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Research article

Idiosyncrasy of feather mite intensity and prevalence across passerine bird species: a comparative study

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Symbionts are key elements of ecosystems, by playing important roles in shaping the biology and ecology of their hosts. However, the factors determining symbiont loads across host species are still unclear. Nowadays, we know that the intensity and prevalence of feather mites, the most diverse group of avian ectosymbionts, differ strongly

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between species. To understand those differences, we studied 17 bird species traits and two feather mite community features (species richness and composition in bird species) potentially related to interspecific differences in feather mite intensity and prevalence across bird species. We analyzed a large dataset of feather mite occurrence across European passerines: for feather mite intensity a sample of 27 424 birds from 119 bird species, and 1 805 566 feather mites counted, and for prevalence a sample of 76 126 birds from 122 bird species. Feather mite intensity and prevalence covaried positively across bird species, reinforcing the previous observation that species differ in feather mite load. Comparative analyses of the association of bird traits and feather mite richness with feather mite intensity or prevalence showed a moderate explanatory power, high model selection uncertainty, inconsistent results for both prevalence and intensity data, and contrasting results with previous comparative studies on feather mite occurrence. Furthermore, even though closely related bird species had similar feather mite communities, there was a low evolutionary conservatism of both the prevalence and intensity of feather mites across bird species (i.e. low phylogenetic signal). Finally, feather mite community composition did not explain feather mite intensity or prevalence across bird species. Overall, our large number of host and mite traits failed to satisfactorily explain the high variability in feather mite occurrence across bird species. We discuss that this difficult-to-understand apparent idiosyncrasy of bird species in their feather mite intensity and prevalence may be the outcome of the interaction between host and symbiont traits.

Keywords: Akaike, Astigmata, data imputation, feather mites, Mantel test, phylogenetic signal

Introduction

Identifying the factors that influence the abundance of organisms is a key question in ecology. Most studies on abundance have focused on free-living organisms (Dobson et al. 2008), while symbiont abundance has received little attention despite symbionts (organisms in close and persistent associations with hosts, Matthews et al. 2023) being the most abundant and species-rich organisms on Earth, and having important roles in ecosystems (Rocha et al. 2016, Larsen et al. 2017). The study of symbiont abundance has traditionally focused on parasites, for example to understand their harmful effects on host individuals and populations, and the ecological and evolutionary consequences of parasitism on host species (Blanco et al. 1999). Moreover, most research on symbiont abundance has been devoted to understanding the causes of its variation among individual hosts of a given species, while the reasons why some host species have more symbionts than others have been poorly explored. This is particularly true for non-parasitic symbionts, such as commensals or mutualists (Mestre et al. 2014). Here we aim to contribute to fill this gap by investigating why bird species differ so much in feather mite occurrence.

Vane-dwelling feather mites (Acariformes: Analgoidea and Pterolichoidea) are a group of taxonomically diverse ectosymbionts of birds present in all avian orders (Gaud and Atyeo 1996, Mironov 1997, Proctor and Owens 2000, Proctor 2003, Mironov and Proctor 2008, Dabert et al. 2015). They live permanently on their hosts, where they concentrate on specific feathers or feather portions that differ among bird species (Choe and Kim 1989, Jovani and Serrano 2004, Jovani et al. 2006, Mestre et al. 2011, Fernández-González et al. 2015, Labrador et al. 2022). They feed on organic matter from the surface of feathers such as bacteria or fungi and possibly preen gland secretions (Dubinin 1951, O'Connor 1982, Gaud and Atyeo 1996, Blanco et al. 2001, Proctor 2003, Walter and Proctor 2013, Doña et al. 2019a). Not only this feeding activity, but also ovoposition occur

during the night in feather mites living on European passerines (Labrador et al. 2022). Feather mites are thought to arrive to birds mainly by direct contact between individuals (Dabert and Mironov 1999, Proctor 2003, Doña et al. 2017a, b). They are dispersal-limited organisms that present different degrees of host specificity, being host-switching an important phenomenon to understand their evolution (Doña et al. 2018, 2019b, Stefan et al. 2018, Mironov and Galloway 2021, Matthews et al. 2023). Despite being abundant and widespread among birds, many questions about the ecology and biology of these symbionts remain unknown (Proctor and Owens 2000, Proctor 2003, Stefan 2016). For example, there is still no consensus on the nature of the relationship between mites and their avian hosts, although most evidence points to a commensalistic or even mutualistic interaction (Blanco et al. 2001, Galván et al. 2012a, b, Doña et al. 2019a, but see Thompson et al. 1997, Figuerola et al. 2003).

Previous studies have investigated the association between particular host species traits and the differences in feather mite presence and numbers among bird species. For instance, Rózsa (1997) and Galván et al. (2008) found that larger bird species, as well as those with a larger preen gland during the breeding season, hold higher feather mite abundance (sensu Bush et al. 1997). Furthermore, according to Poulin (1991) and Figuerola (2000), bird species that are social in winter and those with sexual dichromatism show higher feather mite prevalence (proportion of birds with feather mites; sensu Bush et al. 1997). It has also been showed that feather mite prevalence and intensity (number of feather mites carried by birds with at least one feather mite; sensu Bush et al. 1997) are bird-species characteristics, and interspecific differences hold when studying the same species in different habitats, despite intraspecific variance and environmental factors (Dowling et al. 2001, Díaz-Real et al. 2014, Meléndez et al. 2014). Recently, using the metabolic theory of ecology it has been found that feather mite populations are constrained by host space (number of feather barbs) and not energy/resources available on their hosts, although there exists a large variance

in feather mite intensity among bird species of a given body size (Labrador et al. 2024a). Despite these previous works, we still have a poor understanding of why prevalence and intensity of feather mites differ so widely between bird species.

