

## Ecological correlates of feather mite prevalence in passerines

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The relationship between host ecology and feather mite prevalence was analysed in birds. Feather mites are small arthropods (fam. Pterolichoidea and Analgoidea) commonly found on birds, although the nature of their interactions with the host (commensalism, mutualism or parasitism), still remains unclear. Host body mass and migratory behaviour were unrelated to feather mite prevalence. Contrary to expectation, there was no differences in mite prevalence between colonial and solitary-breeding species. However, winter sociality was associated with increased prevalence, suggesting that winter and breeding sociality affected the distribution patterns of feather mites in different ways. Plumage dichromatism was negatively correlated with feather mite prevalence, a result that is opposite to that predicted by the Hamilton and Zuk hypothesis for the evolution of host secondary sexual characteristics in relation to parasitism.

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Parasites are believed to play an important role in the evolution of bird life history, potentially shaping different aspects of host ecology and behaviour (Hamilton and Zuk 1982, Loye and Zuk 1991, Clayton and Moore 1997). Higher risk of infestation by parasites has been proposed as an important and universal cost of breeding coloniality and of sociality in general (Alexander 1974, Danchin and Wagner 1997). Migratory species may also be exposed to a wider array of parasites than non-migratory species (Møller and Erritzøe 1998, see also Gregory 1990), and habitat use by some species may relate to patterns of parasite abundance (Piersma 1997). These hypotheses, however, have rarely been tested, and when tested most cases have used a univariate approach not controlling for either phylogenetic relationships between hosts or confounding ecological factors (but see Tella et al. 1999).

In this paper I analyse the effects on feather mite prevalence of different variables that have been proposed to be related to the likelihood of feather mite transmission. Feather mites (Pterolichoidea and Analgoidea) feed mainly on detritus and epidermal oil of the host (O'Connor 1982). Some controversy exists about the kind of relationship established between feather mites and their hosts (G. Blanco, J. L. Tella and J. Potti, unpubl.). Blanco et al. (1997, 1999) reported a

positive relationship between mite abundance and host body condition in Red-billed Cough *Pyrrhocorax pyrrhocorax*, and no relationship with body condition in Linnet *Carduelis cannabina*. However, other studies found that infested individuals have poorer body condition, grow shorter wing feathers and have drabber plumage than mite-free individuals (Thompson et al. 1997, Harper 1999). These authors concluded that these results were due to a negative effect of feather mites on body condition, although the opposed relation is also possible. Consequently, I will refer to feather mites as ectosymbionts throughout this paper, without making any assumption about their impact on host fitness, because the prevalence hypotheses tested are fully applicable whether the relationship between feather mites and hosts is one of commensalism, mutualism or parasitism.

Although feather mites probably have no detrimental effects on hosts, and their control is not greatly affected by the host's immune system, I have included a test of the Hamilton and Zuk (1982) hypothesis for the evolution of host secondary sexual characteristics in relation to parasitism, by looking at the relationship between the degree of sexual dichromatism and mite prevalence. Recent support for this hypothesis was reported in studies using feather mites as the model organism

(Thompson et al. 1997, Harper 1999) and assuming a detrimental effect of feather mites on host condition but failing to control for other confounding factors (see Brawnner 1997).

## Material and methods

### Mite prevalence

For the analyses I used McClure's (1989) prevalence data for 43539 passerines of 45 species trapped weekly in two sites in California from 1977 to 1988 (see also Poulin 1991). This data set was supplemented with my own data on feather mite prevalence in 27 species of European passerines (see Appendix 1). Birds were trapped at the Llobregat Delta (41.20N, 02.05E) during six consecutive days at monthly intervals between October and March of the winters 1996–1997 and 1997–1998. The flight feathers on the right wing were examined to detect the presence of any feather mites on or within the barbules. Only species with more than ten examined individuals were included in the analyses, and only data recorded on first capture were considered, to exclude pseudoreplication in the estimates of prevalence. Two species occurred in both data sets, the House Sparrow *Passer domesticus* and the Starling *Sturnus vulgaris*. However, only data from the European study area were considered because both species were introduced in North America by man during the last 140 years (Long 1981). This could have affected the interactions between hosts and potential parasites and symbionts.

