

Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera)

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This study examines the ecological factors expected to determine the abundance of lice on birds. The associations between avian body mass and avian sociality as selected environmental variables and the arithmetic mean of louse abundance per bird individual are evaluated across bird species. Rough data were obtained from the literature. Using host species as statistically independent observations, louse abundance correlates positively with avian body mass. This correlation is not a phylogenetic artefact, being also found after controlling for effects of host phylogeny. Three non-exclusive hypotheses might explain this correlation: (1) larger birds may provide larger 'habitat islands' enabling more lice to coexist; (2) larger birds may provide more topographic refugia for lice to evade host preening and grooming; and (3) larger birds may provide more longevity of 'habitat islands' thus reducing the decimating effects of transmission. Contrary to expectations based on early anecdotal information, avian sociality had no significant effect on louse abundance either with, or without controlling for host-phylogenetic effects.

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Avian lice (the majority of Phthiraptera: Amblycera and Ischnocera) are the only insects to complete their entire life cycle upon the body surface of birds. Their transmission is highly dependent on direct body-to-body contact among hosts. Being larger than any other contagious pathogens of birds, lice are relatively easy to study. Though lice are rather mild parasites exhibiting low pathogenicity (Clayton and Tompkins 1994, 1995), they do influence major aspects of avian life history such as sexual selection (Clayton 1990), metabolic rate (Booth et al. 1993) and survival (Brown et al. 1995). The aim of this study is to examine some ecological factors expected to determine the abundance of lice on birds.

Anecdotal evidence mentioned by Rothschild and Clay (1952) suggests that large-bodied bird species may harbour more lice than small passerines. Marshall (1981) summarized case studies to support his view that host body size influences the abundance of lice, fleas and flies ectoparasitic on mammals.

Aspects of avian sociality, such as colonial breeding and communal roosting have also been mentioned as factors increasing the quantity of lice (Dubinin 1947, Blagoveshchensky 1959). Colonial breeding is routinely mentioned as a factor increasing the level of selective pressure exerted by parasites upon their avian hosts (see e.g. Mooers and Møller 1996). However, in a comparison between the louse assemblages of two Corvid species coloniality appeared to have no effect on the abundance of lice when comparing congeneric species-pairs of lice (Rózsa et al. 1996). Similarly, mean abundance of 12 louse species collected from 8 colonial bird species did not exceed the mean abundance of 15 louse species collected from 7 territorial host species (Rékási et al. 1997). Thus the aim of this study is to test, by interspecific comparisons, whether avian body mass and sociality influence louse abundance.

Closely related species may tend to share many common traits through common descent rather than through independent evolution. Therefore, statistical methods that treat species characters as statistically

independent points may be misleading, since “phylogenetic inertia” may result in covariation of two characters without any adaptive reason (Harvey and Pagel 1991). Since not only body size and sociality, but also the host-specific parasite communities can be treated as inherited characters of host species (Walther et al. 1995, Poulin 1995, 1996), here I also apply a comparative method that controls for avian phylogeny.

Materials and methods

Hereafter the term ‘louse assemblage’ is used to mean all the hatched louse individuals (nymphs and adults) living on the same host individual. Most louse assemblages in the present series of samples are formed by two or more different species of lice. Individuals of different louse species living on the same host species are considered as members of the same ecological guild and pooled together. Louse abundance is expressed as the arithmetic mean of the number of lice collected from conspecific birds (including the 0 values of louse-free birds).

