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RESEARCH ARTICLE

Host space, not energy or symbiont size, constrains feather mite abundance across passerine bird species

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Abstract

1. Comprehending symbiont abundance among host species is a major ecological endeavour, and the metabolic theory of ecology has been proposed to understand what constrains symbiont populations.
2. We parameterized metabolic theory equations to investigate how bird species' body size and the body size of their feather mites relate to mite abundance according to four potential energy (uropygial gland size) and space constraints (wing area, total length of barbs and number of feather barbs). Predictions were compared with the empirical scaling of feather mite abundance across 106 passerine bird species (26,604 individual birds sampled), using phylogenetic modelling and quantile regression.
3. Feather mite abundance was strongly constrained by host space (number of feather barbs) but not by energy. Moreover, feather mite species' body size was unrelated to the body size of their host species.
4. We discuss the implications of our results for our understanding of the bird–feather mite system and for symbiont abundance in general.

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1 | INTRODUCTION

Central goals in ecology are to describe abundance patterns, comprehend the underlying processes driving these patterns, and understand their ecological consequences. These questions have been mainly studied in free-living organisms, while symbiont abundance patterns have received less attention (Cunning & Baker, 2014; Dobson et al., 2008). Symbionts (including mutualists, commensals and parasites) are the most ubiquitous, abundant and diverse organisms on Earth (Larsen et al., 2017; Morand, 2015). They are key components of ecosystems and influence nutrient cycles, food webs, energy flows and community structure (Hatcher et al., 2012), and their abundance can impact individual host performance and drive the evolution of host species (Poulin & George-Nascimento, 2007). Indeed, the abundance of a given symbiont in or on a given host may determine the nature of the host–symbiont interaction (Bronstein, 1994; Holland et al., 2002), with the potential to shift the nature of this relationship between mutualism and parasitism (Hopkins et al., 2017).

Studies on symbiont abundance have mainly focused on parasites rather than on non-parasitic symbionts, and on understanding differences in symbiont abundance among members of a single host species rather than interspecific differences among host species (Mennerat et al., 2021; Turgeon et al., 2018). At the interspecific scale, several studies have found support for Harrison's rule, which postulates that there is a positive covariation between host size and symbiont size. In contrast, when considering symbiont abundance instead of symbiont size, mixed results have been found for its correlation with the body size of either the hosts or the symbionts (Clayton & Walther, 2001; Galloway & Lamb, 2017; Krasnov et al., 2013; Lamb & Galloway, 2019; Poulin, 1999; Presley & Willig, 2008; Rózsa, 1997a, 1997b; Surkova et al., 2018). At macroevolutionary scale, host body size largely explained the variation in feather lice effective population size, which is expected to be positively correlated with symbiont abundance (Doña & Johnson, 2022). Overall, we are still far from understanding why some host species harbour many symbiont individuals of a given taxon, while others carry only a few.

The study of the scaling of symbiont abundance with host body size is an underexplored approach to understand symbiont abundance (George-Nascimento et al., 2004; Hechinger, 2013; Morand & Poulin, 2002; Poulin & George-Nascimento, 2007). Hechinger (2013) developed a hypothesis-driven quantitative framework based on the metabolic theory of ecology (sensu Brown et al., 2004) to disentangle how host and symbiont traits shape symbiont abundance across host species. This framework tries to explain symbiont abundance in different hosts through the comparison of theoretical versus empirical scaling exponents of host and symbiont body size according to energy (e.g. blood or secretions) and space (e.g. surface) provided by the host and according to the metabolic rate and space use of symbionts (see below). Hechinger et al. (2019) used this approach to investigate the relationship between host body size and the abundance of ectosymbiotic mites and lice of 263 bird individuals of 42 species. Their results indicated that the numbers of mites and lice were limited by access to host energy and not by space. However, Hechinger et al. (2019) did not distinguish among ectosymbionts with different diets, for example, blood-feeding mites were equivalent to non-parasitic mites provided that mite body sizes were similar. Here, we implemented Hechinger's (2013) framework by analysing an unprecedented large dataset and parametrizing scaling equations using current knowledge of the biology of a particular host–symbiont system: vane-dwelling feather mites (Acariformes: Astigmata: Analgoidea and Pterolichoidea) from European birds.