### Ecological variables

I included variables that may correlate with variation in feather mite prevalence according to different hypotheses of host-parasite interactions, namely: (1) mean body mass, (2) breeding coloniality, (3) winter sociality, (4) residence status, (5) sexual dichromatism, on a scale of 0 to 12 based on the coding of the colour dimorphism in twelve different body parts (Gray 1996) and (6) study area, to control for any difference due to habitat, geographic region, seasonal differences in trapping effort between both areas (trapping in California took place all year round but only in autumn and winter in Llobregat Delta), or any methodological bias. Côté and Poulin (1995) and Poulin (1991) reported a higher prevalence of ectoparasites in group-living species. However, Tella et al. (1999) reported a significantly higher prevalence of blood parasites in solitary-nesting than in colonial-breeding raptors in Spain, a difference that disappeared when controlling for other ecological factors. Other analyses have also failed to find any effect of host coloniality on lice prevalence (Rózsa et al.

1996, Rékási et al. 1997, Rózsa 1997a). These contradictory results show that the relationship between sociality and parasite prevalence (and by extension the distribution of ectosymbionts) is not clear and underlines the need for detailed analyses separating the effects of breeding coloniality and winter sociality. Data for each species were recorded from field guides (Peterson 1961, Peterson and Chalif 1973, Peterson et al. 1987), handbooks (Dunning 1993, Cramp 1985–1992, Cramp and Perrins 1993–1994) and a previous comparative analysis of feather-mite prevalence in North American passerines (Poulin 1991), see Appendix 1.

### Phylogenetic effects on mite prevalence

Data for different species cannot be considered as independent points in comparative studies because closely related species are more likely to share similar ecological characteristics due to common ancestry (Harvey and Pagel 1991). In this study, I used a nested ANOVA to identify the taxonomic level at which most of the variation in mite prevalence occurs (see Read and Harvey 1989, Herrera 1992, Jordano 1995). Prevalence estimates were arc-sin transformed before analysis. Sibley and Monroe's (1990) taxonomy was followed in this study. The taxonomic level at which most of the variance in mite prevalence occurs was included in the regression analysis as a dummy variable to control for the effects of phylogeny. Given that a complete phylogeny for all the analysed species was not available, a comparative approach based on the taxonomic relationships between species was considered the most suitable method for these analyses (Harvey and Pagel 1991).

### Statistical analyses

General Lineal Modelling was used to examine the relationship between the ecological variables and mite prevalence. A binomial error model with a logit link was implemented using the GENMOD procedure of the SAS program. This procedure uses the number of infested birds as the response variable and the number of examined individuals as the binomial denominator (Crawley 1993), thus controlling for the effect of sample size on the estimates of infestation rate. Discrete variables (both taxonomic classification and most ecological variables) were included as factors in the analyses, whereas body mass and plumage dichromatism were analysed as continuous variables. Deviances from the model were scaled with the square root of the ratio deviance/degrees of freedom. An initial model with all the variables was fitted to the data and a backwards removal procedure was followed to obtain a final model containing only the variables significantly improving the model.

Table 1. Taxonomic distribution of variation in mite prevalence among the 70 passerine species studied. Tabulated values are percentages of total variance occurring at successive taxonomic levels from a nested ANOVA on arc-sin transformed species averages.

|             | Number of taxa | Variance accounted for |
|-------------|----------------|------------------------|
| Superfamily | 5              | 0.00                   |
| Family      | 13             | 0.00                   |
| Subfamily   | 19             | 10.78                  |
| Tribe       | 25             | 24.35                  |
| Genus       | 56             | 16.42                  |

Results

The nested ANOVA showed that most of the variance in mite prevalence concentrated at the level of host Tribe (Table 1). Consequently host Tribe was included as the taxonomic level to be controlled for in the GLM multivariate model.