To answer this fundamental question in feather mite ecology we analyzed here a large dataset compiled in Díaz-Real et al. (2014) to uncover bird and feather mite features that could account for the large variation in feather mite intensity and prevalence among bird species. Our first goal was to explore the consistency of differences in feather mite intensity and prevalence across bird species, testing the covariation between both variables. Second, we aimed to understand which bird traits (and one trait of the feather mite community) may underlie these differences among bird species. To do so, we used phylogenetic generalized least squares (PGLS) analyses to test the association between 17 bird traits (as well as feather mite species richness) with feather mite intensity or prevalence. Among the 17 traits (and six interactions between variables) tested, seven variables and two interactions had been considered in previous studies on the topic (Poulin 1991, Figuerola 2000, Galván et al. 2008). These tested hypotheses included bird traits related to aerodynamic stress (three traits), likelihood of feather mite transmission (five), habitat (two), spatial and food resources for feather mites (two), and six other traits (see Table 1 for a detailed explanation of the hypothesis behind each trait). A third goal of this study was to understand the contribution of bird phylogeny on feather mite intensity and prevalence (estimating the phylogenetic signal of both variables) and on feather mite community composition (using Mantel tests). Finally, we aimed to understand whether feather mite community composition is responsible for the prevalence or intensity patterns across bird species.

Material and methods

Feather mite data

Feather mite data were obtained from 'FeatherMites', the largest dataset on feather mite intensity and prevalence from wild European passerine birds (see Díaz-Real et al. 2014 for details), which contains data collected by 89 observers. One wing of each bird was exposed to sunlight and the number of feather mites was counted on 19 flight feathers (10 primaries, six secondaries, and three tertials). In 853 birds, though, intensity was extrapolated from the number of mites counted on primaries (see Díaz-Real et al. 2014 for details). Overall, data from 27 424 birds of 119 species (belonging to 57 genera and 28 families) with at least one feather mite counted were used to study feather mite intensity (number of birds per species: mean = 230, range = 1–4283; mites counted: 1 805 566). For each bird species, we calculated the median number of feather mites as a robust measure of central tendency in feather mite intensity, given the highly right-skewed distribution of this variable within the bird species studied here (Díaz-Real et al. 2014). Feather mite intensity and some

bird traits (asterisks in Table 1) were $\log_{10}$ transformed to meet normality model assumptions. Prevalence (presence or absence) of feather mites was obtained screening the same 19 wing feathers as for intensity for a total of 76 126 individuals of 122 species belonging to 58 genera and 28 families (mean = 623 individuals per bird species, range = 1–8482). Note that this large prevalence dataset was obtained by adding of 48 702 bird individuals to the 27 424 birds sampled for intensity. For some analyses, only bird species with $n \geq 30$ individuals were included (Table 3). For prevalence analyses this led to 95 species.

For some bird species, feather mite intensities are known to peak in winter until the beginning of the birds' reproductive season in the study areas (Blanco et al. 1997, Pap et al. 2010, Peet et al. 2022), before they are transmitted from parents to offspring in the nest. This increase in mite numbers during the winter is likely explained by the fact that the wetter weather of this season in Europe is more favorable for mites (McClure 1989, Wiles et al. 2000). In addition, mite populations have had several months to grow since the last events of vertical transmission of the previous year. Due to this seasonality in mite numbers, we repeated the analyses only considering birds captured from October to March (both months included, hereafter referred as 'winter'), given that not all species (e.g. migratory species) could be sampled during winter, and even for resident species different proportions of birds were sampled in winter. This subset of 'winter' records contained 8359 bird individuals of 85 species (mean = 70, range = 1–1296; 39; 741 004 feather mites counted; species with $n \geq 30$) for intensity, and 22 967 birds of 95 species (mean = 188, range = 1–4887; 53 species with $n \geq 30$) for prevalence analyses.

Feather mite richness recorded in each bird species was obtained from a review of the taxonomic literature reporting bird-mite associations (Doña et al. 2016). Only bird-mite associations that are probable and not the result of misidentifications or sample contamination (i.e. those coded with a score of 2 in Doña et al. 2016) from birds sampled in Europe and Africa were considered.

Bird traits

We used 17 bird traits (Table 1, Supporting information). Bird body size was not considered as it was highly correlated with other traits included in the analyses (Labrador et al. 2024a). This allowed us to analyze other features related to bird size, such as the number of barbs, which was hypothesized to be more intimately related to feather mite intensity and prevalence. Categorical variables were included as factors in the models.

Some of the bird traits tested here may seem at first glance relevant only to either feather mite prevalence or intensity. For instance, bird traits associated with the transmission of feather mites (e.g. winter bird sociality) are straightforward to relate to prevalence, given that the arrival of mites on a bird is a sine qua non condition for the bird to harbor a population of feather mites. On the other hand, bird traits related to

Table 1. Description of the studied variables (grouped in five categories) and the reasoning underlying their hypothesized effect. The data sources (Ref.) are also shown. * indicates variables $\log_{10}$ transformed in the analyses. All hypotheses apply for prevalence and intensity. Feather mite occurrence is used in this table to include prevalence and intensity.