Feather mites are ectosymbionts found on almost all birds (Walter & Proctor, 2013). Their entire life cycle is spent on their living hosts, mainly on the wing and tail flight feathers, where they are usually

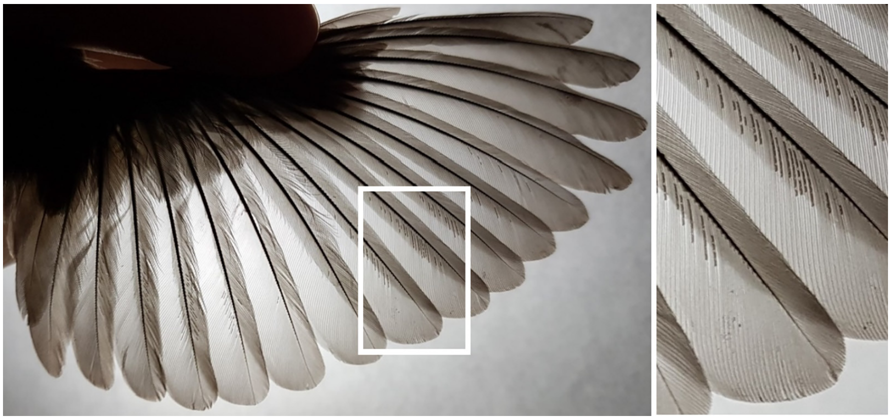

FIGURE 1 Feather mites (*Proctophyllodes sylviae*) on the wing of a *Sylvia atricapilla*. Note their strong aggregation in certain feathers along the wing and in some sections within those feathers, as well as their queuing along feather barbs.

queuing between the feather barbs (i.e. the primary branches of the feather rachis; Figure 1) or next to the rachis (Choe & Kim, 1989; Kelso & Nice, 1963; Yamasaki et al., 2018). They are often said to feed on the preen gland secretions and organic material trapped in them (Dubinin, 1951; Galván et al., 2008; OConnor, 1982; Proctor, 2003; Walter & Proctor, 2013). Still, other evidence suggests a lower relevance of preen waxes as food resources (Pap et al., 2010). Algae are also potential food resources for mites (Blanco et al., 2001). However, Doña, Proctor, et al. (2019) studied the gut contents of a large sample of mites using microscopy and DNA metabarcoding, and found that bacteria and fungi were the main food resources for feather mites, while algae and plant materials were rather anecdotic, and bird tissues such as blood or skin were not found.

Bird species strongly differ in feather mite abundance even when accounting for intraspecific variance between localities (Díaz-Real et al., 2014). While some species consistently have very few feather mites on their wings, regardless of the habitat where they live (such as *Phylloscopus collybita* or *Periparus ater*), other similar-sized ones (such as *Aegithalos caudatus* or *Acrocephalus melanopogon*) often have hundreds of feather mites (Díaz-Real et al., 2014). It is important to note that bird species belonging to different families (as the species mentioned above), can have similar amounts of feather mites. Interspecific differences in feather mite abundance are partly explained by the ecology and morphology of bird species, but a large proportion of the variance remains unexplained after controlling for these traits (Galván et al., 2008; authors' unpublished data). To date, only one interspecific study has related bird species body size to feather mite abundance (Rózsa, 1997b). This study found a positive correlation, albeit based on a relatively small number of host species ($N = 17$), small number of host individuals within species (range of 3–138), and without quantitatively addressing the underlying mechanisms generating the positive relationship between bird size and feather mite abundance.

Here, we applied Hechinger's (2013) quantitative framework to disentangle hosts' energy and space constraints explaining differences in feather mite abundance across 106 passerine bird species. Feather mites are by far the most abundant ectosymbionts in passerines. Bird lice, in contrast, are rare and hardly ever seen on the wing flight feathers of the studied bird species. Thus, feather mites are not likely to compete for energy or space with feather lice, so they can be studied in isolation to understand what spatial and energetic factors constrain their abundance. Here we follow Hechinger's (2013) use of the term ‘size’ to refer to the body mass of hosts and symbionts. According to Hechinger (2013), the metabolic theory of ecology predicts that if energy provided by the host (h) imposes an effective ceiling to the growth of symbiont (*s*) populations, the maximal or carrying-capacity abundance (but also mean abundance under a certain condition) of the symbiont in a given host individual (N_s) will scale with host body size (M_h) and symbiont size (M_s) as