The GLM model explained as much as 90% of the original deviance in mite prevalence (Table 2). No difference in feather mite prevalence was found between migratory and resident species ( $F_{1,39} = 1.01$ ,  $p = 0.32$ ) and mite prevalence was not related to host body mass ( $F_{1,40} = 0.94$ ,  $p = 0.34$ ). The prevalence of mites was lower at the North American locality than in the European study area (Table 2), although this effect could be due to methodological differences between the two studies. Species that form flocks during the winter had higher prevalences (Table 2), but no differences in prevalence were detected between species that breed in colonies and solitary nesters ( $F_{1,41} = 2.25$ ,  $p = 0.14$ ). Plumage dichromatism correlated negatively with mite prevalence, with more dimorphic species being less frequently infested than non-dimorphic species (Fig. 1).

Discussion

The relationship between bird size and ectosymbiont distribution has previously been examined in two studies with opposing results. Poulin (1991) failed to find any relationship between bird length and mite prevalence using McClure's (1989) data for North America. However, Rózsa (1997b) reported a positive relationship between host body mass and the number of mites

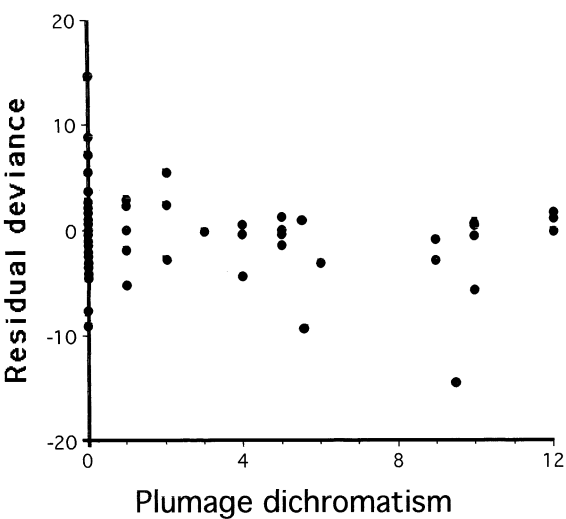


Fig. 1. Relationship between feather mite prevalence and plumage dichromatism. The residual deviance in each species' prevalence from the fitted model without plumage dichromatism was plotted against plumage dichromatism.

for a data set of 17 passerines trapped in Portugal. My results support the conclusions of Poulin (1991), suggesting that although mite abundance could be related to host body size, their prevalence was unrelated to host size, independently of the size estimator used (body mass or wing length).

Migratory species experience a large diversity of environments during their life, and are expected to be more exposed to parasite infestation (Møller and Erritzøe 1998). However, I found no differences in feather mite prevalence between resident and migratory species. This is not surprising if feather mites are contact-transmitted ectosymbionts since the number of congeners that interact with an individual is likely to be more important for their transmission than the migratory behaviour of the host.

Species that live in flocks during the winter had higher mite prevalences than solitary species, while no effect of host coloniality on mite prevalence was detected. Although Poulin (1991) reported a higher prevalence of feather mites in social species, winter sociality and breeding sociality were not separated in these analyses, suggesting that the differences reported were

Table 2. Results of GLM modelling. The reduction of fit of the model when each variable is removed from the final model is shown and its significance tested with an F test. The final model has 42 d.f., a deviance of 955.5, a scale parameter of 4.77 and explains 90% of the original deviance.

| Variable             |               | Estimate           | s.e.   | F     | d.f. | p      |
|----------------------|---------------|--------------------|--------|-------|------|--------|
| Constant             |               | -1.9213            | 0.6543 |       |      |        |
| Locality             |               | 2.6121             | 0.9344 | 10.57 | 1    | 0.002  |
| Winter sociality     | solitary      | -1.4390            | 0.7032 | 5.44  | 1    | 0.02   |
|                      | winter flocks | 0.000              | 0.000  |       |      |        |
| Plumage dichromatism |               | -0.1134            | 0.0426 | 8.13  | 1    | 0.007  |
| Tribe                |               | -19.9106 to 3.1496 |        | 10.73 | 24   | <0.001 |

the result of higher prevalence only in species that form flocks outside the breeding season. Feather mites tend to be transmitted horizontally (between individuals of the same group) rather than vertically (from parents to offspring, O'Connor 1994). In Red-billed Choughs, yearlings were not infested until they joined winter communal roosts, although their parents were heavily infested by feather mites, supporting the view that vertical transmission at the colonies is relatively unimportant compared with horizontal transmission in the roosts (Blanco et al. 1997).

