Oecologia Montana 2000
9, 24 - 28

The biology of the Alpine Accentor *Prunella collaris.* III. The coevolution of Alpine Accentors and lice (Phthiraptera).

M. JANIGA and Ľ. KUBAŠKOVÁ
Department of Biology, Catholic University, SK-03401 Ružomberok, Hrabovská 1, Slovak Republic

Abstract. The species *Philopterus emiliae* is more abundant in the bodies of accentors than *Ricinus subpallidus*. Of the 100 inspected accentors, 36 were insected by *Ph.emiliae*, and 10 by *R. subpallidus*. There is probably no evidence of competition between the two lice. Two birds only harboured both species of lice.

Seasonal change is probably important determinant of population size and sex ratio of lice *Ph. emiliae.* Females of lice are probably capable of adaptive selection of females of accentors for the purposes of vertical transmission and lice dispersal. Species *Ph. emiliae* is also capable of adaptive sex ratio manipulation. Presuming a female bias in the lice departing from large late winter subpopulations to colonize on new hosts (from late May to early August) could explain the female bias of the summer subpopulations. Male bias of louse subpopulation occurred in autumn and early winter.

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

Introduction

Alpine Accentors may be an ideal model for investigating the relationship between specific parasite species and bird host in infavourable and temporary cold conditions. The West Carpathians show typical climate of high mountain regions: large changes in temperature within one day, spells of cold weather can bring temperatures below zero in mid-summer, and late snowfall occurs in June, July and August.

This study is probably the first to compare the ecological measures of lice of sexes of polygynandrous bird species. Host sociality is known to affect louse-bird interactions (Rékási *et al.* 1997), it correlates positively with prevalence but not with abundance of lice (Rózsa *et al.* 1996).

The aim of the study was to investigate the species composition, prevalence, sex ratio and density of lice between seasons, sexes and age classes within the populations of Alpine Accentors. We describe the sampling technique employed and also present the results of a survey of lice in adult wintering birds.

Material and Methods

The Alpine Accentors and their lice were studied from 1988 to 1999 in the three geomorphologic

Fig. 1. Ectoparasite removal apparatus.

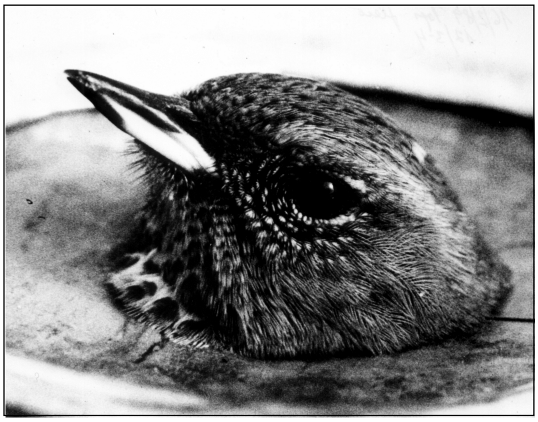

Fig. 2. Each bird was placed in a glass jar with the head out, only plumage of head had to be visually searched for lice. The apparatus is most useful for removing small "non-visible" ectoparasites from wild and living birds such as lice and mites. It reduces the time required for visual inspection.

Fig. 3. *Philopterus emiliae* (Ischnocera), 20 x 2 magnification.

Fig. 4. *Ricinus subpallidus* (Amblycera), 20 x 2 magnification.

Fig. 5. Terminal segments in adult male *Philopterus emiliae* (Ischnocera). 20 x 4 magnification.

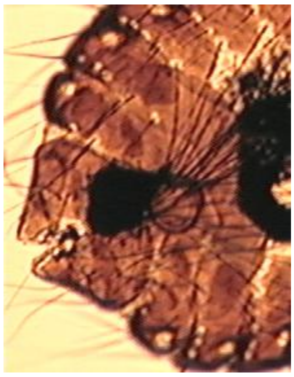

Fig. 6. Terminal segments in adult female *Philopterus emiliae* (Ischnocera). 20 x 4 magification.

areas: high altitude chains of the High and Low Tatra mountains, and the wintering site Malino Brdo, Great Fatra mountains. The summer study regions lie above the timber and dwarf pine line usually between 1,800 and 2,650 m above sea level. The habitats were dominated by alpine meadows and by rocky parts.

For the purpose of this study, 100 Alpine Accentors were mist-netted or caught with food traps. The birds were individually colour-ringed and biometrical data was taken. Adult birds were sexed by the shape of the cloacal protuberance (Nakamura 1990) or by the use of multivariate dicriminant analysis of biometrical 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.