Category/variable	Description	Hypothesis	Ref.
Aerodynamic stress			
Flight (aerial displays and foraging flights)	Presence of aerial movements to forage and/or for courtship displays. 0) no aerial movements, 1) aerial foraging or display, 2) aerial foraging and display	These types of flight (often implying fast movements) would increase stress for mites, and thus lower their occurrence	1–4
Migration	Presence (1) or absence (0) of migratory displacements	Migratory displacements generate stress to the mites, and lower mite occurrences are expected (but see Blanco and Frías 2001)	5
Wing loading*	Bird body mass divided by wing area	High wing loading implies more stress for mites and lower mite occurrences are expected	6
Transmission			
Annual fecundity*	Clutch size multiplied by maximum number of clutches per season	The higher the annual fecundity, the lower the number of mites expected per bird because of a dilution effect during vertical transmission	1, 7–8
Feathers in nest	Use (1) or not (0) of feathers to build the nest	Using feathers (especially from dead birds) to build the nest would favor mite transmission, increasing feather mite occurrence	1, 2, 9
Mating system	Mating patterns within a species. 1) monogamy (<5% polygyny), 2) mostly monogamy but occasional polygyny (5–15% polygyny), 3) mostly polygyny (>15% polygyny), lek, promiscuous, or cooperative breeding	More complex bird mating systems (e.g. cooperative breeding versus monogamy) are expected to enhance mite transmission, and thus, higher mite occurrence	1, 2, 10–16
Nest type	Type of nest according to the exposure of its content. 0) open nest, 1) closed or covered nest	Closed nests would create more protected or wetter environments during mite transmission, thus higher mite occurrences are expected	1, 9, 17, 18
Winter sociality	Formation of interspecific groupings during the wintering season. 0) solitary species, 1) gregarious species	Flocking is known to increase feather mite transmission by enhancing bird-bird contact, so mite occurrence should increase with sociality	1, 2, 15, 19, 20
Habitat			
Habitat	Type of habitat occupied out of the wintering season. 1) open habitat, 2) riparian, groves, wetlands, 3) open woodlands, 4) forest	Dry habitats and a high sun exposure are bad for mites' water balance. Moreover, habitat is correlated with the abundance of bacteria and fungi on feathers, which are food resources for mites. Therefore, wet and closed habitats are expected to favor a higher feather mite occurrence	1, 2, 20
Wintering habitat	Type of habitat occupied during the wintering season. 1) woodland, forest, or wooded savannah, 2) farmland and grassland, dry savannah, or other dry open habitats, 3) wetlands and inland waters		1, 2, 16, 20, 21
Spatial and food resources			
No. barbs*	Total number of barbs of the primary feathers	Most feather mites studied live between the barbs of wing feathers. Mite occurrence is expected to increase with the number of barbs	22 (Sup. Information)
Uropygial gland size*	Volume of the preen gland	It is suggested that feather mites feed on preen gland secretions. The larger the glands, the higher the mite occurrence expected	15, 23
Others			
Diet	Type of food resources consumed. 1) vegetarian 2) carnivore/insectivore	Bird diet could affect preen gland secretion composition and thus, mite intensity and prevalence (but with no specific prediction about which diet would lead to a higher feather mite occurrence)	1, 2, 24

(Continued)

Table 1. (Continued)

Category/variable	Description	Hypothesis	Ref.
Maximum lifespan	Maximum longevity registered in wild individuals (raw uncorrected data)	Species with greater longevity are expected to have higher mite occurrences by providing a more durable environment to be colonized and for populations to grow	25–31
Molts per year (juveniles)	Number of complete annual molts in juveniles	In spite of feather mites seeming to escape from bird molt, molt might affect feather mite performance by reducing the number of feathers (space) available, or the number of feathers with food (old ones). Then, the higher the number of molts per year, the smaller the expected occurrence of mites	1, 18, 32–35
Population size*	Global bird population size	Larger bird population sizes may favor a higher genetic diversity of mites or more generalist mites, and thus, higher feather mite occurrences. Also larger populations may lead to higher intraspecific transmission	36
Sexual dichromatism	Existence (1) or not (0) of plumage color differences between sexes	Sexually dichromatic species should not have more mites as they seem not to be parasites	21, 23, 37
Feather mite species richness*	Number of mite species found in a bird species	Higher mite richness may lead to higher occurrences because of niche partitioning	38

Reference numbers: 1) Cramp and Simmons 1994, 2) del Hoyo et al. 2013, 3) Møller 2009, 4) Møller et al. 2009, 5) Birdlife International 2021, 6) Nudds et al. 2007, 7) Møller et al. 2010, 8) Galván et al. 2012a, b, 9) Harrison 1991, 10) Goymann and Wingfield 2014, 11) Leisler et al. 2002, 12) Møller 1998, 13) Pitcher et al. 2005, 14) Scriba and Goymann 2010, 15) Vincze et al. 2013, 16) David Serrano unpubl. 17) Wikipedia, 18) Carrascal and Salvador 2002, 19) Figuerola et al. 2008, 20) Moreno and Soler 2011, 21) Møller et al. 2008, 22) Labrador et al. 2024a, 23) Galván et al. 2008, 24) Sibly et al. 2012, 25) de Magalhaes and Costa 2009, 26) Borrás et al. 2012, 27) Valcu et al. 2014, 28) Hernández 1999, 29) Laiolo et al. 2008, 30) Aparicio 2015, 31) Fransson et al. 2010, 32) Demongin 2016, 33) Svensson et al. 2015, 34) Shirihaai and Svensson 2018a, 35) Shirihaai and Svensson 2018b, 36) Callaghan et al. 2021, 37) Møller et al. 2011, 38) Doña et al. 2016. See further details about each variable in the Supporting information.

space or energy resources used by mites, such as the number of barbs in feathers and the uropygial gland size (Galván et al. 2008, Labrador et al. 2022) are, however, easier to link to mite intensity. Despite this, we used all bird traits as potential drivers of both prevalence and intensity for two reasons. First, bird traits may shape both variables simultaneously. For example, features negatively influencing feather mite fitness (e.g. bird migration) are expected to cause low feather mite prevalence and intensity. Second, some bird traits may directly influence either intensity or prevalence, but affect the other variable indirectly. For instance, all else being equal, traits favoring high feather mite intensities in a bird species may lead to a higher prevalence indirectly, given that more mites can be transmitted and eventually reach a bird without mites. In the same way, fewer birds would be expected to lose their mite populations because higher intensities may preclude stochastic population extinction (Huang et al. 2015). In summary, we hypothesized that the analyzed bird variables may potentially have the same consequences for both feather mite prevalence and intensity.

Bird phylogeny

We used the latest and most complete bird phylogeny available to control for non-independence of data due to the shared ancestry of species. We downloaded 1000 trees using the Hackett et al. (2008) backbone tree (only sequenced

species) from BirdTree (Jetz et al. 2012, <http://birdtree.org>). Then, we summarized the sample of trees building a single maximum clade credibility tree using the *maxCladeCred* function from the ‘phangorn’ R package (www.r-project.org, Schliep 2011). Finally, we pruned this tree according to the species included in each specific analysis.

