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Wing-feather mite (Acari: Proctophyllodidae) abundance correlates with body mass of passerine hosts: a comparative study

Lajos Rózsa

Abstract: Data from a 4-year study of wing-feather mites on passerines in Portugal (Behnke et al. 1995. *Exp. Appl. Acarol.* 19: 443–458) were used to investigate whether avian body mass influences the abundance of mites. When 17 host species were used as statistically independent observations, the mite infestation score correlated positively with avian body mass. This correlation is not a phylogenetic artefact, having been also found when avian phylogeny was controlled for. Three non-exclusive hypotheses might explain this finding: (1) larger birds may provide larger “habitat islands,” enabling more mites to coexist; (2) larger birds may provide more topographic refugia for mites to evade host preening; (3) larger birds may provide greater longevity of habitat islands, thus reducing the decimating effects of transmission.

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Résumé : Les données d'une étude de 4 ans sur les acariens des plumes des ailes de passereaux au Portugal (Behnke et al. 1995. Exp. Appl. Acarol. 19: 443–458) ont été utilisées dans le but de déterminer si la masse corporelle des oiseaux influence le fardeau de parasites. Dix-sept espèces d'oiseaux ont été utilisées comme variables indépendantes; les infestations d'acariens sont en corrélation positive avec la masse corporelle des oiseaux. Cette corrélation n'est pas un artéfact phylogénétique, puisqu'elle persiste même après que l'effet de la phylogénie des oiseaux ait été éliminé. Trois hypothèses non exclusives peuvent être invoquées pour expliquer ce phénomène : (1) les oiseaux plus gros constituent des « îlots » plus grands qui permettent la coexistence d'un plus grand nombre d'acariens; (2) les oiseaux plus gros comportent plus de refuges topographiques permettant aux acariens d'échapper aux effets du toilettage de l'hôte; (3) les oiseaux plus gros assurent la longévité plus grande des îlots, réduisant ainsi les effets de la décimation encourue au cours de la transmission.

[Traduit par la Rédaction]

Introduction

Feather mites are contagious ectoparasites of birds that include the family Proctophyllodidae, a group of mites inhabiting the primary wing feathers of birds. They are numerous on birds; however, since they have little pathogenic effect on their hosts, their natural history is rarely subjected to ecological study and so is poorly understood (for mite communities on seabirds cf. Choe and Kim 1987, 1988, 1989). In the case of passerines, the main source of information is a study by Poulin (1991), who analysed prevalence data published by McClure (1989) and showed that avian sociality correlated positively with mite prevalence across host species, while avian body length and migratory habit did not. Prevalence is the proportion of infested individuals within a sample of hosts (Margolis et al. 1982).

Here I analyse data on the abundance of wing-feather mites. Abundance is the mean number of individuals of a particular parasite species per host examined (Margolis et al. 1982). Data were obtained from a 4-year study in Portugal describing the quantities of wing-feather mites on 17 species of passerines carried out by Behnke et al. (1995). This data set describes the occurrence of *Proctophyllodes pinnatus*, *P. truncatus*, *P. sylviae*, *P. serini*, *P. clavatus*, *P. stylifer*, and *Pteronyssoides obscurus* without revealing a clear causality behind the observed patterns. Contrary to expectations based on previous evidence, no correlation between avian sociality and mite abundance was found. The argument about whether the bill structure of the host (either insectivore or granivore) influences mite infestations remains inconclusive and there is a lack of statistical support (Behnke et al. 1995). The major advantage of this data set is its quantitative nature; unlike previous sources, this one refers not only to prevalence but also to the abundance of mites. Sample sizes are rather small in this data set (ranging from 3 to 138 individuals per host species, mean \pm SD = 27.5 \pm 37.0), but this is not expected to cause false correlations due to statistical artefacts. The expected arithmetic mean of a sample (i.e., the mean of the arithmetic means of many samples) does not correlate with sample size but equals the true population mean (Fulford 1994). Of course, this would hold neither for geometric means (Fulford 1994) nor for the median of arithmetic sample means (Gregory and Woolhouse 1993). Indeed, mite abundances do not correlate with log(sample size) in the present data set (sample size was log-transformed to meet the assumptions of normality, linear regression, $F_{116} = 0.3890$, $p > 0.54$).