$$N_s \propto M_h^{\sigma_h - \gamma_h} M_s^{-\alpha_s}. \tag{1}$$

Thus, symbionts would be more abundant in larger hosts (that provide more metabolic resources to symbionts) and when symbionts are smaller (they consume less resources per capita, allowing higher carrying-capacity infracommunity sizes in a host). $-\gamma_h$ is the scaling exponent for host mass-specific metabolic rate and equals to $\alpha - 1$, where α is the scaling exponent for whole-organism metabolic rate to body size. α is ~3/4 across multicellular species (Hechinger, 2013), although it is estimated in 0.668 for the particular case of passerines (Gavrilov et al., 2022). Thus, $-\gamma_h = -0.332$, and $-\alpha_s = -3/4$. However, $-\gamma_h$ can be further tuned to better predict the host metabolic rate that will eventually become available to symbionts, and this depends on the use that symbionts do of host energy. Current knowledge points to two main energy (food) resources for feather mites:

1. Organic matter (mainly fungi and bacteria) available on feathers' surface (Doña, Proctor, et al., 2019; Dubinin, 1951; Labrador et al., 2022). There is very little information on the amount of this resource present for mites in different bird species, and we only have a rough measure of its abundance in a snapshot (using qPCR; Labrador et al., 2022), but not the rate at which it appears on feathers, which is the parameter that the model needs. In any case, we performed a tentative analysis of this variable with the information available (see Discussion).
2. Waxes produced by the uropygial gland that birds spread on feathers (Doña, Proctor, et al., 2019; Galván et al., 2008). Uropygial gland size is positively correlated, at least within species, with the amount of waxes it produces (Møller et al., 2009; Pap et al., 2010). Therefore, the size of this gland may be a good proxy of the energy resources for feather mites produced by the hosts (Martín-Vivaldi et al., 2009). We used uropygial gland size allometry to tune $-\gamma_h$ to show the rate at which waxes are available to feather mites in each bird species (see below).

Lastly, σ_h is the spatial exponent for host body size. This is usually parametrized as 1 when the symbiont occupies the host in a volumetric way (e.g. endosymbionts), or 2/3 when they occupy the surface of the host. Here, however, we have parametrized $\sigma_h = 1$ because we already tuned $-\gamma_h$ according to the allometry of the uropygial gland size, and because all the waxes produced by the uropygial gland are spread on the surface of feathers, where mites live. Thus, there is no need to further tune the exponent of M_h in Equation 1.

Alternatively, space provided by the host can also impose an effective ceiling on symbiont populations, and then the maximal or carrying-capacity symbiont abundance in a given host individual would scale with host and symbiont body size as

$$N_s \propto M_h^{\sigma_h} M_s^{-\sigma_s}. \tag{2}$$

Here, σ_h indicates how the host body portion that the symbiont inhabits scales with host body size (Hechinger, 2013; Hechinger et al., 2019). Again, theoretical σ_h values are 1 when the studied symbionts use the host volumetrically, or 2/3 if symbionts inhabit the host surface. Ideally, σ_h should be calculated empirically for each particular study system (Hechinger, 2013). We hypothesized that feather mite infracommunities (all of the mite infrapopulations within a single host; Bush et al., 1997) could be spatially constrained by wing area, which is the largest scale habitat for these mites. Feather mites could otherwise be constrained by the number or the length of feather barbs of the wing because they (except the genus *Trouessartia*) live in the corridors between feather barbs in the ventral side of feathers (Figure 1; Mironov, 2022). Moreover, *Trouessartia* spp., despite living on the dorsal surface of feathers (where there are not such well-defined corridors), also queue along feather barbs (fig. 1 in Mironov & González-Acuña, 2013; authors' personal observation). Thus, we studied the scaling of wing area and the number and length of barbs to bird species body size to parameterize σ_h in Equation 2. Similarly, $-\sigma_s$ is the relevant aspect of symbiont bodies that determines their spatial packing on host bodies. Since feather mites line up in a single row between adjacent feather barbs and their body width does not affect how many can fit in these interbarb spaces (Figure 1), feather mite length would be the most relevant aspect to understand feather mite abundance. Thus, we parametrized $-\sigma_s$ as $-1/3$ because this is how mite length scales to mite body size (in µg) (Supporting Information).