Data imputation

Only species with data for all traits can be used to build alternative and comparable multiple regression models. This demand for a complete dataset leads to the exclusion of several species from the analyses, which increases the likelihood of biasing parameter estimates and reducing statistical power (Nakagawa and Freckleton 2008, 2011). An appropriate approach to deal with missing data is to impute them into the dataset where data were originally not available. We followed a three-step approach to decide which variables could be imputed. First, we evaluated the suitability for imputation of the five continuous variables with missing values for some bird species (annual fecundity, barb amount, maximum lifespan, uropygial gland size and wing loading). For this purpose, we used the function *phylo.d* in the ‘caper’ (Orme et al. 2013) R package to investigate whether or not the missing values of the five traits were spread across the phylogeny. This function computes the D parameter (Supporting information), which allows to identify if the distribution of

Table 2. Multivariable PGLS regression models aimed to explain feather mite intensity and prevalence across passerine bird species. Each group of models refers to a dependent variable and a period constraint (i.e. 'all year' or 'winter'). Only the models within two AICc points from the highest AICc ranked model are shown. A circle indicates the presence of a variable in a model, circle color denotes whether the variable was informative (black) or not (grey). For informative variables, circle background indicates whether the estimate of the variable supported our predictions (grey) or not (white). A particular case of black circles with white background is the variable Diet (for which we had no clear hypothesis on the direction of its effect), and Flight in the dataset 'Prevalence all year' (given that the interaction between Flight and Migratory was included in the model). Variables are grouped as in Table 1. Sample size is indicated in each model (for prevalence in winter: n bird species = 79 and n bird individuals = 21 938).

Aerodynamic stress										Transmission			Habitat		Food Resources		Others			Interactions					
Dataset	Flight (FI)	Migratory (MI)	Wing Loading (WL)	Annual Fecundity (AF)	Feathers in Nest	Mating System	Nest Type	Winter Sociality	Habitat (Ha)	Winter Habitat (WH)	Barb Amount	Uropygial Gland Size (UGS)	Diet	Maximum Lifespan	Molts per Year	Population Size	Sexual Dichromatism	Feather mite Richness	FI*WL	MI*Ha	MI*FI	MI*UGS	MI*WH	MI*WL	
Intensity all year N=96 bird species N=25,933 bird individuals N=60,217 mites	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●						
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Intensity winter N=71 bird species N=7,878 bird individuals N=41,584 mites	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●						
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Prevalence all year N=96 bird species N=22,621 bird individuals	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●						
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Prevalence winter	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●						
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Table 3. Phylogenetic signal of feather mite intensity and prevalence calculated with different sample size (n) and study period constraints. n constraint indicates the minimum number of individuals required for a species to be included in the analysis. no. species is the number of bird species satisfying that constraint. p-values < 0.05 are shown in bold.

Variable	Period	n constraint	no. species	λ , p-value	K, p-value
Intensity	All year	n > 0	119	0, 1	0.210, 0.406
		n > 30	59	0, 1	0.200, 0.687
	Winter	n > 0	85	0, 1	0.208, 0.718
		n > 30	39	0, 1	0.386, 0.632
Prevalence	All year	n > 0	122	0.294, 0.005	0.053, 0.894
		n > 30	94	0.385, 0.004	0.213, 0.388
	Winter	n > 0	95	0.203, 0.110	0.265, 0.275
		n > 30	52	0.426, 0.045	0.251, 0.556

the missing values was random with respect to the phylogeny ($D=1$), more overdispersed than the random expectation ($D > 1$), or distributed as expected under Brownian motion ($D=0$). Missing data evenly distributed throughout the phylogeny can be more easily estimated if information on the phylogenetic relatedness of species is included in the approach. Second, by using the function *phylosig* in the 'phytools' R package (Revell 2012), we estimated the phylogenetic signal of the traits (Supporting information). A high phylogenetic signal improves the imputation accuracy (Fisher et al. 2003, Cardillo et al. 2008, Guénard et al. 2013, Swenson 2014). Third, we evaluated the performance of the imputation approach for the five variables to decide the traits in which the estimation would finally be undertaken. To do this, we randomly deleted 40% of the values of each variable and estimated these values with the *phylopars* function in the 'Rphylopars' package (Goolsby et al. 2017). We repeated this imputation process 50 times and calculated the mean of the estimated values for each variable and species. Next, we compared the original values with the imputed ones with the *cor.test* function in the 'stats' R package (www.r-project.org), to check imputation accuracy (Supporting information). After the three steps, we decided to impute missing values for four out of the five continuous bird traits: annual fecundity (values imputed for two species), number of barbs (78 species), preen gland size (32 species), and wing loading (49 species). Maximum lifespan was not suitable for data imputation. Final sample sizes (number of species) used in each PGLS are shown in Table 2. In addition, analyses that did not allow weighting by species sample size (below) were repeated considering only species with at least 30 sampled individuals (an arbitrary limit), in order to strongly reduce uncertainty in parameter estimates (Jovani and Tella 2006, Table 3, 4).

Statistical analyses

To study the covariation between feather mite intensity and prevalence, we performed phylogenetic generalized least squares (PGLS, Martins and Hansen 1997) regressions using the *gls* function in the R package 'nlme' (Pinheiro et al. 2022). We calculated the Pagel's λ parameter by a maximum-likelihood estimation (Freckleton et al. 2002).

We also used PGLS regressions to further explore the association of bird traits and feather mite richness (Table 1) with

feather mite intensity and prevalence across bird species. We used the *dredge* function in the 'MuMIn' R package (Barton 2022) to build models with all possible combinations of variables, but we limited to six the number of variables included simultaneously in a model to avoid overfitting. This was decided after running simulations where the presence of more than six independent variables made some simulated models to spuriously lead to $R^2 > 0.2$. Among the candidate models, we also included the null model, i.e. without any explanatory variable. Phylogenetic linear models were weighted by the sample size ($\log_{10}$ transformed number of individuals) of each bird species to control for the sampling effort, as there is higher uncertainty in data coming from smaller sample sizes. Pagel's λ of the models were initially optimized towards its maximum likelihood value. However, in all four cases, estimated λ values were outside the 0–1 range, and the inspection of the plots of the likelihood profile (Supporting information) strongly suggested to fix λ at 0 (Garamszegi and Mundry 2014). Thus, multivariable (and null) models for feather mite prevalence and intensity were run by setting $\lambda=0$.

To rank our candidate (including null) models according to the balance between goodness-of-fit and number of estimated parameters, we used the Akaike's information criterion corrected for small sample sizes (AICc) and selected the models

Table 4. Spearman's rank correlation coefficients (r) between the distance in feather mite communities of pairs of bird species and their differences in feather mite intensity or prevalence. A statistically significant correlation means that bird species with more similar feather mite communities have more similar feather mite intensity or prevalence values. n constraint indicates the minimum number of individuals required for a species to be included in the analysis. no. species is the number of bird species analysed (i.e. satisfying the constraint).