Considering the influence of avian sociality on mite infestation, there is an apparent contradiction between the results of Poulin (1991) and Behnke et al. (1995). Though the

latter authors did not describe how the test was performed, the main difference appears to be in the measures used in the two studies. Poulin studied mite prevalence, while Behnke et al. compared means of mite abundance across host species. Clearly, the same number of parasites can exhibit higher prevalence if distributed more equally (i.e., are less aggregated) within a sample of hosts. This is the situation in avian lice (Insecta: Phthiraptera), the only other contagious ectoparasite arthropods on birds. In lice, avian sociality correlates positively with prevalence (and also with other distribution measures) but not with mean abundance (Rózsa et al. 1996; Rékási et al. 1997). This is due to differences in louse distribution, not in louse abundance. On the other hand, louse abundance correlates positively with host body size (L. Rózsa, unpublished data).

Since feather lice and feather mites share many features of their natural history, I hypothesize that environmental factors affect their statistical distribution and abundance in similar ways. Here I use the data set of Behnke et al. (1995) and a cross-species comparison to test one of the predictions of this hypothesis: the abundance of wing-feather mites is correlated with avian body mass.

Materials and methods

Behnke et al. (1995) developed a novel method to quantify mite abundance without causing harm to the host. This method relied on visual inspection of primary wing feathers and assignment of subjective infestation scores to individual feathers, the sum of these scores constituting the primary total mite infestation score (PTMIS). Seventeen species of passerines were characterised by the arithmetic means of PTMIS.

Avian body sizes were obtained from Dunning (1993) and log-transformed to meet the assumption of normality. The data set is summarised in Table 1.

Using host species as statistically independent observations, the influence of avian body mass on mean PTMIS is quantified by linear regression. Computations were carried out using Microsoft Excel 5.0 for Power Mac.

Closely related species may tend to share many characters through common descent rather than independent evolution. Therefore, statistical methods that treat species characters as statistically independent points may be misleading, since "phylogenetic inertia" may result in two characters being found together for no adaptive reason (Harvey and Pagel 1991). Since both body size and measures of specific parasite faunas can be treated as inherited characters of host species (Walther et al. 1995; Poulin 1995, 1996), I used the comparative method to control for avian phylogeny.

A simplified phylogenetic tree was constructed by interpreting the taxonomy of Sibley and Monroe (1990) as a phylogeny. This tree is used in a phylogenetically controlled test performed by means of comparative analysis of independent contrasts (CAIC)

Fig. 1. Positive correlation of avian body mass with mean PTMIS when host species are used as statistically independent observations.

