

0 Feather mites (Acari: Astigmata) and body condition of their avian hosts: a large correlative study 53 55

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25 Feather mites are arthropods that live on or in the feathers on birds, and are among the commonest avian ectosymbionts. However, the nature of the ecological interaction between feather mites and birds remains unclear, some studies reporting negative effects of feather mites on their hosts and others reporting positive or no effects. Here we use a large dataset comprising 20 189 measurements taken from 83 species of birds collected during 22 yr in 151 localities from seven countries in Europe and North Africa to explore the correlation between feather mite abundance and body condition of their hosts. We predicted that, if wing-dwelling feather mites are parasites, a negative correlation with host body condition should be found, while a mutualistic interaction should yield positive correlation. Although negative relationships between feather mite abundance and host body condition were found in a few species of birds, the sign of the correlation was positive in most bird species (69%). The overall effect size was only slightly positive (r = 0.066). The effect of feather mite abundance explained < 10% of variance in body condition in most species (87%). Results suggest that feather mites are not parasites of birds, but rather that they hold a commensalistic relationship where feather mites may benefit from feeding on uropygial gland secretions of their hosts and birds do not seem to obtain a great benefit from the presence of feather mites. 80 85 90

40 Parasites are organisms that live at the expense of others (their hosts), causing some kind of damage to or removing valuable resources from the latter. Thus, parasites generally exert negative effects on the body condition of their hosts (Møller 1997, Møller et al. 1998). Plumicolous feather mites (Astigmata: Analgoidea, Pterolichoidea) are obligatorily symbiotic arthropods living permanently on the feathers of live birds, and are among the commonest ectosymbionts on birds (Dabert and Mironov 1999, Proctor and Owens 2000, Proctor 2003). The nature of the ecological interactions between feather mites and their bird hosts is still controversial. Although no clear mechanism has been proposed by which feather mites might harm their hosts (see below), some authors have hypothesized that feather mites are parasites and have provided correlative and experimental evidence of detrimental effects of these organisms to their hosts (Thompson et al. 1997, Harper 1999, Pérez-Tris et al. 2002, Figuerola et al. 2003). Other studies, by contrast, suggest that feather mites provide benefits to their hosts (Blanco et al. 1997, Jovani and Blanco 2000, Blanco and Frías 2001, Brown et al. 2006, Galván and Sanz 2006, Campos et al. 2011) or do not affect their hosts 95 100 105

Methods

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Field methods

A total of 20189 individuals from 83 different species of passerine birds were inspected for feather mite abundance between 1989 and 2010 in 151 localities from seven different countries (Fig. 1, Supplementary material Appendix 1). The birds were captured in the field, mostly with mist nets but also using alternative techniques of capture for certain species, and weighed, and their tarsus (Tar1, following Eck et al. 2011) and wing length (Wmax, following Eck et al. 2011) were measured as alternative indices of body size. Size-independent body mass was considered as an index of body condition. To determine whether tarsus or wing length was the best index of body size, we regressed both variables separately on body mass for each species, and selected the one explaining a greater proportion of variance in body mass. Therefore, we used either tarsus length or wing length as a covariate in the general linear models testing for a correlation between body condition and feather mite abundance (see below). In any case, the results were very similar using either tarsus length or wing length as index of body size (results not shown).

Feather mites were counted by extending and exposing the wings of the birds to daylight. Only one wing was used, as the numbers of feather mites on both wings of the same bird are highly positively correlated (Jovani and Serrano 2004). The total number of feather mites in primary, secondary and tertial feathers was used as an index of feather mite abundance (according to terminology in Bush et al. 1997). To avoid pseudo-replication, only the first observation of each individual bird was used in the analyses. Including the individual bird as a random factor