Some colorations and ornaments may have evolved as indicators of health, quality or parental care capacity (Zahavi and Zahavi 1997). Hamilton and Zuk (1982) proposed that plumage brightness in birds has evolved as an indicator of resistance to parasites. In this case, brighter individuals should be less parasitized and have more efficient immune systems. At the interspecific level the hypothesis predicts a positive association between parasite prevalence and plumage brightness. Comparative tests have produced contradictory results (Møller 1990), probably due to the different effects that parasites could have on hosts (Dufva and Allander 1995, Figuerola et al. 1999). The negative correlation between plumage dichromatism and feather mite prevalence was in the opposite direction to that predicted under the Hamilton and Zuk (1982) hypothesis. However, feather mite ecology differs from those of parasites used to formulate or test the hypothesis. Feather mites are not affected by immune system activation or capacity, so cycles of adaptation between host genetic disease resistance and parasite virulence are not likely to occur. For ectoparasites, time devoted to feather cleaning and plumage maintenance could be more important for parasite population regulation, through self preening, grooming or anting (see e.g. Clayton 1991). In this case, low levels of infestation could be related to a bird's capacity to devote time to self-maintenance activities. However, no evidence has been provided that birds attempt to remove feather mites (see Blanco et al. 1997), and the effects of feather mites on host fitness is, at most, very small. Møller (1996) suggested that not only do parasites affect sexual selection of their hosts, but host sexual selection should also affect the population biology of parasites. This hypothesis predicts a negative relationship between intensity of sexual selection and parasite prevalence for those parasites that do not depend on intermediate vectors. This is the case for feather mites, independently of the true nature of feather mite-bird interactions (parasitic, mutualistic or commensal). Plumage dichromatism has been shown to correlate positively with intensity of sexual selection in birds (Møller and Birkhead 1994), and consequently the negative relationship I found between mite prevalence and plumage dichromatism supports Møller's (1996) proposal.

In conclusion, I provide the first interspecific evidence of a relationship between feather mite prevalence and plumage characteristics of the avian host. The direction of the relationship favours the hypothesis that host ecology affects feather mite distribution more than the opposing view that feather mites have favoured the evolution of plumage dichromatism. The common assumption of higher prevalence in colonial-breeding species needs further testing, on a wide range of ectosymbionts and parasites, whilst controlling for the effect of winter sociality on prevalence.

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**Appendix 1.** Data used in the analyses. Body mass (in grams); number of individuals examined and number infested; breeding coloniality: solitary (1) or colonial (2); winter sociality: solitary (1) or flocking (2); residence: migrant (1) or present all year (2); locality: Llobregat Delta (1) or California (2); plumage dichromatism (increasing from 0 to 12).