Variable	Period	n constraint	no. species	r, p-value
Intensity	All year	n > 0	104	−0.006, 0.595
		n > 30	54	0.003, 0.437
	Winter	n > 0	75	0.027, 0.156
		n > 30	34	−0.040, 0.791
Prevalence	All year	n > 0	104	−0.006, 0.602
		n > 30	83	−0.003, 0.536
	Winter	n > 0	83	−0.012, 0.696
		n > 30	46	0.004, 0.465

with the lowest score. Models whose AICc values differed from the best ranked model by less than two units were considered as equivalent (Burnham and Anderson 2002, Arnold 2010, Symonds and Moussalli 2011). Best models ranked according to AICc scores may contain uninformative variables (Arnold 2010). Their inclusion in the models does not improve them, and increases the type I error (Anderson et al. 2001, Leroux 2019). Then, they would be ignored in the discussion of the models (Table 2). To detect uninformative variables in the models, we employed the function *intervals* of the 'nlme' R package (www.r-project.org) in order to obtain the 85% confidence interval of the partial regression coefficients (following Arnold 2010). Variables were considered as uninformative in a given model when the estimated confidence interval overlapped zero. Cumulative weights were used to estimate the relative importance of each predictor variable in explaining feather mite prevalence or intensity. These were calculated by summing Akaike model weights across all models that included that variable as informative (again, ignoring uninformative variables).

Finally, apart from evaluating the goodness-of-fit of the models in explaining feather mite intensity and prevalence, the present study also aimed at exploring the power of the combination of bird traits and feather mite species richness to explain feather mite intensity and prevalence. Thus, to complement the multi-model inference approach, we calculated the variance explained by the top-ranked model (the one with lowest AICc value) of each dataset, but only including those variables that met the 85% CI criterion described above. Due to the inclusion of weights in our models, R^2 was unspecified. Thus, we roughly estimated R^2 as

$$1 - \left(\frac{\text{Sum of squares of the residuals of the multivariable model}}{\text{Sum of squares of the null model}} \right)$$

where both models used the same lambda value.

Phylogenetic signal (Blomberg's K and Pagel's λ) of feather mite intensity and prevalence, that represents how both variables are spread along the bird phylogeny, was calculated with the *phylosig* function of the 'phytools' R package (Revell 2012).

Mantel tests were used to evaluate the effect of feather mite community composition on the intensity and prevalence of mites and to study the effect of bird phylogeny on feather mite community composition. To determine whether bird species with more similar feather mite communities also had more similar intensity or prevalence, we studied the correlation between the feather mite community Jaccard distance matrix (built with the *dist.binary* function of the 'ade4' package, Dray and Dufour 2007) and the intensity or prevalence distance matrix (built with the *dist* function of the 'stats' R package, www.r-project.org). To test whether phylogenetically close bird species harbored similar feather mite species, we compared the mite community distance matrix with a phylogenetic distance matrix (latter built with the *cophenetic.phylo* function of the 'ape' package, Paradis and

Schliep 2019). Mantel tests were performed using 1000 permutations with the *mantel* function of the 'vegan' package (Oksanen et al. 2020).

Results

Feather mite intensity and prevalence covaried across bird species (PGLS $t_{117} = 8.424$, slope = 0.889, $p < 0.001$, $\lambda = 0.059$, Fig. 1). Results were similar when only birds sampled in winter were considered (PGLS $t_{83} = 8.261$, slope = 0.974, $p < 0.001$, $\lambda = 0$, Supporting information).

When we fitted candidate regression models of bird traits on mite intensity and prevalence, we found several top-ranked PGLS models that showed very low and similar Akaike weights (Table 2). Values of pseudo- R^2 were moderate (intensity all year dataset: 0.101, intensity winter: 0.199, prevalence all year: 0.141, prevalence winter: 0.189). Models using different datasets and filtering (intensity/prevalence, 'all year' data/'winter' data) revealed contrasting results in terms of which traits were informative (see the black circles in Table 2). Less than half of the informative variables showed estimate values in the direction of our predictions (see the gray background in Table 2, see Table 1 for predictions).

The cumulative model weight of a given predictor across models was inconsistent when comparing values for prevalence with those for intensity models, but also when comparing across different sampling periods ('all year' or 'winter', Fig. 2). However, some patterns proved consistent. For instance, wing loading was among the variables with the highest cumulative Akaike weight (Fig. 2) for both intensity and prevalence models and in both sampling periods, showing a positive correlation with feather mite intensity and prevalence for the top-ranked models (Table 2), contrary to our prediction (Table 1). Bird species population size or

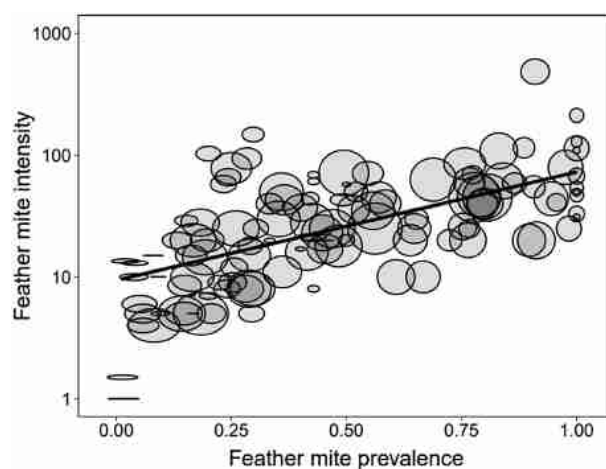


Figure 1. Relationship between feather mite prevalence and median intensity ($\log_{10}$ scale) across bird species. Ellipse size is proportional to the $\log_{10}$ (sample size) used to calculate species' feather mite intensity (height of the ellipse) and prevalence (width).