In sum, we used empirical data to complete the parametrization of Equations 1 and 2, and then compared predicted scaling exponents with the empirical exponents obtained by phylogenetic generalized least squares regressions and quantile regressions for the abundance of feather mites across bird species, following Hechinger (2013). We show, using a large dataset on feather mite abundance, how a biologically informed parametrization of the metabolic theory of ecology proposed by Hechinger (2013) is a powerful approach to help understand why symbiont abundance differs between host species.

2 | MATERIALS AND METHODS

2.1 | Feather mite morphometric data

Body size in Hechinger's (2013) equations (M_h, M_s) refers to host and symbiont species' body masses. Given that M_s data were available for only one of the mite species studied here, we calculated them from feather mite species' biometry following the equation provided by Edwards (1967; Supporting Information). To do so, we gathered data from adult female morphology because they are typically the largest (e.g. Atyeo & Braasch, 1966; Santana, 1976) and more abundant life stage (e.g. Marčanova & Janiga, 2021; Muzaffar & Jones, 2005). Feather mites ranged from the 394 µm length and 0.989 µg weight of *Scutulanyssus nuntiaeveris* [Berlese] to the 1121 µm and 22.85 µg of *Joubertophyllodes modularis* [Berlese]. Then, to obtain a reliable measure of the mean M_s on each bird species, we calculated the weighted mean body size (in µg) of the feather mite species reported for each bird species as $\text{weighted mean}(M_s^z)$, where z will take different values depending on what is parameterized (see below): the mean body mass of mites ($z=1$), the mean metabolic rate of the mites ($z=-3/4$, Equation 3) or the use of bird space by mites ($z=-1/3$, Equations 4–6). The weighted mean was calculated using the number of records reported by Doña et al. (2016) for each mite species in each bird species (i.e. the number of studies published where a feather mite species is reported to occur on a given bird species), using only the most reliable bird–mite associations (i.e. those with quality score = 2; see Doña et al., 2016 for more details). Doña et al. (2016) consisted of an extensive and thorough review of taxonomic studies reporting bird–feather mite species associations. Most of these studies were seeking to characterize feather mite communities of bird species from a given area. The information in Doña et al. (2016) can be considered the best description of the feather mite species occurring in the bird species studied here. Consequently, we used the number of records in Doña et al. (2016) as a proxy of the relative abundance of the feather mite species present in each bird species. This is supported by a strong correlation between (1) the $\text{weighted mean}\left(M_s\right)$ calculated with the approach described above with (2) the $\text{weighted mean}\left(M_s\right)$ calculated using as weights the relative abundance of each mite species in each bird species from a metabarcoding study (Doña, Serrano, et al., 2019) on 71 of the bird species (1130 individual birds) studied here (unpublished analyses).

2.2 | Feather mite abundance data

Data were obtained from *FeatherMites*, the largest dataset available on feather mite abundances (see Díaz-Real et al., 2014 for details), where, for each bird individual, the total number of vane-dwelling feather mites was counted (i.e. without differentiating between mite species) on the 19 flight feathers (10 primaries, six secondaries and three tertials) of one wing. Because we aimed to understand the mechanisms setting the upper limit for feather mite abundance, birds without feather mites were not included in the analyses. Therefore, according to parasitological terminology, we analysed feather mite intensity (or infracommunity size; Bush et al., 1997), that is, the number of feather mites counted in each individual bird with at least one mite, but we use the term 'abundance' hereafter due to its general use in the ecology literature. Since we could not find data on the morphology of certain feather mite species in our dataset, some bird species were not included in the analyses, leading to a final dataset of 26,604 individual birds from 106 passerine species.

Given the non-normal frequency distribution of feather mite abundance (Díaz-Real et al., 2014), we used quantiles of mite counts at regular intervals from the 5th (Q5) to the 95th quantile (Q95) to characterize feather mite abundance in each bird species. Special relevance was given to Q95 as the best surrogate for the carrying capacity of the abundance of feather mites of each bird species, following Hechinger et al. (2019).