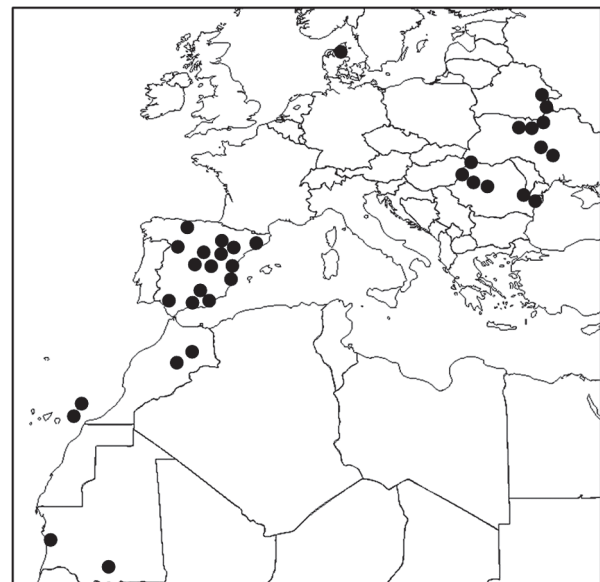


Figure 1. Location of the 151 study sites. Superimposed localities are grouped under same black dots. The number of localities per country were: Belarus (6), Denmark (28), Mauritania (2), Morocco (2), Romania (22), Spain (76; 2 of them in the Canary Islands), Ukraine (15).

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0 (Blanco et al. 1999, Dowling et al. 2001, Pap et al. 2005, 2010). Therefore, the nature of the interaction between feather mites and their hosts remains an open question whose solution would have diverse evolutionary implications because feather mites are present in almost all groups of birds (Proctor 2003).

5 Since the reasons by which feather mites should be parasites are weak, much evidence suggest that these organisms have a mutualistic or commensal relationship with their hosts (reviewed by Blanco et al. 2001). This non-parasitic relationship is supported by the diet of feather mites, mainly based on the lipidic secretions produced by the host's uropygial gland that are smeared onto the plumage during preening (Blanco et al. 2001, Proctor 2003). These substances, which protect the plumage of birds from degradation due to external factors, are highly stable and can remain on feathers for long periods of time (Sweeney et al. 2004). It has been shown that an excess of waxes makes the plumage lose its capacity for heat retention (Sandilands et al. 2004). Thus, feather mites may benefit birds by removing old waxes and associated microorganisms (bacteria, fungi, algae) and debris (pollen) that accumulate on feathers (Blanco et al. 1997, 2001, Reneerkens 2007). Moreover, there is evidence of a positive association between feather mite abundance and uropygial gland size both within and among bird species (Galván and Sanz 2006, Galván et al. 2008, Møller et al. 2010, Haribal et al. 2011; but see Pap et al. 2010). In contrast, no mechanisms have been proposed to explain why feather mites could negatively affect their bird hosts (Blanco et al. 2001). Finally, it has been proposed that the interaction between feather mites and birds may be a case of conditional outcomes (Blanco et al. 2001); birds impaired from normal preening by injury or disease may accumulate an excess of uropygial gland secretions, thus increasing the abundance of feather mites. In this context, feather mites would be especially beneficial by helping birds to maintain their plumage (Blanco et al. 2001).

35 Correlative studies, despite being limited in their ability to control for confounding factors, represent a powerful approach to find general patterns in ecology, particularly when performed with huge datasets. However, correlative studies on the relationship between feather mite abundance and the body condition of their hosts have until now been performed with relative small sample sizes, with single species of birds or with a limited number of species (Blanco et al. 1997, Harper 1999, Jovani and Blanco 2000, Pap et al. 2005, 2010, Campos et al. 2011). Here we make the first correlative study of the relationship between feather mite abundance and body condition for a large sample of individuals and species of birds. Our aim was to determine the magnitude of the association between body condition of birds and feather mite abundance in different species. If feather mites are parasites, we expected a negative relationship between feather mite abundance and host body condition within species, while the opposite should result if the interaction between feather mites and their hosts is mutualistic and birds benefit from having feather mites on the plumage. A commensal interaction would result in a lack of association.

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0 in the analyses was not possible because of convergence
problems due to the large number of individuals sampled
only once. It must be considered that feather mites were
only counted on wings and not on tail or body feathers,
so we are dealing with a subset of the total feather mite
5 abundance of birds. The species of feather mites in many
of the bird host species considered here have been already
reported elsewhere (Galván et al. 2008).