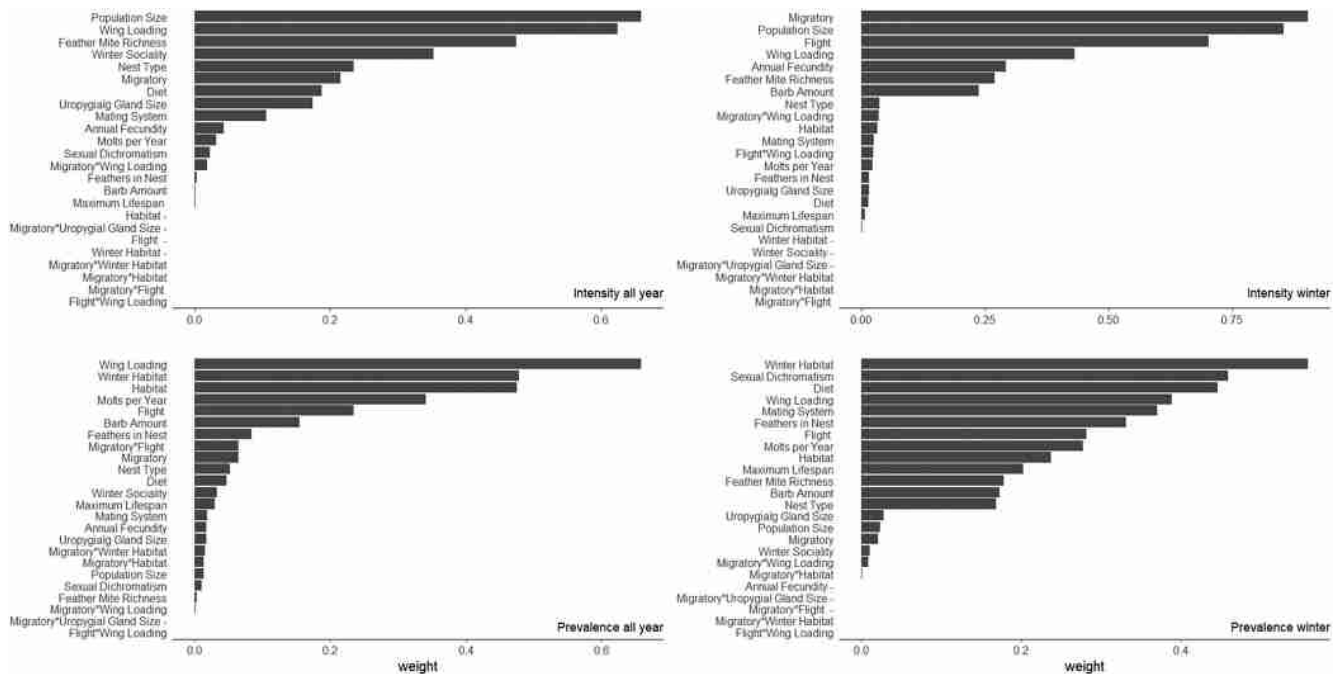


Figure 2. Cumulative Akaike weights of the explanatory variables used in the PGLS regression models. A dash next to the variables indicates a very low (but > 0) weight.

feather mite species richness showed high cumulative weights for intensity in both sampling periods, although the weight was much reduced for prevalence models. Conversely, interactions among variables seldom contributed to explain the differences in feather mite prevalence or intensity.

The phylogenetic signal of feather mite intensity did not differ significantly from 0 (Blomberg's $K=0.210$, $p=0.406$, Pagel's $\lambda=0$, $p=1$, $n=119$ species, Fig. 3). Similarly, feather mite prevalence did not show any phylogenetic signal using Blomberg's K ($K=0.053$, $p=0.894$, $n=122$), but a low phylogenetic signal using Pagel's λ ($\lambda=0.294$, $p=0.005$, $n=122$, Fig. 3). These estimates were robust to different combinations of sample size and sampling period constraints (Table 3).

Closely related bird species carried similar communities of feather mites (Mantel $r=0.2576$, $p<0.001$, $n=104$ bird species, Fig. 4). However, bird species carrying more similar feather mite communities (i.e. sharing more feather mite species) did not present more similar feather mite intensities (Mantel $r=-0.006$, $p=0.595$, Fig. 5a) or prevalence (Mantel $r=-0.006$, $p=0.602$, Fig. 5b). Results were robust to different combinations of sample size and sampling period constraints (Table 4).

Discussion

Feather mite prevalence and intensity were highly variable among species. They were also highly correlated with each other in agreement with previous studies (Behnke et al. 1995, Díaz-Real et al. 2014). These findings altogether show a robust pattern and raises an important ecological question:

Why do some bird species have feather mite prevalence close to 100% with host individuals often carrying hundreds of feather mites, while other bird species have prevalence close to 0% and intensities rarely above a few mites?

PGLS analyses trying to explain these differences between bird species did not provide a clear answer. The only variable that appeared consistently in the best models of all data subsets and with remarkable Akaike weights was wing loading (Table 2). Regarding variable weights, other variables such as bird species population size, habitat, winter habitat or feather mite species richness appeared well positioned and with relatively high cumulative Akaike weights only for intensity or prevalence.

We expected more uniform results between intensity and prevalence models due to their strong interdependence (Table 1). Consistent results were even more expected between 'all year' and 'winter' data, given that 'winter' data are a subset of 'all year' data. However, our findings did not meet clearly these expectations. Additionally, we found contrasting results in comparison to existing literature. For instance, Figuerola (2000) found that bird species that are social in winter showed higher feather mite prevalence, while Galván et al. (2008) found the interaction between migratory status and uropygial gland size to be correlated with feather mite intensity in the breeding season. None of these results were corroborated by our models based on this updated and much larger database (the 'FeatherMites' database). On the other hand, habitat variables showed opposite results: while 'winter habitat' supported our hypothesis (bird species inhabiting more humid habitats and with more vegetation cover had more feather mites), 'habitat' showed results against it