| Species                                | Body mass | Exam.  | Infest. | Breed. | Winter | Resid. | Locality | Dichromat. |
|----------------------------------------|-----------|--------|---------|--------|--------|--------|----------|------------|
| <i>Empidonax difficilis</i>            | 10        | 39     | 1       | 1      | 1      | 1      | 2        | 0          |
| <i>Myarchus cinerascens</i>            | 27.2      | 14     | 3       | 1      | 1      | 1      | 2        | 0          |
| <i>Sayornis nigricans</i>              | 18.65     | 34     | 0       | 1      | 1      | 2      | 2        | 0          |
| <i>Lanius ludovicianus</i>             | 47.4      | 18     | 5       | 1      | 1      | 2      | 2        | 0          |
| <i>Aphelocoma coerulescens</i>         | 80.2      | 311    | 52      | 1      | 2      | 2      | 2        | 0          |
| <i>Bombycilla cedrorum</i>             | 31.85     | 56     | 35      | 1      | 2      | 1      | 2        | 3          |
| <i>Phainopepla nitens</i>              | 24        | 18     | 0       | 1      | 2      | 1      | 2        | 12         |
| <i>Catharus guttatus</i>               | 31        | 360    | 48      | 1      | 1      | 1      | 2        | 0          |
| <i>Catharus ustulatus</i>              | 30.8      | 14     | 1       | 1      | 1      | 1      | 2        | 0          |
| <i>Turdus merula</i>                   | 113       | 18     | 10      | 1      | 1      | 1      | 1        | 12         |
| <i>Turdus migratorius</i>              | 77.3      | 19     | 6       | 1      | 2      | 1      | 2        | 5          |
| <i>Turdus philomelos</i>               | 67.75     | 29     | 16      | 1      | 2      | 1      | 1        | 0          |
| <i>Erithacus rubecula</i>              | 18.2      | 196    | 101     | 1      | 1      | 1      | 1        | 0          |
| <i>Luscinia svecica</i>                | 18.2      | 25     | 25      | 1      | 1      | 1      | 1        | 2          |
| <i>Phoenicurus phoenicurus</i>         | 14.6      | 13     | 2       | 1      | 1      | 1      | 1        | 9          |
| <i>Saxicola torquata</i>               | 15.3      | 10     | 5       | 1      | 1      | 1      | 1        | 5          |
| <i>Sturnus vulgaris</i>                | 82.3      | 10     | 8       | 1      | 2      | 2      | 1        | 0          |
| <i>Mimus polyglottos</i>               | 48.5      | 180    | 20      | 1      | 1      | 2      | 2        | 0          |
| <i>Toxostoma redivivum</i>             | 84.4      | 75     | 4       | 1      | 1      | 2      | 2        | 0          |
| <i>Campylorhynchus brunneicapillus</i> | 38.9      | 16     | 0       | 1      | 1      | 1      | 2        | 0          |
| <i>Thryomanes bewickii</i>             | 9.9       | 131    | 0       | 1      | 1      | 2      | 2        | 0          |
| <i>Troglodytes aedon</i>               | 10.9      | 51     | 1       | 1      | 1      | 2      | 2        | 0          |
| <i>Troglodytes troglodytes</i>         | 9.9       | 15     | 9       | 1      | 1      | 1      | 1        | 0          |
| <i>Remiz pendulinus</i>                | 9.3       | 91     | 55      | 1      | 2      | 1      | 1        | 0          |
| <i>Parus inornatus</i>                 | 17.5      | 22     | 6       | 1      | 2      | 2      | 2        | 0          |
| <i>Parus major</i>                     | 19        | 28     | 20      | 1      | 2      | 2      | 1        | 0          |
| <i>Aegithalos caudatus</i>             | 8.2       | 27     | 24      | 1      | 2      | 1      | 1        | 0          |
| <i>Psaltiriparus minimus</i>           | 5.3       | 232    | 0       | 1      | 2      | 2      | 2        | 1          |
| <i>Regulus calendula</i>               | 6.65      | 161    | 0       | 1      | 1      | 1      | 2        | 1          |
| <i>Cisticola juncidis</i>              | 7.05      | 19     | 9       | 1      | 1      | 2      | 1        | 0          |
| <i>Acrocephalus melanopogon</i>        | 11        | 49     | 39      | 1      | 1      | 1      | 1        | 0          |
| <i>Cettia cetti</i>                    | 14.25     | 195    | 135     | 1      | 1      | 2      | 1        | 0          |
| <i>Phylloscopus collybita</i>          | 7.5       | 1116   | 119     | 1      | 1      | 1      | 1        | 0          |
| <i>Phylloscopus trochilus</i>          | 8.7       | 50     | 1       | 1      | 1      | 1      | 1        | 0          |