Faunistic surveys aimed at describing all the lice collected from samples of conspecific birds were reviewed for the present study. Since data on avian behaviour were restricted to the Western Palearctic realm (see below), louse data were collected from this area exclusively. Minimum sample size was arbitrarily set at 40 conspecific birds per sample. Defining a minimum value for sample size serves to decrease the variability of abundance and to reduce ‘publication bias.’ This characteristic bias of faunistic reports is caused by the low probabilities of publishing results after a few or no lice were found compared to the high probabilities of publishing results after many lice were found. Thus uniting several small samples published by different authors would cause an overestimation of louse abundance. Here, though some samples referring to the same host species were pooled, each individual sample was equal to or above the minimum sample size before pooling. The samples of birds reviewed here were either trapped (e.g. mist-netted) or shot for the purpose of collecting lice. All birds were free-ranging and fledged individuals. All available surveys that are consistent with the criteria described above were incorporated into the data set (see Table 1 for sources). Abundances were transformed as $\log(\text{mean abundance} + 1)$. Body size data for birds were taken from Dunning (1993) and were log-transformed. Avian sociality was scored as:

1 – birds that neither show regular flocking behaviour nor colonial breeding (family groups, small parties, occasional gathering at food patches and loosely co-ordinated flocks during migration may occur);

- 2 – birds that show regular flocking behaviour but not colonial breeding, or birds with colonial breeding but without regular flocking behaviour, or birds with facultative colonial breeding and moderate flocking behaviour;
- 3 – birds with regular flocking behaviour and obligate colonial breeding.

Since verbal descriptions of social behaviour are often hard to quantify, intermediate scores (1.5 and 2.5) were also applied. Behavioural scores are based on descriptions by Cramp (1984, 1985, 1988) and Cramp and Perrins (1993, 1994a, 1994b). The types of pair-bond, such as monogamy or polygamy were not evaluated. The data set is summarized in Table 1.

Using host species as statistically independent observations, the influence of avian body mass on louse abundance was quantified by linear regression. A significant correlation between $\log(\text{abundance} + 1)$ and $\log(\text{body mass})$ (see below) yielded a regression line that was used to calculate predicted values of $\log(\text{abundance} + 1)$. Predicted values were subtracted from the observed values to obtain log-residuals. The influence of avian sociality scores on these residuals was checked by Spearman rank correlation.

A simplified phylogenetic tree was constructed by interpreting the taxonomy of Sibley and Monroe (1990) as a phylogeny (Fig. 1). This tree was used in a phylogenetically controlled test performed by CAIC (Comparative Analysis of Independent Contrasts, Purvis and Rambaut 1994). This program identifies sets of phylogenetically independent comparisons within the branching pattern of a phylogenetic tree. Independent differences (linear contrasts) are created by comparing the values of sister taxa. The program assumes a Brownian motion model of evolution. Values for ancestral nodes in the phylogeny are estimated as the mean of the values at daughter nodes, inversely weighted by the lengths of the branches from the daughter nodes to the higher node. Differences that evolved since the splits of lineages are considered as independent evolutionary events. A linear regression forced through the origin indicated a significant interaction between contrasts of $\log(\text{body mass})$ and contrasts of $\log(\text{abundance} + 1)$ (see below). The resultant linear regression line was used to calculate predicted values of contrasts of $\log(\text{abundance} + 1)$. Predicted values were subtracted from the observed ones to obtain residuals. The influence of the contrasts of avian sociality scores on these residuals was checked by Spearman rank correlation.

Computations were carried out with InStat 2.01.

Results

$\log(\text{abundance} + 1)$ was a linear function of $\log(\text{body mass})$ (linear regression, $r = 0.745$, $F = 42.499$, $d.f. =$

Table 1. Host species included in the analyses, avian sociality scores, body mass, the number of bird and louse individuals respectively and the sources of data.

