice. Vertical transmission is the dispersal of lice from parents to offspring. Horizontal transmission is the dispersal of lice between less related host individuals (Clayton and Tompkins 1994, Rózsa *et al*. 1996). The Alpine Accentors and their lice show great promise as a model system for studying louse – bird interactions in high mountain conditions. Transmission of *Philopterus emiliae* lice between individual hosts is known to be vertical (between parent bird and its offspring - Janiga and Kubašková 2000). The birds nest in rocky caves or holes in polygynandrous families and our previous data indicate that the care for nestlings is probably the most important activity of accentors which facilitates the lice transmission. Females of accentors are important for the transmission of summer generations of lice because female birds perform the main portion of parental care. They perform the entire incubation of their eggs alone, and they also feed and warm the chicks shortly after hatching (Heer 1994). Males start to bring food usually from the third day of the nestling-rearing period, but the females perform the majority of the feeding, the male feedings are short and less frequent than the contributions of females.

In earlier study (Janiga and Kubašková 2000) we also hypothesized that rare direct contacts among host birds in winter may be considered as a factor increasing the horizontal transmission of lice. The importance of horizontal transmission of lice in winter was mainly described by Brooke and Nakamura (1998) and Lindholm *et al*. (1998) in cuckoos. The authors suggest that the most likely transmission route for cuckoo lice is from adult to juvenile birds during feeding aggregations on the wintering grounds. In this study, we completed our previous data on species composition, seasonal occurrence, prevalence and sex ratio in lice and we checked the validity of our earlier results. Our aim here was also to assess the relationship between the wintering of accentor males and potential horizontal transmission of lice.

Material and Methods

We conducted the study in the High Tatra, Low Tatra and Great Fatra mountains (the West Carpathians, Slovakia, Table 1). For the purpose of our research 105 individuals of Alpine Accentors (*Prunella collaris*) were mist-netted or caught with food traps from 1988 to 2001. The birds were individually colour-ringed and measured. Adult birds were sexed by the shape of the cloacal protuberance (Nakamura 1990) or by the use of multivariate dicriminant analysis of biometric data (Heer 1994). One-year old birds were aged by the colouring of the middle and greater wing-coverts. Some of the birds were ringed as nestlings. Lice were removed by exposing live birds to chloroform fumes in a glass fumigation chamber, while keeping the head of the bird outside the chamber. For details on sampling technique and methods of collection,

Locality Ph.e.	Nymp. *Ph.e.*	Males *Ph.e.*	Femal. *Ph.e.*	Total
Malino Brdo (GF)	8	14	24	46
Mala Studena valley (HT)	1	-	2	3
Velicka valley (HT)	10	13	14	37
Ďumbier - Štiavnica (LT)	2	2	3	7
Poľana (LT)	-	-	1	1
Chopok – Konské (LT)	-	-	1	1
Skalnata valley (HT)	2	15	17	34
Polish crest (HT)	1	-	1	2
Rysy (HT)	13	8	22	43
Belianske Tatry (HT)	2	3	5	10
Batizovské lake (HT)	-	-	1	1

Table 1. Locations of collections of *Philopterus emiliae.* At the locality Malino Brdo, the lice were collected from the wintering males of Alpine Accentors. GF – Great Fatra National Park, HT – High Tatra National Park, LT – Low Tatra National Park. Shown are the censuses of sexes and nymphs, unidentified individuals are excluded from the table.

slide preparation and species and sex determination of lice see previous study by Janiga and Kubašková (2000). Using anesthesia jar offers the possibility of sampling several birds simultaneously what is very efficient in unfavourable windy alpine conditions (cf. Walther and Clayton 1997).