10 Statistical analyses

10 The association between body condition of birds and
feather mite abundance was tested by means of general linear
models with body mass as response variable and body size
(either tarsus or wing length) and feather mite abundance
15 as covariates. We also controlled for seasonal effects on
feather mite abundance (Blanco et al. 1997, Blanco and
Frias 2001, Galván et al. 2008, Pap et al. 2010), adding a
categorical variable to the models with the values of 0 (i.e.
observation between June and October) or 1 (i.e. obser-
20 vation between November and May). This is because we
found that the average abundance of feather mites was
lower during the former period than during the latter in our
entire dataset of birds (results not shown). A separate model
was performed for each bird species.

25 The age and sex of the birds may also represent confound-
ing variables if body condition and feather mite abundance
were both affected by these variables. Unfortunately, the
age and sex of birds can be determined in the field in only
some of the species considered here, so this information
30 was not always available. However, we determined whether
the exclusion of age and sex in the models influenced the
results by comparing the slope of the effect of feather mite
abundance estimated from the models including age and
sex as categorical variables with the slope estimated from
35 the same models but excluding these variables, using a
dataset from nine species for which information on both
age and sex was available for a fraction of the individuals.
This dataset comprised 9745 individuals that had infor-
mation on age and sex. The slopes were compared using
40 t-tests (Zar 1999). None of the nine comparisons of
slopes was significant ($0.07 < t < 1.45$, $48 < DF < 9062$,
 $0.073 < p < 0.471$, median p-value = 0.388). Therefore, the
exclusion of age and sex from the models testing the asso-
45 ciation between the body condition of birds and feather
mite abundance is unlikely to influence the estimation of
the slope of body condition regressed against feather mite
abundance.

Another variable potentially affecting our results is
observer identity. However, it has previously been reported
50 that estimates of wing-dwelling feather mite abundance are
highly repeatable among observers (Galván et al. 2008).
Moreover, differences between individual birds are large
enough to suggest that feather mite counts are robust
between observers (e.g. in this study feather mite abundance
55 ranged from 0 to 2928 mites). However, to further test for
any influence of observer identity in our analyses, we used
a subset of data from two species in which several observers
had been involved in determining feather mite abun-
dance (bearded tit *Panurus biarmicus*, n = 197 birds, seven
60 observers; great tit *Parus major*, n = 99 birds, 10 observers).

For each of these subsets, we estimated the slope for effect
of feather mite abundance as described above and ignored
the identity of observers and compared it with the slope
estimated from the same model, but including observer
65 identity as a random factor in a general linear model. The
slopes were again compared using t-tests, and none of these
tests was significant (bearded tit: $t_{390} = 0.03$, $p = 0.488$;
great tit: $t_{194} = 0.01$, $p = 0.496$). Therefore, the exclusion
of observer identity from the models testing for an asso-
70 ciation between body condition of birds and feather mite
abundance might not influence the estimation of the slope
of body condition regressed against feather mite abundance.

Finally, we tested whether year and locality of cap-
75 ture represented confounding variables for our analyses of
the relationship between body condition and feather mite
abundance. With this aim, we chose 10 species of birds
with large sample sizes and that were captured at several
different localities and years. We then compared the slope
of the effect of feather mite abundance estimated from
80 the models including locality and year as random variables
with the slope estimated from the same models but exclud-
ing these variables. The dataset comprised 11376 indi-
viduals with information from a number of localities that
ranged between 9 and 64 and from a number of years
85 that ranged between 7 and 20. From the 10 comparisons
of slopes, only one (the greenfinch *Carduelis chloris*: $t_{2528} =$
 4.52 , $p < 0.0001$) was significant, while the remaining nine
comparisons were non-significant ($0.00 < t < 1.17$, $942 <$
 $DF < 12053$, $0.120 < p < 0.499$, median p-value = 0.294).
90 Therefore, the exclusion of locality and year from the mod-
els testing the association between the body condition of
birds and feather mite abundance is unlikely to influence the
estimation of the slope of body condition regressed against
feather mite abundance.