Species	Sociality	Mass (g)	N birds	N lice	Sources
<i>Alauda arvensis</i>	2	39.95	46	5	Blagoveshchensky (1951)
<i>Apus apus</i>	3	37.6	87	168	Lee and Clayton (1995)
<i>Cinclus cinclus</i>	1	59.8	50	93	Fowler and Hodson (1991)
<i>Coccothraustes coccothraustes</i>	1.5	54	50	213	Shumilo and Lunkashu (1972)
<i>Columba livia</i>	2	354.5	285	6744	Černý (1970), Rózsa (1990)
<i>Corvus frugilegus</i>	3	488	139	6115	Shumilo and Lunkashu (1972)
<i>Corvus monedula</i>	2.5	246	113	667	Shumilo and Lunkashu (1972)
<i>Delichon urbica</i>	3	14.5	114	1485	Shumilo and Lunkashu (1972)
<i>Dendrocopos major</i>	1	81.6	68	329	Shumilo and Lunkashu (1972)
<i>Emberiza citrinella</i>	2	26.5	60	157	Shumilo and Lunkashu (1972)
<i>Emberiza bruniceps</i>	2	23.5	55	59	Blagoveshchensky (1951)
<i>Emberiza schoeniclus</i>	2	18.3	370	639	Fowler and Williams (1985), Blagoveshchensky (1951)
<i>Fringilla coelebs</i>	2	21.4	101	105	Shumilo and Lunkashu (1972)
<i>Galerida cristata</i>	1.5	40.45	198	1885	Blagoveshchensky (1951), Shumilo and Lunkashu (1972)
<i>Garrulus glandarius</i>	1	161	115	1079	Shumilo and Lunkashu (1972)
<i>Hydrobates pelagicus</i>	2.5	25.2	240	1395	Fowler and Miller (1984)
<i>Lanius collurio</i>	1	29.9	42	105	Shumilo and Lunkashu (1972)
<i>Merops apiaster</i>	3	56.6	41	649	Shumilo and Lunkashu (1972)
<i>Oceanites oceanicus</i>	2	32	61	404	Fowler and Price (1987)
<i>Oceanodroma leucorhoa</i>	2	31.7	100	149	Fowler and Hodson (1988)
<i>Passer domesticus</i>	2.5	27.7	112	563	Shumilo and Lunkashu (1972)
<i>Passer hispaniolensis</i>	3	24.2	61	121	Blagoveshchensky (1951)
<i>Passer montanus</i>	2.5	22	131	177	Blagoveshchensky (1951), Shumilo and Lunkashu (1972)
<i>Phoenicurus erythronotus</i>	1	18.5	47	74	Blagoveshchensky (1951)
<i>Pica pica</i>	1.5	177.5	107	1958	Shumilo and Lunkashu (1972)
<i>Puffinus puffinus</i>	3	453	230	12298	Fowler and Show (1989)
<i>Riparia riparia</i>	3	14.6	169	225	Balát (1966), Shumilo and Lunkashu (1972)
<i>Sitta europaea</i>	1	22	41	0	Shumilo and Lunkashu (1972)
<i>Streptopelia decaocto</i>	2	149	43	195	Černý (1970)
<i>Streptopelia turtur</i>	1	132	64	475	Shumilo and Lunkashu (1972)
<i>Sturnus roseus</i>	3	66.5	42	163	Blagoveshchensky (1951)
<i>Sturnus vulgaris</i>	2.5	82.3	264	2187	Blagoveshchensky (1951), Shumilo and Lunkashu (1972)
<i>Turdus merula</i>	1.5	113	92	1818	Shumilo and Lunkashu (1972)
<i>Turdus philomelos</i>	1	67.75	69	360	Shumilo and Lunkashu (1972)
<i>Turdus pilaris</i>	2.5	106	43	617	Shumilo and Lunkashu (1972)
<i>Turdus viscivorus</i>	1.5	115	40	551	Shumilo and Lunkashu (1972)

35, $P < 0.0001$, Fig. 2). The linear regression line $Y = 0.73X - 0.50$ was used to calculate the residuals, i.e. the differences between observed and predicted values of $\log(\text{abundance} + 1)$. These residuals were not significantly influenced by avian sociality scores ($r_s = 0.283$, $p > 0.09$, $N = 36$).