For the purpose of this study we use data on 221 specimen of lice, 196 individuals of *Philopterus emiliae* and 25 *Ricinus subpallidus.*

Results

Of the 105 inspected accentors, 52 birds yielded lice (Fig. 1.), Species *Ph. emiliae* highly prevailed to *R. subpallidus.* (Fig. 2). Only four birds were infested by both species. The data on birds which hosted more than four individuals of lice are presented in Table 2. The percentage of infested accentors varied throughout the year (Table 3). There was an apparent decrease in the number of lice *Ph. emiliae*

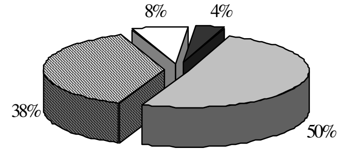

Fig. 1. The prevalence of *Philopterus emiliae* and *Ricinus subpallidus* on 105 individuals of alpine accentors (50 % - individuals infested by lice, 38 % - individuals infested by *Philopterus emiliae*, 8 % - individuals infested by *Ricinus subpallidus*, 4 % - individuals infested by both species).

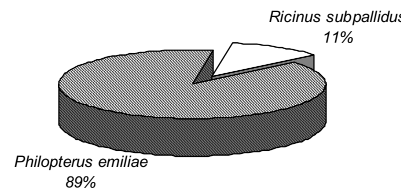

Fig. 2. Species composition of lice (n=221) on Alpine Accentors.

in August and late autumn (October - November) but 85 per cent of the accentors caught in September yielded *Philopterus* lice. In total, we collected 221 specimen of lice, 89 % (196) of all individuals were *Ph. emiliae* and only 11 % were *R. subpallidus*.

Sex ratio of Philopterus. The ratio males: females was biased towards females from summer to winter (Table 4 and Fig. 3). The female-biased sex ratios indicate that there is a differential dispersal between the sexes, with a sex ratio bias in favour of the more

Species	Dec.- Febr.	March- May	June- July	Aug.	Sept.	Oct. - Nov.
Ph.e.	50%(6)	45%(42)	48%(23)	0%(8)	85%(13)	0%(13)
R.s.	0%(6)	14%(42)	9%(23)	13%(8)	8%(13)	8%(15)

Table 3. Percentage of infested accentors in different months of a year (total numbers of examined birds are in brackets).

Prunella collaris Number	Sex	Month	Year	Locality	*Ph. emiliae* Number*	*Ric.subp.* Number
6.	male	March	1988	M. Brdo (GF)	15 (4:10:0:1)	-
8.	male	April	1988	M. Brdo (GF)	6 (2:3:1:0)	-
22.	x	October	1988	Chopok (LT)	-	6
45.	male	April	1990	Skalnata valley (HT)	8 (2:6:0:0)	-
65.	female	April	1990	Skalnata valley (HT)	5 (2:3:0:0)	-
66.	male	April	1990	Skalnata valley (HT)	-	5
86.	female	April	1990	Skalnata valley (HT)	6 (1:4:1:0)	5
89.	male	May	1990	Velicka valley (HT)	38 (13:11:10:4)	-
98.	male	June	1990	Ďumbier (LT)	5 (1:1:2:1)	-
224.	male	September	1997	Rysy (HT)	19 (6:6:5:2)	-
227.	x	September	1997	Rysy (HT)	7 (1:6:0:0)	-
228.	female	September	1997	Rysy (HT)	10 (0:3:6:1)	-
236.	juvenil	June	1998	Belianske Tatry (HT)	7 (2:3:1:1)	-
247.	male	February	1999	M. Brdo (GF)	11 (2:4:5:0)	-
260.	male	September	2000	Rysy (HT)	5 (0:5:0:0)	-

Table 2. Louse species richness on some individuals of alpine accentors. * - ratio of males:females:nymphs:undetermined. x = undetermined sex of alpine accentor. GF – Great Fatra National Park, HT – High Tatra National Park, LT – Low Tatra National Park.