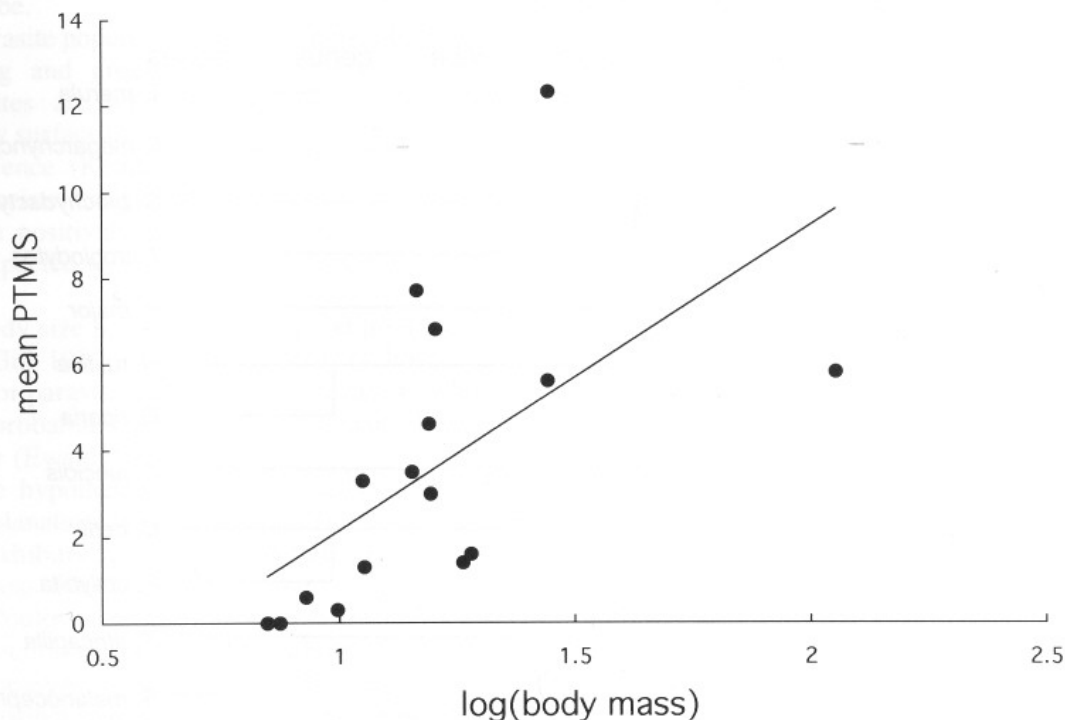


Table 1. Host species included in the analyses, sample sizes, body masses (g), and mean primary total mite infestation scores (PTMIS).

	Sample size	Body mass (g)	Mean PTMIS
<i>Carduelis carduelis</i>	53	12	3.0
<i>Carduelis chloris</i>	21	15	12.3
<i>Certhia brachydactyla</i>	15	12	0.6
<i>Cettia cetti</i>	10	14	3.5
<i>Cisticola juncidis</i>	4	10	0.0
<i>Estrilda astrild</i>	4	9.5	0.0
<i>Hirundo rustica</i>	5	15	6.8
<i>Luscinia megarhynchos</i>	5	16	1.4
<i>Parus major</i>	5	14	1.6
<i>Passer domesticus</i>	95	15	5.6
<i>Phylloscopus collybita</i>	9	11	0.0
<i>Riparia riparia</i>	3	12	7.7
<i>Serinus serinus</i>	11	11	3.3
<i>Sylvia atricapilla</i>	138	14	4.6
<i>Sylvia melanocephala</i>	36	13	1.3
<i>Troglodytes troglodytes</i>	32	9	0.3
<i>Turdus merula</i>	21	25	5.8

Note: Data are from Dunning (1993) and Behnke et al. (1995).

program (Purvis and Rambaut 1994), which identifies sets of phylogenetically independent comparisons within the branching pattern of a phylogenetic tree. Independent differences (linear contrasts) are created by comparing the values for sister taxa. The program assumes a Brownian motion model of evolution. Values for ancestral nodes in the phylogeny are estimated as the means 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 after lineages split are considered to be independent evolutionary events and are analysed by linear regression forced through the origin.

Results

A linear regression with 17 species as independent observations showed a significant positive correlation between avian body mass and mean PTMIS (linear regression: $Y = 7.028 \times X - 4.874$; the slope differs significantly from zero: $F_{[16]} = 3.882$, $p < 0.02$; Fig. 1).

A phylogenetic tree of 12 branch points was fitted to the 17 species (Fig. 2). Analysing independent contrasts on this tree revealed a significant positive correlation between contrasts of avian body mass and contrasts of mean PTMIS (linear regression through the origin: $Y = 13.513 \times X$, the slope differs significantly from zero: $t = 3.878$, 11 df, $p < 0.01$; Fig. 3).

Discussion

Our current understanding of the processes influencing the distribution and abundance of feather mites is mostly based on nonquantitative observations and is therefore insufficient to allow quantitative predictions to be made about the occurrence of mites on birds. Thus, comparative analyses of large numbers of mite assemblages collected from different host species provide the possibility of identifying some of the major environmental factors shaping the patterns of parasite abundance. This approach needs the appropriate statistical methods to distinguish between phylogenetic and ecological influences on mite communities.

In accordance with expectations based on similarities between the natural histories of feather mites and avian lice, mean PTMIS correlated positively with avian body size. This correlation is not a phylogenetic artefact, having also been found when controlling for avian phylogeny. Three hypotheses may explain this correlation.