A phylogenetic tree with 24 branching points was fitted to the 36 species. Analysing independent contrasts on this tree revealed a significant positive correlation between contrasts of avian body mass and contrasts of louse abundance (linear regression forced through the origin, $t = 4.249$, d.f. = 23, $P < 0.001$, Fig. 3). The linear regression line $Y = 1.04X + 0.00$ was used to calculate predicted values of linear contrast of $\log(\text{abundance} + 1)$. Predicted values were subtracted from the observed ones to obtain residuals. Contrasts of avian sociality scores did not correlate with these residuals ($r_s = 0.019$, $p > 0.92$, $N = 24$).

Discussion

Our current understanding of the processes structuring louse communities is mostly based on non-quantitative

observations which are insufficient to allow quantitative predictions about louse infestation in birds. Comparative analyses of large numbers of lice collected from different host species should help to identify some of the major factors shaping the patterns of parasite abundance. This approach needs the appropriate statistical methods to distinguish between phylogenetic and ecological influences on louse communities. It is still questionable, however, to what extent parasites can be interpreted as host characters inherited along host phylogeny. The parasite communities of closely related host species are likely to be similar partly because they share a recent common ancestor community that parasitised the common ancestor of the host species (Poulin 1995, 1996a). Although the extinction of some parasite species and the invasion by some others may have partially changed the species composition of the community, we can still presume that the majority of parasite species were not replaced and thus the present parasite community can be viewed as a descendant of an ancestral community.

This assumption is much less realistic when interactions between host and parasite species are considered.

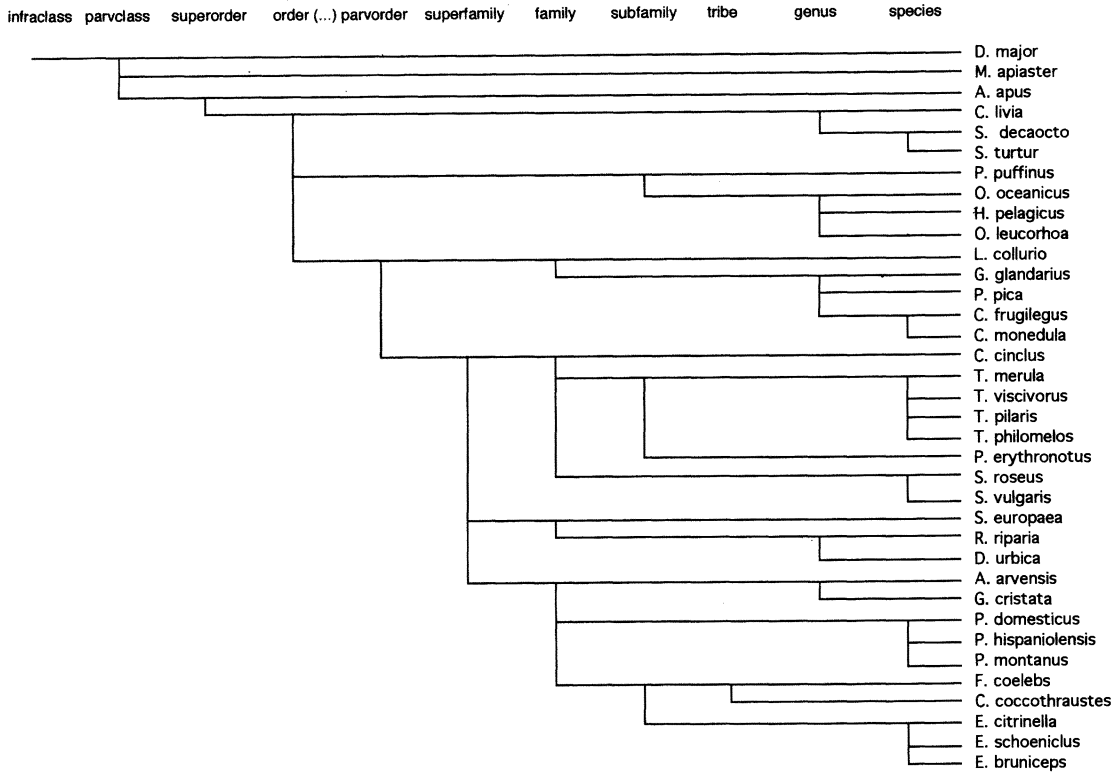


Fig. 1. A simplified avian phylogeny used in a comparative test that controls for phylogenetic effects. All the 24 branching points – illustrated here as vertical lines – are represented in the comparative test. Two levels of the hierarchy, suborder and infraorder are not illustrated.