Season	*Pr. collaris*	*Philopterus emiliae* total	nymph	male	female	X
Winter	7	37 (100%)	7 (18.9%)	11 (29.7%)	19 (51.4%)	5.3
Spring	15	78 (100%)	13 (16.7%)	31 (39.7%)	34 (43.6%)	5.2
Summer	11	20 (100%)	4 (20.0%)	5 (25.0%)	11 (55.0%)	1.8
Autumn	11	50 (100%)	15 (30.0%)	8 (16.0%)	27 (54.0%)	4.5

Table 4. Frequency of occurrence of males, females and nymphs of *Philopterus emiliae* in different seasons. X = average number of *Philopterus* lice per one host.

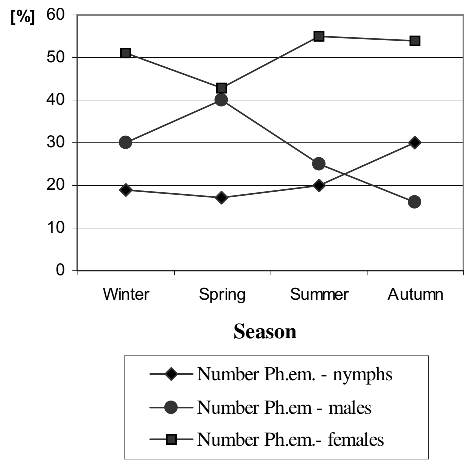

Fig. 3. The relative numbers of males, females and nymphs of *Philopterus emiliae* collected in different seasons.

Philopterus emiliae	Number of lice found on *P. collaris* juveniles	males	females	Total
Nymphs	3(25.0%)	27(21.8%)	4 (12.9%)	34(20.4%)
Males	4(33.3%)	42(33.8%)	7 (22.6%)	53(31.7%)
Females	5(41.7%)	55(44.4%)	20(64.5%)	80(47.9%)
Total *Ph.e.*	12 (100%)	124 (100%)	31 (100%)	167 (100%)

Table 5. Frequency distribution of nymphs and sexes of lice *Philopterus emiliae* on 44 individuals of Alpine Accentors. Indetermined lice are not included.

dispersive sex. Towards the males, the sex ratio of lice tended to be biased in the spring. The relative numbers of nymphs increased in the autumn. The average number of louse individuals was the lowest in summer, 1.8 on individual alpine accentors. The density of lice on individual bird rapidly increased in other seasons (Table 4).

Among adult birds, the female accentors were more often infested by females than males of *Ph. emiliae* (Table 5). The female-biased sex ratios in lice and female louse loads of the females of accentors clearly signalize that there is the vertical transmission in lice in summer and autumn. The same sex ratio of lice, approximately 2:1 towards the lice females, was also found in wintering males of accentors (Table 1), what indicates potential horizontal transmission of lice in winter.

Discussion

Our results support the view that probably site segregation stabilizes the coexistence of the two louse species. Under a model of site segregation it is typical that there are a frequent and a rare parasite species (Reiczigel and Rózsa 1998, Lindell *et al.* 2002). Ischnoceran lice are approximately three times more abundant on bird bodies than amblyceran species (Eichler 1963). There is probably no direct interaction like resource limitation between *Ph. emiliae* and *R. subpallidus*. These species apparently have their own site preferences because they have different ecology and morphology (Eichler 1963).

We surveyed populations of lice on adult accentors and their offspring over the course of the host´s breeding season, molting, autumn and spring aggregations, and male wintering. The number of lice varied considerably among individual birds. Parasites generally show an aggregated frequency distribution among hosts, with most individuals having few parasites and a few individuals having many parasites (Table 2) (Tompkins *et al.* 1996, Whiteman and Parker 2004, Szczykutowicz *et al.* 2005).