First, host individuals have often been referred to as habitat islands for parasites (cf. Kuris et al. 1980); the larger

Fig. 2. A simplified avian phylogeny used in a comparative test with a control for phylogenetic effects. This tree was made by interpreting the taxonomy of Sibley and Monroe (1990) as a phylogeny.

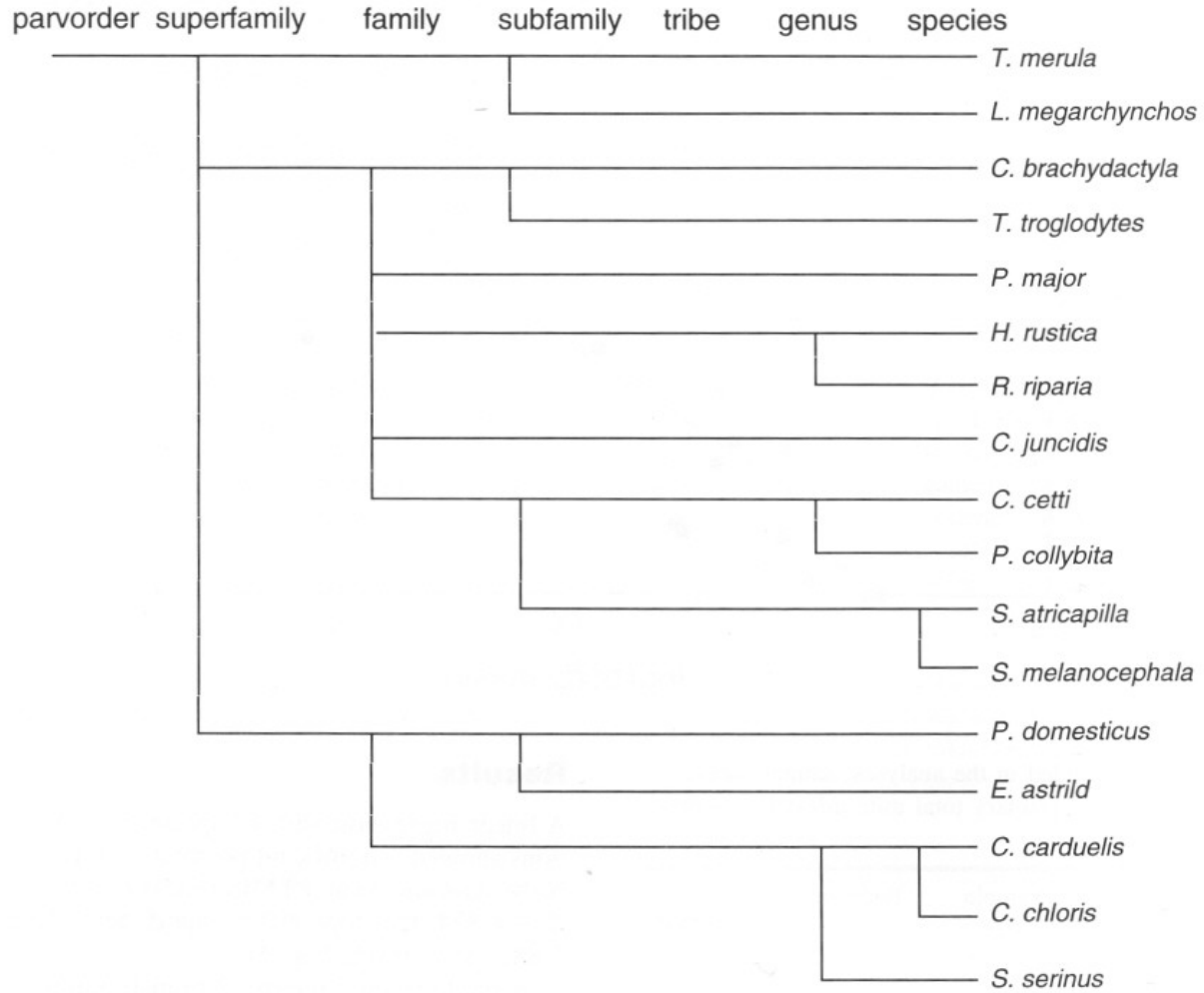
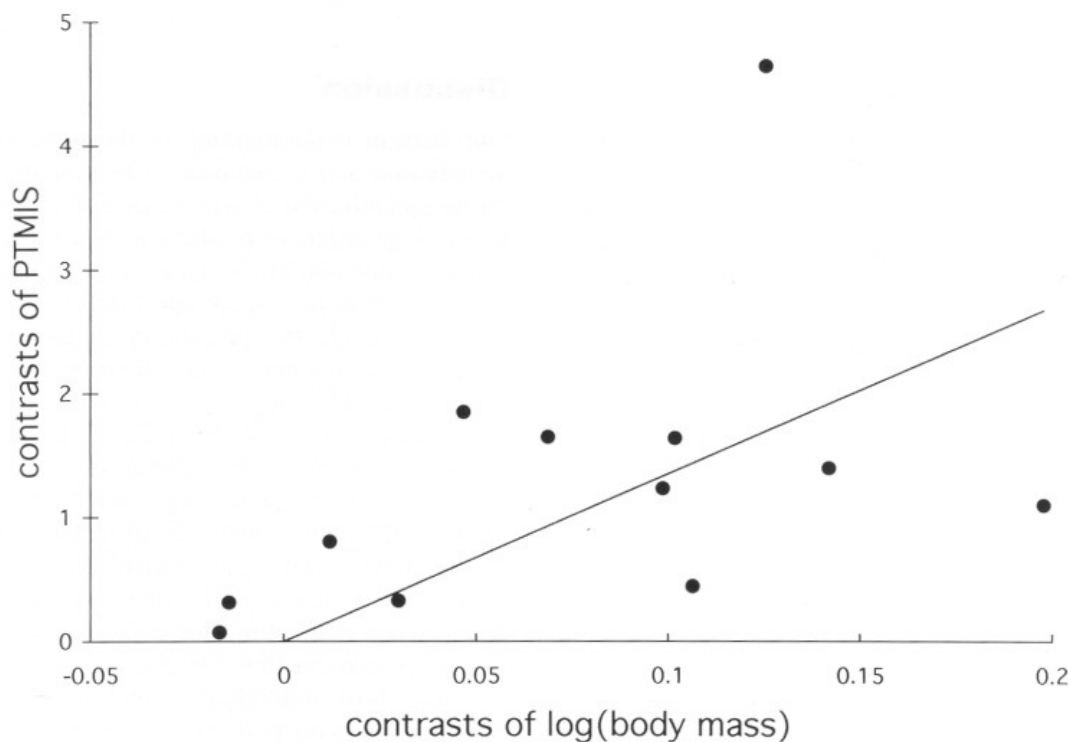