Prevalence and intensity of infection are not properties of the host or the parasite but of the host-parasite system. It is impossible to control for both host and parasite phylogeny simultaneously, as they are not necessarily congruent (Poulin 1996b). Furthermore, a host-switch, i.e. the emergence of a new parasite population or species

due to colonisation on a new host species, may result in a new species interaction that is not the descendant of any previous one. Although species interactions may follow the host phylogeny if parasites co-speciate with hosts, interactions that emerged as new ones are likely to confuse the phylogeny of these interactions.

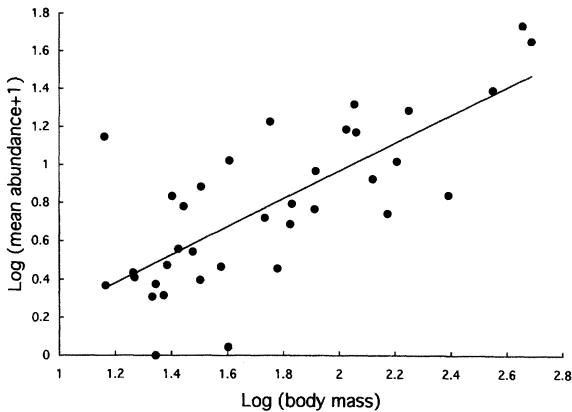


Fig. 2. Using host species as statistically independent observations, avian body mass correlates positively with louse abundance.

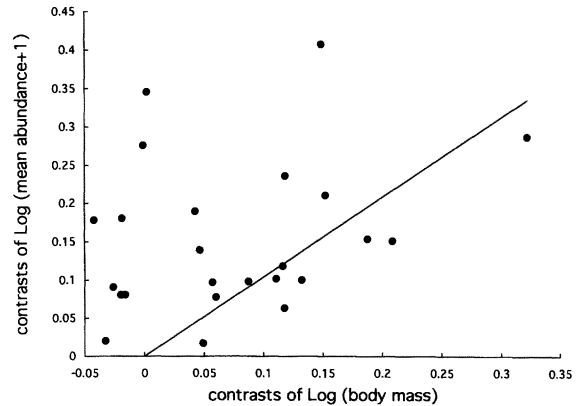


Fig. 3. The line of regression between phylogenetic contrasts (differences between sister taxa) of avian body mass and those of arithmetic mean louse abundance.

Thus, controlling for avian phylogeny in the present context is justified by two circumstances. First, lice have no free-living developmental stages which could be subjected to environmental limitations outside of their avian hosts. Second, louse abundance was defined here as a community measure.

In accordance with early anecdotal evidence, avian body size correlated positively with louse abundance. This correlation was not a phylogenetic artefact, as it was found also after controlling for avian phylogeny. Three hypotheses can explain this correlation:

(1) Host individuals have often been referred to as habitat islands for parasites (but see Kuris et al. 1980). The larger an island is, the more abundant insect assemblage is expected to inhabit it.