2.3 | Bird morphology data

Three morphological traits for the studied bird species were retrieved from the literature (not from the birds from which feather mites were counted; Table 1): body size (expressed as body mass in g), wing area and uropygial gland size (see Supporting Information for details). Moreover, the number of feather barbs was calculated for each bird species by multiplying the sum of primary feather lengths for 40,346 birds (sample size: mean = 917, min-max = 1–9506 birds per species) captured from 1994 to 2015 at the Manecorro Ringing Station (Doñana National Park, SW Spain) by feather barb density of the innermost primary feather (P1) (see Supporting Information for details, and Table 1 for the number of bird species for each morphological variable). Total barb length was estimated by multiplying the number of barbs calculated above by the mean barb length obtained by averaging the length of three inner vane barbs at the middle of the P1 feather using FeatherBase website (*N* species = 43; *N* individuals per species range = 1–5).

2.4 | Statistical analyses

Phylogenetic generalized least squares (PGLS) regressions (Symonds & Blomberg, 2014) were performed to retrieve (from the slope of the log–log regressions; following Hechinger, 2013) the scaling exponents between bird species' body size ($\log_{10}$ transformed) and the four variables ($\log_{10}$ transformed) hypothesized to constrain feather mite infracommunity sizes: uropygial gland size, wing area, total length of barbs and number of barbs of primary feathers.

We also used PGLS regressions to contrast Equations 3–6 with empirical allometry of feather mite abundance. To do so, we fixed the exponent of M_s by assuming that $M_s^{-3/4}$ in Equation 3 is the proper estimate of feather mites' metabolic rate and $M_s^{-1/3}$ in Equations 4–6 is the best way to estimate how mites pack in bird feathers. The exponent of M_h was estimated empirically. We did so by taking logarithms at both sides of the equations: $\log_{10}\left(N_s / M_s^z\right) = \text{slope} \times \log_{10}\left(M_h\right) + \text{intercept}$. Next, for each of 19 equally spaced quantiles of feather mite abundance (*Ns*) from 5 to 95, we run two PGLS regressions, one fixing $z = -3/4$ and another for $z = -1/3$. Quantile 5 (Q5) would be closer to the minimum number of feather mites in a given species. Q50 is the median abundance, and Q95 would represent a robust non-parametric measure of the maximum abundance of feather mites.

We used the *gls* function of the *caper* R package (Orme et al., 2012) to perform the PGLS regressions, which ensure the statistical independence of our samples, correcting the model estimates by the phylogenetic relatedness of the studied species. We obtained information on the phylogenetic relationship among bird species by downloading a distribution of 1000 trees from BirdTree (Jetz et al., 2012, http://birdtree.org) using the Hackett backbone tree (only sequenced species; Hackett et al., 2008). Then, following Rubolini et al. (2015), trees were summarized by computing a single 50% majority-rule consensus tree in SumTrees v 4.5.1 in DendroPy (Sukumaran & Holder, 2010, 2015).

In each PGLS model, we allowed the phylogenetic signal in the residuals (i.e. Pagel's lambda, λ) to be optimized towards its maximum likelihood value (Symonds & Blomberg, 2014). These models were also weighted by the sample size ($\log_{10}$ transformed) of each bird species to incorporate the higher uncertainty associated with feather mite abundance data from host species with smaller sample sizes.

To further study the factors constraining feather mite infracommunities, we performed a quantile regression for the $\log_{10}$(Q95) of feather mite abundance, using the same approach as for PGLS analyses (Cade & Noon, 2003; Koenker & Bassett, 1978). We were especially interested in the quantile regressions at the largest τ values because these would reflect the maximum feather mite abundance that bird species can harbour, considering their body size and

TABLE 1 Variables employed in the present study and their sample size. All analyses were done at the species level (i.e. one value of each variable for each bird species). *N* individuals show individual-level field data used to calculate feather mite abundance quantiles and mean primary feather length at the species level. *N* species for M_s indicates the number of feather mite species with which we calculated the weighted mean M_s of the 106 bird species. See Supporting Information for further details.