Our data confirm that in the species of avian lice (Phthiraptera: Ischnocera) the female bias tended to be more pronounced in small subpopulations. The sex ratio of the whole population of adult *Philopterus* lice was 1:1.3 (males:females) in the adult males, and 1:2.3 in adult females of accentors (Janiga and Kubašková 2000). Females of lice are probably capable of adaptive selection of females of accentors for the purposes of colonization and dispersal (cf. Potti and Merino 1995, Rózsa 1997). The intensity of lice that we observed on birds remained fairly constant from autumn to next spring, averaging five lice per bird. In the breeding season of accentors - summer, the intensity was low, averaging approximately two lice per bird. To our knowledge, this is the first study to quantify lice in alpine habitats during all seasons. Considering that only in the spring the ratio of male to female lice did not differ from unity and in the other seasons the lice females prevailed to males, we suppose two important peaks of transmission of lice during a year. In the breeding period of hosts, young birds were infested with lice as early as a few days of age (Janiga and Kubašková 2000), by which time the tips of their developing feathers had emerged. The lice on nestlings must have come from the parent birds, especially from females. Alpine Accentors live in polygynandrous groups in which a dominant male, and a few unrelated and usually younger males, share a group territory within which a few unrelated females have overlapping ranges. The species is not a typical social one, members of group do not move around together within their group territory (Davies *et al.* 1995, Nakamura 1995, Heer 1996). During copulation period, body-to-body contacts between male and female are very brief (0.15 sec. - Cramp

1988, Nakamura 1990) and main postures and movements related to copulatory behaviour do not enable, in our opinion, any transmission of lice. Therefore, females of accentors are extremely important for the transmission of summer generations of lice because female birds perform the main portion of parental care such as territory defence against other females, choice of nest-site, nest-building, incubation, brooding and feeding of nestlings. We hypothesize that transmission of lice between bird mates may occur during the nest construction and egg-laying periods when male birds often inspect the nest-site before and during the egg-laying. Although the males never assist in nest construction nor incubate the eggs or chicks, sometimes they sing after entering the nest site (Heer 1994). The female performs the entire incubation of her eggs alone, and it also feeds and warms the chicks shortly after hatching (Heer 1994). Males start to bring food usually from the third day of the nestling-rearing period, but the females perform the majority of the feeding, the male feedings are short and less frequent than the contributions of females. The transmission of lice from parents to offspring is probably mainly by nymphs. Relatively more nymphs than adult lice were found on young nestlings (Table 5). After the summer peak of infestation, the number of lice decreased to zero in August. The generation time of most lice is about a month (Obenberger 1957, Marshall 1981). Therefore one would expect nymphs transmitted to nestlings to mature and begin laying eggs one month later.The incubation period of the louse eggs may last 4 - 5 days (Stockdale and Raun 1965). September was precisely the period when the second peak of louse occurrence was detected. The number of nymphs increased (Fig. 3), the female bias was recorded, and the louse generation was significantly smaller in the body size than winter and spring individuals (Mičková 2004). September is the time of molting of accentors. Samples of lice from September are evidence that there si the second peak of transmission from old to new plumage. Our data are consistent with scenario published by Lee and Clayton (1995) in swifts. The authors showed that the ratio of nymphal to adult *Dennyus* lice on nestling swifts *(Apus apus)* was far higher than that on adults. Lice from younger donors were themselves younger than lice from older donors. In experimental study, Tomkins and Clayton (1999) showed that lice from adult donors showed double the mortality of control lice from nestling donors. In October when accentors form larger pre-migrating feeding aggregations, the abundance of lice decreased to minimum. Our collections from winter and spring seasons seem to indicate that species *Ph. emiliae* is probably capable of adaptive sex ratio manipulation. In the late winter, the abundance of lice in a subpopulation reached its maximum (Janiga and Kubašková 2000) what is also known in other species of lice (Balát 1959, Eichler 1963, Nelson 1972). Population size of lice positively correlated to overall body size of lice (Mičková 2004, and cf. Tryjanowski *et al.* 2005). It also appears that the louse species is highly adapted to the „alpine“ style of living of accentors. Presuming a female bias in the lice departing from late winter subpopulations, the capability of lice to manipulate sex ratio could explain the equal number of males and females in the spring. The female bias then again occurred in the small summer subpopulations. In the species of avian lice, the female bias was found to be more pronounced in small subpopulations (Rózsa *et al.* 1996, Szczykutowicz *et al.* 2005). Moreover, female bias tends to occur in the breeding period of birds. Zlotorzycka (1972) and Rem and Zlotorzycka (1981) found that females of lice *Columbicola columbae* prevailed in summer what is the main breeding period of hosts - feral pigeons in Poland (Johnston and Janiga 1995). Accentors also breed in summer. In the common passerine species which do not live in the alpine habitats, a marked peak of seasonal infestation occurs just prior to the birds´ breeding season and there is marked reduction in the infestation of adult birds after the breeding season. A peak for blackbirds usually occurs in February, for chaffinch in April. Robins usually reach a peak of infestation earlier than the chaffinches, in March, with a more gradual reduction in late summer to zero in September and October.Unfortunately, many species of birds show an increase of infestation in winter months (Ash 1960).