(2) The population growth of avian lice is typically limited by preening (by the bill) and scratching (by feet) (Clayton 1991). Ectoparasites are adapted to use certain topographic regions of the body surface as refugia to evade host defence (Kethley and Johnston 1975). Larger birds provide refugia that are not available in the plumage of small ones, thus habitat diversity within the avian plumage is likely to correlate positively with avian body size. For example, lice with an elongate body shape can insert themselves between the barbs of primaries and retrices, thus practically disappear from the surface of feathers. This topographical refugium is not available on small passerines, apparently because lice cannot be small enough to utilise it. Interestingly, wing feather mites (Acari: Proctophyllodidae) are small enough to inhabit these refugia on small passerines. Larger birds provide more diverse types of the refugia used by lice to avoid host defences.

(3) Body size in birds is known to be a good predictor of longevity (Gill 1990). Long life-span of hosts is a major advantage for parasites of low pathogenicity, to whom low transmission probability per time unit is a major limit to population growth (Ewald 1994). Lice of small birds need to transfer from host to host frequently and parasite mortality is presumed to be high at, and soon after transmission.

If hypothesis (1) explains the correlation between host body mass and parasite abundance, then it would also predict the same relationship within a narrowly defined taxon of ectoparasites consisting of species utilising the same type of refugium or even within a species. Wing feather mites, although not related to lice, are members of the same ecological guild and offer a good example. These mites are dependent upon a single type of topographic refugia on the surface of primaries, and in spite of that, their abundance was shown to be significantly influenced by the body mass of their passerine hosts (Rózsa 1997). Furthermore, only one species of lice parasitised the population of Swifts *Apus apus* studied by

Lee and Clayton (1995). Still, there was a significant positive correlation between host body size and louse abundance. Larger swifts apparently provided more resources to maintain lice. In the context of this hypothesis, it is also worth mentioning that louse body size correlates positively with avian body size (see e.g. Clay 1962). Thus, more lice on larger birds should not necessarily be predicted.

Hypothesis (2) predicts more individuals and also more taxa of lice to be found on larger birds. Price (1980) mentioned anecdotal evidence suggesting that large-bodied bird species may harbour more species of lice than do small passerines. Louse species richness was shown to correlate positively with louse abundance in Peruvian birds (Cotgreave and Clayton 1994, based on data from Clayton et al. 1992). In a study of gastrointestinal helminths of vertebrates, Poulin (1995) showed that host body size correlates positively with parasite abundance and species richness suggesting that this correlation may be a more general feature of animal parasitism. Here, I do not test whether louse species richness correlates with avian body mass because parasite species richness is strongly influenced by host sample size (Gregory 1990, Walther et al. 1995) which varied within one order of magnitude (40–370) in the present data set.

Finally, hypothesis (3) cannot be tested here since the life expectancies of the bird species involved in the present study are not known.

The above three hypotheses are mutually non-exclusive and the possibility that further hypotheses will be suggested by future authors cannot be ruled out.

Contrary to previous expectations based on anecdotal evidence (Dubinin 1947, Blagoveshchensky 1959), avian sociality had no significant influence on louse abundance in the present series of samples. One cannot exclude the possibility that the lack of influence may be an artefact caused by the rough method used to quantify avian behaviour and the low number of species involved. However, data available at present indicate that this factor has no significant effect on louse abundance.

The finding that avian lice are not more abundant in more social birds first appeared in Rózsa et al. (1996) and was verified in a study dealing with the distribution patterns of individual host-parasite species pairs (Rékási et al. 1997). Now it is further supported by the present study based on a different data set describing the abundance of lice of 36 avian species. Our result is opposing the widespread view that avian coloniality results in a relatively high level of parasitism. It must be emphasised that this widely accepted view has mostly been based on studies of ectoparasitic arthropods with free-ranging infective forms, such as ticks, mites, fleas and flies (see Rékási et al. 1997 for a citation list). The

present results suggest that the correlation established for these particular parasites cannot be extended to all parasites. Louse abundance is apparently not affected by avian sociality, and this may apply to contagious parasites in general. Moreover, since louse distribution is less aggregated in colonial than in territorial birds (Rékási et al. 1997), lice – and perhaps other contagious parasites – may exert a weaker selective pressure on colonial birds than on territorial ones.

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