Fig. 3. Phylogenetic contrasts created by comparing the values for sister taxa. Values for ancestral nodes in the phylogeny are estimated as the means of the values at daughter nodes inversely weighted by the lengths of the branches from the daughter nodes to the higher node. Differences that evolved after lineages split are considered to be independent evolutionary events. The phylogenetic contrasts of the arithmetic mean of primary total mite infestation score (PTMIS) are positively correlated with the contrasts of avian body mass.



an island is, the more abundant the mite population inhabiting it is likely to be.

Second, ectoparasite population growth is typically limited by avian preening and grooming as predation (Clayton 1991). Ectoparasites are adapted to certain topographic regions of the body surface in order to utilize them as refugia to evade host defence (Kethley and Johnston 1975). The quantity of appropriate refugia available in the plumage is likely to correlate positively with avian body size. Thus, more mites are expected to survive host defences on larger birds.

Third, avian body size is known to be a good predictor of avian longevity (Gill 1990). A long life-span of hosts is a major advantage for parasites of low pathogenicity, to whom low transmission probability per unit time is a major limit to population growth (Ewald 1994).

Note that these hypotheses are not mutually exclusive. Whatever the explanation is, Poulin's (1991) finding that host body length exhibited no influence on mite infestation in a comparison across bird species does not contradict the present finding. Poulin analysed prevalence, an index that refers to the distribution rather than the quantity of parasites as an infestation measure. Thus, two correlations, the positive correlation between mite prevalence and avian sociality and the positive correlation between mite abundance and avian body size, suggest that the environmental factors determining the distribution and abundance of feather mites on birds may well be similar to those that act on avian lice.

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