Horizontal transmission. Investigations into the parasite–host sociality nexus have focused on colonially breeding host species or those that form nonbreeding aggregations. However, little attention has been given to cooperative breeders, despite abundant data on other aspects of their biology (Heer 1994,1996, Nakamura 1995). Well documented intraspecific variation in sociality, a characteristic of some cooperative breeders, is a key advantage when relating host density to parasite abundance (Rózsa *et al.*, 1996, Whiteman and Parker 2004). From spring to autumn, the horizontal louse transmission in accentors is likely to be very low because birds maintain individual distances, also during nighting and sleeping. There are only few observations especially from very cold winter nights when two - three wintering birds slept together touching their bodies (Janiga, not published). This situation could predict horizontal transmission in winter. Polyandrous Galapagos hawks within small groups harbored similarly aggregated (where most hosts harbored few parasites and few hosts harbored many parasites) distributions of two (ischnoceran and amblyceran) louse species. As host group size increased, however, the more mobile amblyceran (*Colpocephalum turbinatum*) was less aggregated among hosts than the less mobile ischnoceran (*Degeeriella regalis* - Whiteman and Parker 2004). Rózsa *et al.* (1996) found similar patterns between colonial and territorial crow (*Corvus* spp.) host species. The amblycerans (*Myrsidea* spp.) were less aggregated within the population of the colonial host species relative to those found within that of the territorial. Such situation occurs in the accentors in winter - the Ischnoceran *Ph. emiliae was found* at 50 % of birds while Amblyceran *R. subpallidus* was not detected (Table 3). The highest examples of concentrations of *Ricinus* lice were found in April when the accentor females returned from the breeding sites (Table 2). The results suggest that the taxonomic richness of different parasite taxa is influenced by different host defenses, and they are consistent with the hypothesis that increasing host allocation to immune defense influences Amblyceran prevalence and dispersal (Moller and Rózsa 2005). Amblycerans tend to walk directly on the host skin, often feed on the excretions and fragments of the skin, and also chew the emerging tips of developing feathers to obtain blood. They move fastly, so their horizontal transmission in winter conditions cannot be excluded. On the basis of careful field work, Brooke and Nakamura (1998) concluded that the Common Cuckoo (*Cuculus canorus*) must acquire its host-specific lice sometime between leaving the nest in summer and returning from migration the following spring. None of the 21 cuckoo nestlings they examined had cuckoo lice. Nor were any cuckoo lice found in 19 nests containing cuckoo eggs that had yet to hatch. However, cuckoos making their first return to the breeding grounds from the wintering grounds had as many lice as did older birds. The authors therefore suggest that the most likely transmission route for cuckoo lice is from adult to juvenile birds during feeding aggregations on the wintering grounds.

Our results show that current ecological conditions may play an important role in maintaining the host-specifity of lice in the alpine habitats. The lice adopt to shortened breeding cycle of birds in the mountains and are able to behaviorally alter their microhabitat selection. Further exploration of host-parasite size relation patterns within lice will need to take into account more species living in the alpine resorts, including an assessment of the number of host and coexisting species.

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