For the removing of ectoparasites from birds, we used simple and quick method which is a modification of an apparatus designed by Fowler and Cohen (1983) and Bear (1995). Each caught bird was placed in a glass jar so that its body was inside the plastic sack in the jar (Figs. 1 and 2). Retaining linoleum clip held the bird head outside. Chloroform vapors in the apparatus killed the parasites, which fell to the sack in the jar. These method enabled processing more birds at a time. Birds were kept in the collector approximately 15 minutes, the interval depended on the season and bird behaviour. In the warm days, the chloroform vapors probably earlier killed parasites than in winter. The head plumage was visually searched for lice. In the laboratory, the parasites were preserved in 70 % alcohol. Species, sexes and nymphs of lice were identified (Balát 1959, Zlotorzycka 1972b, 1977), and the number of each group was recorded. The sexes and nymphs were determined using a microscope Olympus B 201 connected to a Pentium PC computer running image analysis software Image Pro Plus (Media Cybernetics). Determination of lice was verified by Dr. J. Rékasi. Our nomenclature of lice follows his advices.

Results

Parasite species and intensity of infection. Two most important lice species in Alpine Accentors are *Philopterus emiliae* (Balát 1959) *and Ricinus subpallidus* (Blagoveščenskij 1953) - Figs. 4 -7. Two accentors were infested by both species. Of the 100 inspected accentors, eight birds were only infested by more than three individuals of *Ph. emiliae,* and three birds by more than three individuals of *R. subpallidus* (Table 1). The highest density of lice per individual bird occurred in the late winter and early spring (Table 1). 8% of examined birds harboured 56 % of collected individuals of *Ph. emiliae,* and 65 % of all *R. subpallidus* specimen were found on the bodies of three (3 %) inspected birds (Table 1). In total, we collected 126 specimen of lice, 82 % (103) of all individuals were *Ph. emiliae* and only 18 % were *R. subpallidus.*

The load of the *Philopterus* lice varied throughout the year (Table 2). There was an apparent decrease in the number of lice in August and late Autumn

P. collaris	*Ph.emiliae*			
sex	number**	month	year	locality
male	14(4:8:x)	March	1988	G. Fatra
male	12(1:5:6)	February	1999	G. Fatra
male	7 (3:3:1)	March	1988	G. Fatra
juvenile	7 (2:2:1,)	June	1998	Bel. Tatras
male	5	April	1988	G. Fatra
female	5(2:3:0)	April	1990	H. Tatras
female	4(2:2:0)	April	1990	H. Tatras
juvenile	4	March	1998	G. Fatra
	Ric.s.			
x	6	October	1988	L. Tatras
male	5	April	1990	H. Tatras
female *	4	April	1990	H. Tatras

x - sex undetermined,
* - founded also 3 individuals of *Philopterus emiliae*
**- male/female/nymph ratio, if known

Table 1. Number of lice found on the most infested birds

(October - November). From ten birds loaded by *R. subpallidus,* 6 infested birds were caught in April, one in June, one in August and two in October.

Prevalence is defined as the percentage of infected individuals in the sample during the time period of the survey. Infestation by *Ph. emiliae* was found in 44 % of all examined birds, and *R. subpallidus* infestation was found in 10 %. The most prevalent parasite was *Ph. emiliae,* and we therefore chose to analyze only the prevalence of this species between the sexes of accentors. There were no differences in prevalence of lice between the sexes of accentors (Table 3). The prevalence of lice tended to be higher among old than young birds.

Sex ratio of Philopterus. The ratio males: females: nymphs was biased towards females from early spring to summer (December: 2:1:0; February: 1:5:6; March: 8:14:1; April: 12:18:1; June: 3:5:1, July 0:2:0; September: 5:2:2). Of the 103 examined individuals of lice, 53 % of all were females and 36 % males. The female-biased sex ratios in spring and summer indicate that there is a differential dispersal between the sexes, with a sex ratio bias in favour of the more dispersive sex. In August, October and November no *Philopterus* lice were found on 20 birds (Table 2). Towards the males, the sex ratio of lice tended to be biased in autumn and early winter. Among adult birds, lice abundance was higher in males than in females of accentors but the female birds were more often infested by females than males of *Ph. emiliae* (Table 4).