Therefore, we calculated the slope of the effect of
95 feather mite abundance in the models with body mass as
the response variable and season as a covariate. As the value
of the slope depends on the value of body mass, and there is
a 21-fold variation in body mass across the 83 species of
birds considered here (from 5.6 to 117.8 g), we transformed
100 the effect size t to the Pearson r as

$$r = \sqrt{\frac{t^2}{t^2 + DF}}$$

105 where DF is the number of degrees of freedom of
the model's error (Rosenthal 1984). We used r as an index
of the magnitude of the correlation between feather mite
abundance and the body condition of birds in our com-
parisons between species. We also calculated the magnitude
110 of the partial, pure effect of feather mite abundance by
running the same models after excluding feather mite abun-
dance, and then regressing the residuals of these models
against feather mite abundance. The percentage of vari-
ance in the residuals explained by feather mite abundance
115 was considered as the magnitude of the pure effect of that
variable. Using the software Meta-Analysis 5.3 (available
at http://userpage.fu-berlin.de/~health/meta_e.htm), we
calculated an overall effect size and p-value for the relation-
ship between body condition and feather mite abundance by
121 a meta-analysis.

0 Results

A total of 27 out of the 83 bird species (33%) showed a statistically significant slope of the regression between body condition and feather mite abundance, and only three out of the 27 significant slopes were negative (Supplementary material Appendix 1; greenfinch, European serin *Serinus serinus* and common blackbird *Turdus merula*). The overall p-value associated with the effect size for this relationship calculated from a meta-analysis was highly statistically significant ($p < 0.0001$). All slopes, represented by the effect size (r-value), ranged from -0.27 to $+0.81$, although 53% of the species had slopes very close to 0, ranging between -0.15 and $+0.15$ (Fig. 2a). Both positive and negative slopes were found in all bird families for which we had information on more than one species, with the exceptions of Muscicapidae (two species), Paridae (four species), Prunellidae (two species) and Sturnidae (two species) (Supplementary material Appendix 1), thus suggesting that the phylogenetic signal in the effect of feather mites on the body condition of birds might be low. The mean magnitude of the slope was negatively correlated with sample size (Pearson $r = -0.29$, $n = 83$, $p = 0.008$; Fig. 3a), and it was more variable in species with smaller sample

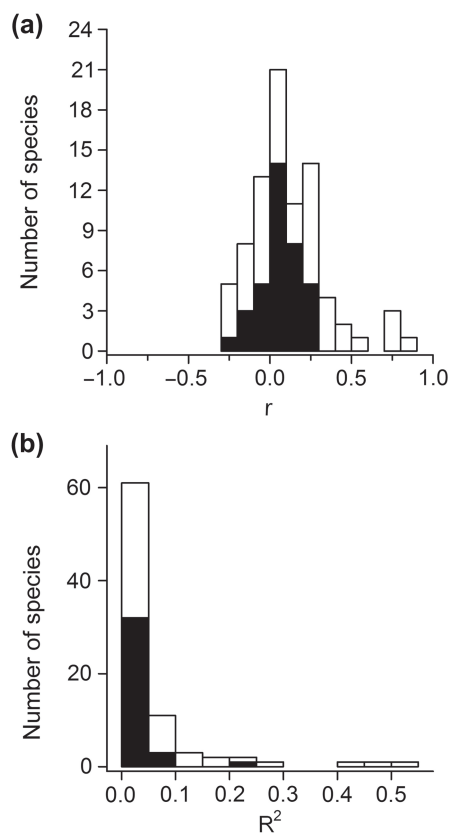


Figure 2. Histograms showing the distribution of Pearson r-values (a); i.e. effect size of the slope of the regression between host body condition and feather mite abundance) and R^2 (b); i.e. pure effect of feather mite abundance on host body condition after controlling for effect of season) in 83 species of birds. Black bars represent counts for the best sampled species (i.e. those with $n > 100$ birds).