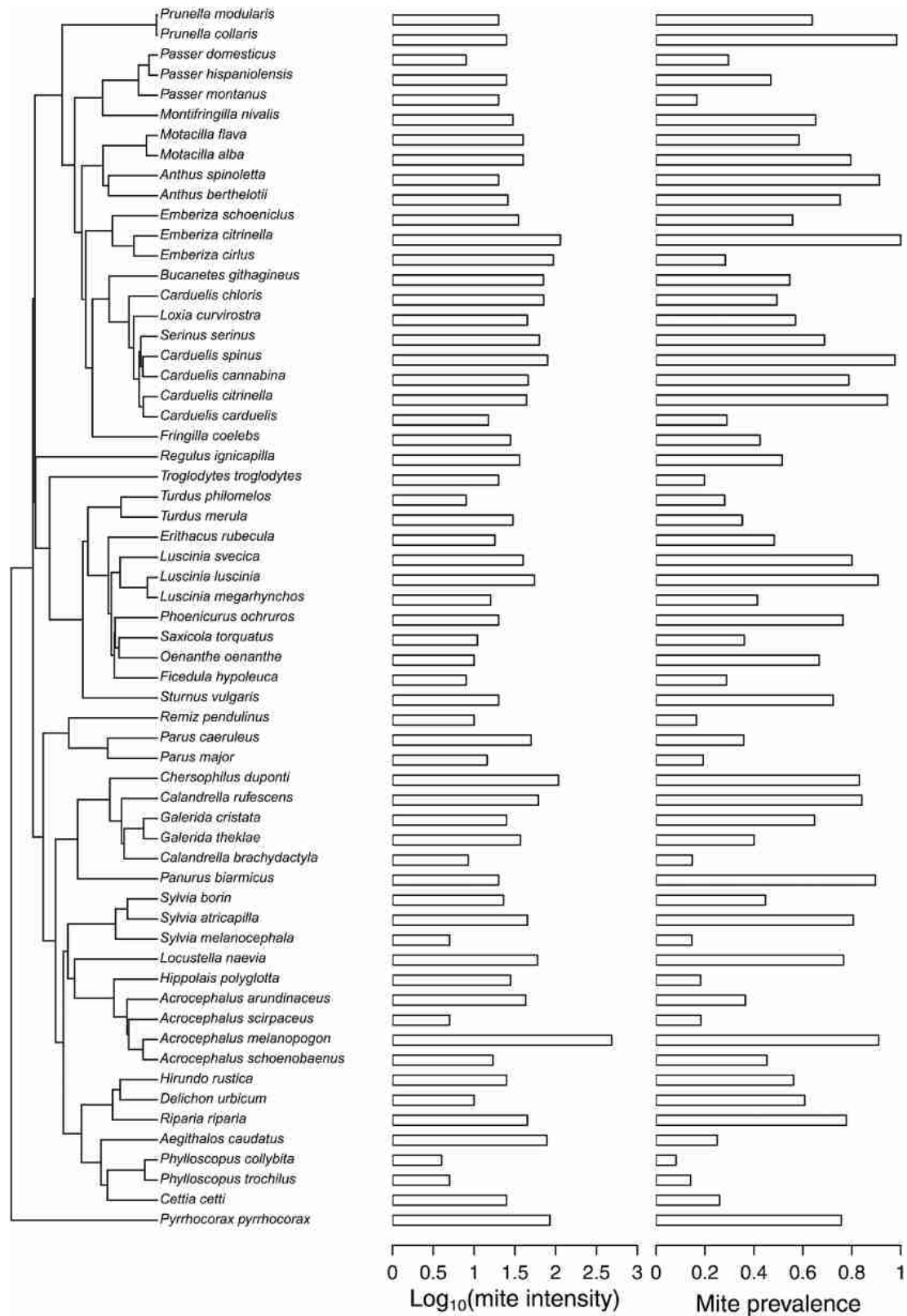


Figure 3. Feather mite intensity and prevalence mapped across the passerine phylogeny. For display purposes, only species with $n \geq 30$ individuals are shown.

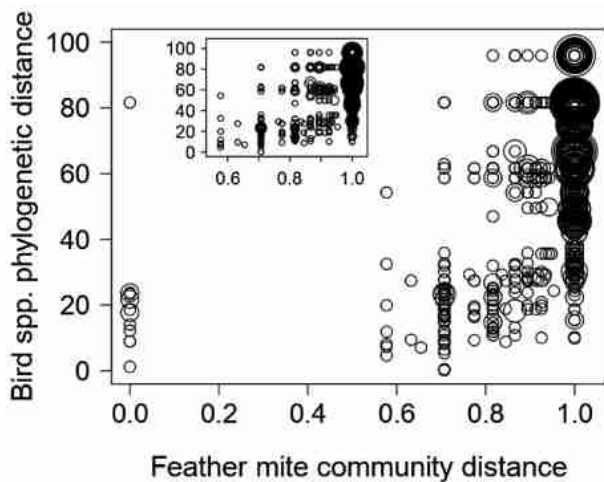


Figure 4. Relationship between the dissimilarity (Jaccard index) in feather mite community composition of pairs of bird species and the phylogenetic distance between them. Dot size is proportional to the natural logarithm of the number of bird species pairs sharing a same combination of distance values. Inset plot shows the same data, but excludes bird species pairs with identical feather mite communities (note the different x-axis ranges), showing that the positive correlation holds even when excluding those data. The inset plot does not hide any point of the main plot.

(bird species from open habitats hold more feather mites than those inhabiting wetlands). Other variables also presented effects opposing what we predicted on both intensity and prevalence (Table 2). This is the case of bird population size or wing loading. Bird population size could be seen as a proxy of intraspecific proximity and contact between individuals, and therefore of transmission rate. However, higher population sizes did not result in higher numbers of feather mites (pattern found in other systems, Stanko et al. 2006), suggesting a dilution effect (feather mites would be distributed among more hosts). Finally, our newly proposed hypotheses (Table 1) were also not supported.

To sum up, we found no evidence for one model clearly outperforming the rest. Also, cumulative Akaike weights were low for almost all traits studied, and were similar among alternative data subsets. Indeed, while the explanatory power of our PGLS models were comparable to those of other large-scale phylogenetic comparative studies, where R^2 is usually below 10% (Møller and Jennions 2002), much variance remained unexplained despite the large number of host predictors (Table 2). All of this means that our PGLS analyses have not identified any single or group of bird traits that clarify why some bird species have a higher mite intensity and prevalence than others.