Discussion

Abundance, density and sexual structure of lice

Our data confirm that in the species of avian lice (Phthiraptera: Ischnocera, and maybe also Amblycera) the female bias tended to be more pronounced in small subpopulations. In the three quarters of infested accentors, we collected less than four individuals of lice per bird. 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. The data is giving support to the hypothesis that colonizing individuals in this species of lice tend to be females (cf. Rózsa 1997). 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). It is highly probable thatcolonizing individuals in this species of lice are foremost females. They can colonize on new hosts probably only in nesting period. In all seasons, accentors maintain an individual distance between individuals. In winter period, antagonism between wintering males usually arises from individual-distance encroachments

Decemb.-February	March-April*	June-July	August	Septemb.	October-Novemb.
75% (4)	44%(41)	43%(23)	0%(8)	45%(11)	0% (12)

*****individuals collected on May, 2nd are included in the sample

Table 2. Seasonal prevalence = percentage of infected accentors (total number of birds is in brackets).

male	female	nestlings and fledglings	independent immatures
41%(41)	40%(27)	30%(13)	38%(8)

adults	juveniles
41%(68)	33%(21)

Table 3. Prevalence of *Philopterus emiliae* in the sexes and immatures of Alpine Accentors.

Phil.emiliae	Sum.	on juveniles 1	on juveniles 2	on males	on females
nymphs	10,9% (10)	10% (1)	0% (0)	80% (8)	10% (1)
males	35,9% (33)	9,1% (3)	9,1% (3)	63,6% (21)	18,2% (6)
females	53,3% (49)	6,1% (3)	8,2% (4)	57,1% (28)	28,6% (14)
Sum. *Ph.e.*	100% (92)*	7,6% (7)	7,6% (7)	62% (57)	22,8% (21)

*Adult lice of indetermined sex are not included
1- nestlings and fledglings
2-juveniles independent on parents

Table 4. Relative numbers of lice *Ph. emiliae* found on juveniles and adult males and females of accentors. Absolute numbers are in brackets.

(Janiga, not published). Samples of lice from September are evidence that the parasites are able to survive the unfavourable bird molting period in late August and September (in September, we found one lice on the body of moulting adult bird). From August to next May, the louse transmission 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 a male bias of louse population in autumn and winter. In human head louse, Rózsa (1997) had showed that limited possibility of transmission of lice between individual hosts could increase inbreeding in lice, and in the case of high abundance of parasites this effect had resulted in a male bias. Our collections from September and December (Table 3) 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 (Table 3) what is also known in other species of lice (Balát 1959, Eichler 1963, Nelson 1972) 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 large late winter subpopulations (see seasonal ratios in Results and Table 1) to colonize on new hosts (in the nesting period from late May to early August) could explain the female bias (Table 3) of the small summer (one to three specimen of lice in a sample) subpopulations. In the species of avian lice, the female bias was found to be more pronounced in small subpopulations (Rózsa *et al.* 1996). Moreover, female bias tends to occur in the breeding period of birds. Zlotorzycka (1972a) 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.

Horizontal vs. vertical transmission

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). 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). Our results suggest that very rare direct contactcs among host birds had infrequently been considered as a factor increasing the horizontal transmission of lice.

Vertical transmission. Our data indicate that the care for nestlings is probably the most important activity of accentors which facilitates the lice transmission. 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. Females of accentors are extremely important for the transmission of summer generations of lice (especially adult females of lice - Table 5) 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. From this point of view, the nymphs, males and females (Table 5) of lice are mainly transmitted to squabs by female birds. We have evidence that lice may appear on nestlings of a few days in age, or when the vane starts to spread from the rachis of the growing feather. We found both species of lice on squabs, shortly after fledging. It is possible that direct contact of lice with their hosts is not the indispensable condition to shift from one bird to another. This phenomenon was described in amblyceran lice (Eichler 1963, Rem and Zlotorzycka 1981).

Species richness and parasite coexistence

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). 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). Our data derived from the sample of polygynandrous species living in extremely unfavourable conditions coincide with recent concerns that the two louse species do not possess resource limitations within host individuals. Our findings may be probably better explained by a "low density populations living in resource-rich habitats" model (Reiczigel and Rózsa 1998) than "resource competition" model (Kéler 1969, Zlotorzycka 1972).

Acknowledgements

We thank Jozsef Rékasi and Jadwiga Zlotorzycka for the help in determination of lice and Lajos Rózsa for providing valuable sources of literature. For suggestions on early drafts we thank Ján Guli̇čka. We are also greatly indebted to all people who helped us in the field work.