| <i>Chamaea fasciata</i>                | 14.65     | 181    | 5       | 1      | 1      | 2      | 2        | 0          |
| <i>Sylvia atricapilla</i>              | 15.5      | 190    | 175     | 1      | 1      | 1      | 1        | 1          |
| <i>Sylvia melanocephala</i>            | 11.3      | 35     | 20      | 1      | 1      | 2      | 1        | 4          |
| <i>Passer domesticus</i>               | 27.7      | 64     | 34      | 2      | 2      | 2      | 1        | 5          |
| <i>Passer montanus</i>                 | 22        | 76     | 53      | 2      | 2      | 2      | 1        | 0          |
| <i>Anthus pratensis</i>                | 18.4      | 44     | 24      | 1      | 2      | 1      | 1        | 0          |
| <i>Anthus spinoletta</i>               | 23.9      | 21     | 19      | 1      | 1      | 1      | 1        | 0          |
| <i>Motacilla alba</i>                  | 21        | 22     | 22      | 1      | 2      | 1      | 1        | 1          |
| <i>Carduelis carduelis</i>             | 15.6      | 10     | 5       | 1      | 2      | 2      | 1        | 0          |
| <i>Carduelis chloris</i>               | 27.8      | 12     | 11      | 1      | 2      | 2      | 1        | 4          |
| <i>Carduelis psaltria</i>              | 9.5       | 153    | 16      | 1      | 2      | 2      | 2        | 9.5        |
| <i>Carpodacus mexicanus</i>            | 21.4      | 20 600 | 13 655  | 1      | 2      | 2      | 2        | 5          |
| <i>Serinus serinus</i>                 | 11.2      | 118    | 117     | 1      | 2      | 2      | 1        | 2          |
| <i>Aimophila ruficeps</i>              | 18.7      | 106    | 5       | 2      | 2      | 2      | 2        | 0          |
| <i>Chondestes grammacus</i>            | 29        | 154    | 68      | 1      | 2      | 1      | 2        | 0          |
| <i>Emberiza schoeniclus</i>            | 18.3      | 58     | 41      | 1      | 2      | 1      | 1        | 6          |
| <i>Junco hyemalis</i>                  | 19.6      | 707    | 146     | 1      | 2      | 1      | 2        | 5.6        |
| <i>Melospiza lincolni</i>              | 17.4      | 67     | 3       | 1      | 1      | 2      | 2        | 0          |
| <i>Melospiza melodia</i>               | 20.75     | 261    | 22      | 1      | 1      | 2      | 2        | 0          |
| <i>Passerculus sandwichensis</i>       | 20.05     | 31     | 13      | 1      | 2      | 2      | 2        | 0          |
| <i>Passerella iliaca</i>               | 32.3      | 16     | 6       | 1      | 2      | 1      | 2        | 0          |
| <i>Pipilo erythrophthalmus</i>         | 40.5      | 507    | 126     | 1      | 2      | 2      | 2        | 10         |
| <i>Pipilo fuscus</i>                   | 44.4      | 986    | 296     | 1      | 2      | 2      | 2        | 0          |
| <i>Spizella passerina</i>              | 12.3      | 16     | 6       | 1      | 2      | 1      | 2        | 0          |
| <i>Zonotrichia atricapilla</i>         | 29.8      | 491    | 132     | 1      | 2      | 1      | 2        | 0          |
| <i>Zonotrichia leucophrys</i>          | 29.4      | 9066   | 3668    | 1      | 2      | 1      | 2        | 0          |
| <i>Dendroica coronata</i>              | 12.55     | 607    | 31      | 1      | 1      | 1      | 2        | 5.5        |
| <i>Geothlypis trichas</i>              | 10.1      | 78     | 0       | 1      | 1      | 2      | 2        | 2          |
| <i>Vermivora celata</i>                | 9         | 31     | 2       | 1      | 1      | 2      | 2        | 4          |
| <i>Wilsonia pusilla</i>                | 6.9       | 33     | 0       | 1      | 1      | 1      | 2        | 1          |
| <i>Passerina amoena</i>                | 15.5      | 48     | 4       | 1      | 2      | 1      | 2        | 10         |
| <i>Pheucticus melanocephalus</i>       | 42        | 36     | 2       | 1      | 1      | 1      | 2        | 10         |
| <i>Agelaius phoeniceus</i>             | 52.55     | 48     | 5       | 2      | 2      | 1      | 2        | 12         |
| <i>Euphagus cyanocephalus</i>          | 60.4      | 1461   | 64      | 2      | 2      | 2      | 2        | 9          |
| <i>Icterus galbula</i>                 | 33.75     | 84     | 7       | 1      | 2      | 1      | 2        | 12         |
| <i>Molothrus ater</i>                  | 43.9      | 223    | 12      | 1      | 2      | 2      | 2        | 10         |