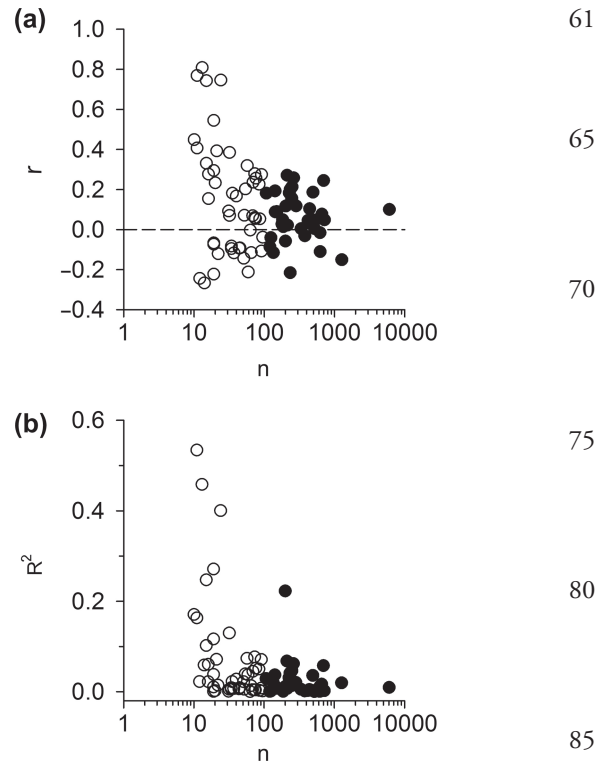


Figure 3. Relationship between number of individual birds sampled per species and Pearson r-values (a); i.e. effect size of the slope of the regression between host body condition and feather mite abundance) and R^2 (b); i.e. pure effect of feather mite abundance on host body condition after controlling for effect of season) in 83 species of birds. The best sampled species (i.e. those with $n > 100$ birds) are represented by black solid dots.

sizes ($F_{40,41} = 5.43$, $p < 0.0001$). Note, however, that this negative correlation indicates that the larger the sample size the weaker the correlation between body condition and feather mite abundance. In fact, we also found a negative correlation between sample size and the absolute value of the slope ($r = -0.51$, $n = 83$, $p < 0.0001$). Indeed, a majority (53%) of the best sampled species (those with $n > 100$ birds) had r-values between -0.09 and $+0.09$, and thus slope estimates were close to 0 in the majority of species (Fig. 2a). A total of 57 out of the 83 species considered (68.7%) had positive slopes (Supplementary material Appendix 1), indicating that the relationship between host body condition and feather mite abundance was mainly positive, although the magnitude of the effect was weak as reflected by the low overall effect size calculated from a meta-analysis ($r = 0.066$; Fig. 2).

The partial, pure effect of feather mite abundance on body condition of the bird hosts was small, as the percentage of variance explained in body condition was $< 10\%$ in 86.7% of all species and in 97.2% of species with sample size above 100 birds (Fig. 2b). Furthermore, the pure effect of feather mite abundance was negatively correlated with the number of individuals sampled per species ($r = -0.41$, $n = 83$, $p < 0.001$; Fig. 3b), suggesting that the few high R^2 -values obtained were the result of small sample sizes leading to spurious high R^2 -values.

0 Discussion

The nature of the ecological interaction between feather mites and birds is still controversial after several correlational studies (Blanco et al. 1997, 1999, Thompson et al. 1997, Harper 1999, Jovani and Blanco 2000, Blanco and Frías 2001, Dowling et al. 2001, Pérez-Tris et al. 2002, Brown et al. 2006, Galván and Sanz 2006, Campos et al. 2011) and experimental manipulations of feather mite abundance (Figuerola et al. 2003, Pap et al. 2005). These studies were, however, based on single species of birds and relative small sample sizes. Our results, based on a dataset comprising >20 000 measurements of feather mite abundance in 83 species of birds, shed new light on this question. We report that the association between feather mite abundance and the body condition of their hosts is weak, as the slope of the regression between body condition and feather mite abundance was very close to zero in most species, and the overall slope calculated from a meta-analysis was very small ($r = 0.066$). The pure effect exerted by feather mite abundance on host body condition was also small, and the variance in body condition explained by feather mite abundance was <10% in most species. Therefore, our results indicate that feather mites are probably not parasites of birds, as in such a case a negative relationship between feather mite abundance and host body condition would be expected (Møller 1997, Møller et al. 1998). Our results suggest, in contrast, that the symbiotic relationship between feather mites and birds is better defined as commensal, as some authors had previously suggested (Blanco et al. 1999, Dowling et al. 2001, Pap et al. 2005, 2010), because the body condition of birds does not seem to be affected by the presence of feather mites on their feathers.