References

Balát, F. 1959: Řád všenky-*Mallophaga*. In *Klíč zvířeny ČSR, díl III* (ed. J. Kratochvíl), pp.243-269. CAV, Praha.

Bear, A. 1994: An improved method for collecting bird ectoparasites. *J.Field Ornithol.,* **66**:212-214.

Clayton, D.H. and Tompkins, D.M. 1994: Ectoparasite virulence is linked to mode of transmission. *Proccedings of the Royal Society of London B,* **256:**211-217.

Cramp, S.**(ed.)**1988 :*Prunella collaris.* In *Handbook of the Birds of Europe the Middle East and North Africa.* pp.574-584. Oxford University Press, New York.

Davies, N.B., Hartley, I.R., Hatchwell, B.J., Desrochers, A., Skeer, J. and Nebel, D. 1995: The polygynandrous mating system of the alpine accentor, *Prunella collaris,* I. Ecological causes and reproductive conflicts. *Anim. Behav.,* **49:** 769-788.

Eichler, W. 1963: Phtiraptera 1. Mallophaga. In *Klassen und Ordnungen des Tierreichs* (ed. H.G. Browns*)*, pp. 1-267. Leipzig Akademidche Verlagsgesellschaft Geest und Portig K.-G.

Fowler, J.A. and Cohen, S. 1983: A method for quantitative collection of ectoparasites from birds. *Ring. Migrat.,* **4:**185-189.

Heer, L.. 1994: Zur sozialen Organisation und Brutbiologie der Alpenbraunelle *(Prunella collaris).* MSc. thesis, University Bern.

Heer, L. 1996: Cooperative breeding by Alpine Accentors *Prunella collaris:* Polygynandry, territoriality and multiple paternity. *J. Orn.,***137:** 35-51.

Johnston, R.F. and Janiga, M. 1995: Feral Pigeons. Oxford University Press, New York, Oxford.

Kéler **,** S. (1969): Mallophaga (Federlinge und Haarlinge). In *Handbuch der Zoologie* (ed. W. Kukenthal) pp.1-72, Berlin.

Nakamura, M. 1990: Cloacal protuberance and copulatory behavior of the Alpine Accentor *(Prunella collaris). The Auk,* **107:** 284-295.

Nakamura, M. 1995: Territory and group living in the polygynandrous Alpine Accentor *Prunella collaris. Ibis,* **137:** 477-483.

Nelson, C. 1972: A revision of the New World species of *Ricinus* (Mallophaga) occuring on Passeriformes (Aves). University of California Press, Los Angeles.

Potti, J. and Merino, S. 1995: Louse loads of pied flycatcers: effects of host's sex, age, condition and relatedness. *J. Avian. Biol.,***26:** 203-208.

Reiczigel, J. and Rózsa, L. 1998: Host-mediated site segregation of ectoparasites: An individual-based simulation study. *J. Parasitol.* **84:** 491-498.

Rem, R. and Zlotorzycka, J. 1981: An experimental study of the survival rate of some Mallophaga outside of *Columba livia* dom. body. *Acta parasit. pol.,* **28:** 179-185.

Rékási, J., Rózsa, L. and Kiss, B.J. 1997: Patterns in the distribution of avian lice (Phthiraptera: Amblycera, Ischnocera). *J. Avian Biol.,***28:** 150-156.

Rózsa, L. 1997: Adaptive sex-ratio manipulation in *Pediculus humanus capitis:* Possible interpretations o Buxton's data. *J. Parasitol.,* **83:** 543-544.

Rózsa, L., Rékási, J. and Reiczigel, J. 1996: Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). *J. Anim. Ecol.,***65:** 543-544.

Zlotorzycka, J. 1972a:Wszoly (Mallophaga) ptaków i ssaków udomowionych. PWN, Warsaw - Wroclaw.

Zlotorzycka, J. 1972b: Klucze do oznaczania owadów polski. Cześć XV. Wszoly - Mallophaga - Zeszyt 1. Nadrodziny Gyropoidea; Laemobothrioidea. PWN, Warszawa .

Zlotorzycka, J. 1977: Klucze do oznaczania owadów polski. Cześć XV. Wszoly - Mallophaga - Zeszyt 4. Nadrodzina *Philopteroidea* : rodzina Philopteroidea. PWN, Warszawa.

Received 1 July 2000; accepted 12 August 2000.