This may be partly the result of our decisions when coding and collecting data for each bird trait, so the possibility that relevant bird traits for feather mite occurrence were missing in the analyses cannot be discarded. However, our other analyses also did not provide a clear answer as to why bird species differ in feather mite occurrence. Although closely-related bird species share many phenotypic traits (Cicero et al. 2020)

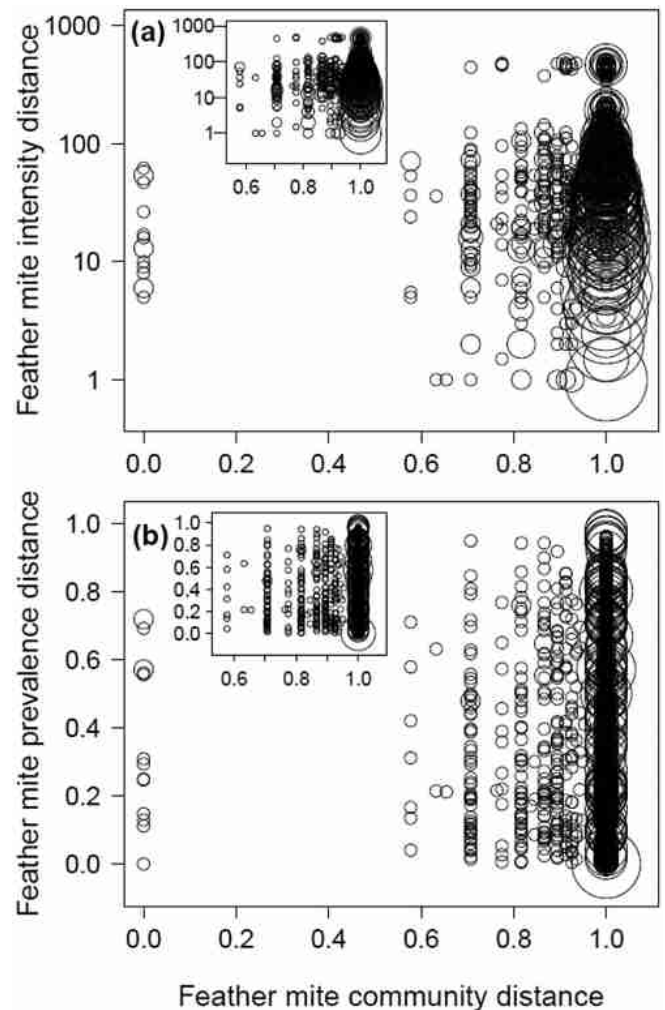


Figure 5. Relationship between the dissimilarity (Jaccard index) in feather mite community composition between pairs of bird species and the distance (difference) in (a) their median feather mite intensity + 1 on $\log_{10}$ scale or (b) their feather mite prevalence. Dot size is proportional to the natural logarithm of the number of bird species pairs sharing a same combination of distance values (i.e. summarizing number of data points in identical coordinates in the plot). Inset plots show the same data as their main plots, but excluding bird species pairs with identical feather mite communities (note x-axis range). The same lack of correlation holds even when excluding those data. Inset plots do not hide any point of the main plots.

and were the only ones holding similar feather mite communities (present study, Stefan et al. 2023), they did not show similar feather mite numbers. In the same way, similar feather mite communities did not result in similar prevalence or intensities. These findings suggest that host and feather mite traits cannot provide a simple general explanation for interspecific differences in prevalence and intensity of feather mites. In other words, our results suggest that feather mite prevalence and intensity are idiosyncratic.

This idiosyncrasy does not mean that bird and mite traits are not important to understand feather mite occurrence, but rather we suggest that what may be relevant is the interaction

between bird and mite traits. This hypothesis is supported by our current knowledge of the host specificity of feather mites. Taxonomic literature (compiled in Doña et al. 2016) traditionally showed that most feather mite species occur on one or few bird species, but that others are polyxenous and have the ability to inhabit many bird species (Doña et al. 2018, Matthews et al. 2023). Moreover, we currently know that feather mites have higher dispersal capabilities between host species than previously appreciated. For instance, a metabarcoding study found ca 5% of feather mite individuals studied were carried by unexpected bird species according to the taxonomic literature (Doña et al. 2019b). Also, several authors have found host-switching to be more common than cospeciation in feather mite evolution (Doña et al. 2017b, Matthews et al. 2018, 2023, Dabert et al. 2022). Despite so, most feather mite species occur on one or few bird species, often in the same bird genus (Doña et al. 2018). Therefore, the high host-specificity of many feather mite species is likely driven by habitat filtering (Doña et al. 2019a), thus implying an important role of the interaction between feather mite species preferences and bird species traits. This could explain our difficulties in finding general explanations for why some bird species have more feather mites than others.

Importantly, idiosyncrasy may arise from combinations of same bird and mite traits. For instance, bird habitat and feather mite humidity requirements may lead to different outcomes in each association (e.g. a bird species with high sun exposure may have more or fewer mites depending on the humidity requirements of its feather mite community). This gives some hope that this idiosyncrasy does not imply that in each bird–mite association the traits involved are different, but that the same traits of birds and mites may be responsible for the different outcomes of feather mite numbers across bird species.

Future studies on feather mite intensity and prevalence variability among bird species may benefit from new ways of coding the same variables used here, incorporating other bird traits or collecting a larger sample size. Also, taking into account data on feather mite occurrence on tail feathers or wing coverts would also be advisable as they are often occupied by the same mite species as those occurring on the wing flight feathers studied here (Dubinin 1951). However, we want to specially encourage focusing on feather mite species features that may be important for their interaction with bird species' traits (e.g. mite morphology, or diet, temperature and humidity requirements). This proposal to focus on mite traits also implies the need to study feather mite intensity at the mite species level, and how a same feather mite species performs on different bird species. Furthermore, it would be worthy employing a community ecology approach with mite–mite interactions and other pterosphere organisms (e.g. feather fungi and bacteria eaten by feather mites, or potential competitor taxa such as feather lice), which might also be relevant players in the bird–feather mite interaction (Labrador et al. 2021).

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Data availability statement

Data are available from the Figshare Repository: <https://figshare.com/s/af8b97fa6f9d80192ce8> (Labrador et al. 2024b).

Supporting information

The Supporting information associated with this article is available with the online version.

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