Commensalism is probably common among animals, but the existence of this kind of interaction is difficult to demonstrate because significant effects on hosts are always easier to detect than their absence (Dickman 1992, Leung and Poulin 2008). Our large dataset allows us to suggest that the interaction between feather mites and birds probably represents commensalism. Feather mites would benefit by feeding on wax secreted by the uropygial gland of birds (Blanco et al. 2001, Proctor 2003, Galván and Sanz 2006, Galván et al. 2008, Haribal et al. 2011; but see Pap et al. 2010) while the latter would be not affected by feather mites, thus constituting one of the few examples of commensalism among animals in the field (Dickman 1992, Casadevall and Pirofski 2000). This, however, must still be taken with caution until further experimental studies on the abundance of feather mites on birds are conducted. Although the magnitude of the association between feather mite abundance and host body condition was weak, the sign of the effect was positive in the majority of host species. This suggests that, although detrimental effects of feather mites on their hosts can be discarded at least as a general trend among birds, it is still possible that feather mites provide some benefits to some of their bird hosts. Furthermore, it should be considered that ecologists rarely can explain >5–10% of the variance in the studied variables (Møller and Jennions 2002), so it is possible that we are undervaluing the magnitude of the effect caused by feather mites on their hosts. However, although it is possible

that feather mites benefit some of their bird hosts by removing old waxes and debris contained therein and associated micro-organisms from feathers (Galván et al. 2008), especially in birds that present some diseases that limit their ability for preening (Blanco et al. 2001), our large sample size allows us to state that the effect caused by feather mites on their hosts is, in general among species of birds, closer to be neutral than to be positive, given the low overall effect size calculated for all species of birds considered here (see above).

An alternative explanation for our results may be that feather mites are parasites but that birds have evolved tolerance mechanisms (Svensson and Råberg 2010) compensating for any damage caused by feather mites, which is probably the outcome when the parasite growth rate in natural conditions can be completely tolerated by the host (Miller et al. 2006). However, this possibility is not likely either. It is unlikely that we have not been able to include a great variability in tolerance to feather mites among the 83 species of birds included in our study comprising >20 000 observations and thus detect a significant proportion of hosts being negatively affected by feather mites (only a small proportion of species had negative correlations between host condition and mite load). Therefore, if feather mites were initially parasites, almost all species of hosts considered here have evolved tolerance mechanisms so that the initial parasitism has evolved into commensalism (Miller et al. 2006). However, our study only included passerine birds so more studies on other groups of birds are necessary to generalize our conclusions to the entire avian class. We should not discard the possibility that bird species differ in the magnitude by which they are affected by feather mites, as phylogenetic, physiological and ecological characteristics may make some species particularly susceptible to the effects of feather mites; however, no convincing hypothesis has been so far posed to explain how feather mites can seriously harm their hosts (reviewed by Blanco et al. 2001).

Given the correlational nature of our study, we are unable to establish a cause-effect relationship. Our starting hypothesis posits that parasites negatively affect the body condition of their hosts as measured by size-corrected weight. However, we should not discard the possibility that feather mites could be affected by the body condition of their hosts, as has been previously observed in some parasites (Tschirren et al. 2007) and even in feather mites at the intraspecific level (Blanco and Frías 2001, Pap et al. 2005). Thus, the overall positive correlation between feather mite abundance and host body condition we have reported here can also be explained by birds in better condition producing a greater amount (or higher quality) of waxes from the uropygial gland (Galván and Sanz 2006), leading to an increase in feather mite abundance as these organisms would be better fed. Future experimental studies should disentangle the causation of the relationship between feather mite abundance and host body condition. Additionally, future studies should consider the diversity of feather mites that can be found on birds' feathers (Proctor 2003). While we are dealing with the abundance of all feather mites observed on the remiges of birds (which in passerines are principally members of the families Trouessartiidae and Proctophylloidae), it is

- 0 possible that effects on host body condition are differentially
exerted by different species of feather mites.
- In conclusion, we have found that feather mites apparently exert weak and mostly positive effects on the body condition of their bird hosts, discarding the view of these
5 organisms as parasites at least as a general rule among passerine birds and supporting the interesting possibility that commensalism or mutualism exists between feather mites and birds. These results should be complemented with future studies that experimentally manipulate feather mite loads and consider the entire diversity of feather mites, which will surely expand our knowledge on the commonest ecological interactions between birds and mites.
- 10
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