Variable	Units	*N* species (*N* individuals)	Source
Feather mite abundance (N_s)		106 (26,604)	Díaz-Real et al. (2014)
Bird species body size (M_h)	g	106	Dunning (2007) Birds of the World website
Feather mite species body size (M_s)	µg	103	Santana (1976) Edwards (1967)
Uropygial gland size	mm^3	76	Vincze et al. (2013)
Bird wing area	m^2	88	Nudds et al. (2007) Pap et al. (2015) Bruderer and Bolt (2001)
Number of barbs (a × b)			
a: P1 barb density	barbs/cm	44	Pap et al. (2015)
b: Length of primary feathers	cm	44 (40,346)	Doñana National Park, SW Spain
Total barb length (c × Number of barbs)			
c: P1 mean barb length	mm	43	Featherbase website

that of their feather mites. But we also explored other τ values to obtain a more complete picture of the scaling of Q95 feather mite abundance. We used the *quantreg* R package (Koenker 2015) and assessed the slopes of the quantile regression models for different τ values from 0.05 to 0.95. Quantile regression analyses were also weighted by the sample size ($\log_{10}$ transformed) of each bird species.

Estimated mean λ for Q95 in the PGLS regressions explained above was 0.413 (95% CI: 0.077–0.749). Thus, a phylogenetic modelling approach to the quantile regression would require the phylogenetic scaling factor to be adjusted to $\lambda < 1$. However, we were unaware of any tool able to perform such partial phylogenetic correction in a quantile regression analysis (see Jovani et al., 2016). Consequently, we present the results based on a non-phylogenetically corrected quantile regression and assume that phylogeny is unlikely to be a confounding factor.

Current information on the annual cycle of feather mites on European birds indicates that their abundance peaks from winter until the onset of birds' reproductive season (Blanco et al., 1997; Peet et al., 2022), when mites are transmitted from parents to offspring birds, causing a lowering of feather mite abundance in adult birds (Doña, Potti, et al., 2017; Mironov & Malyshev, 2002). As migratory species overwintering in Africa were mainly captured and studied during the breeding season, when feather mite populations are at their lowest annual level, migratory species may suffer from an underestimation of their feather mite abundance compared to the sedentary species in our dataset. To test whether our results were robust against this uneven sampling of bird species, we repeated all the analyses on feather mite abundance for the subset of birds captured from the beginning of October to the end of March (hereafter 'winter'). This restriction reduced the sample size to 8066 individual birds of 77 species.

3 | RESULTS

3.1 | Empirically setting the exponents of Equations 1 and 2 under different scenarios

Uropygial gland size showed a scaling exponent of 0.902 (Figure 2a, Table S1). Thus, we tuned $M_h^{-\gamma_h}$ (with $-\gamma_h$ calculated in the Introduction as −0.332) as follows: $M_h^{-0.332}/M_h^{(1-0.902)} = M_h^{-0.430}$; that is, the exponent of M_h decreased because the uropygial gland size did not scale isometrically with bird species body mass. Given that $\sigma_h = 1$ here (see Introduction), $\sigma_h - \gamma_h = 0.570$. Therefore, if energy provided by the gland waxes of the host was the main constraint to feather mite infracommunities, Equation 1 would predict that the maximum feather mite abundance would scale with bird and mite body size as follows

$$N_s \propto M_h^{0.570} M_s^{-3/4}. \tag{3}$$

Wing area scaled with bird species body size to 0.676 power in accordance with the theoretical 2/3 scaling exponent for external host surfaces, the total length of barbs scaled with a slope of 0.459, and the number of barbs scaled with a slope of 0.264 (Figures 2b–d, Table S1). Thus, if feather mite infracommunities were limited by wing area, total length of barbs or the number of barbs, Equation 2 would be respectively

$$N_s \propto M_h^{0.676} M_s^{-1/3}, \tag{4}$$

$$N_s \propto M_h^{0.459} M_s^{-1/3}, \tag{5}$$

$$N_s \propto M_h^{0.264} M_s^{-1/3}. \tag{6}$$

Thus, Equations 4–6 predicted a positive effect of bird body size upon feather mite abundance (larger birds provide more space to mites, with different scaling slopes depending on the spatial constraint), and a negative effect of feather mite size (fewer large mites would fit on a host of a given size).

3.2 | Predicted versus empirical scaling rules

PGLS models showed a positive correlation between bird species' body size and the abundance of their feather mites (Figure 3, Tables S2 and S3), holding consistently from the Q45 to the Q95. Empirical slopes were in close agreement with the slopes predicted for the number of barbs (Equation 6), less so for the total

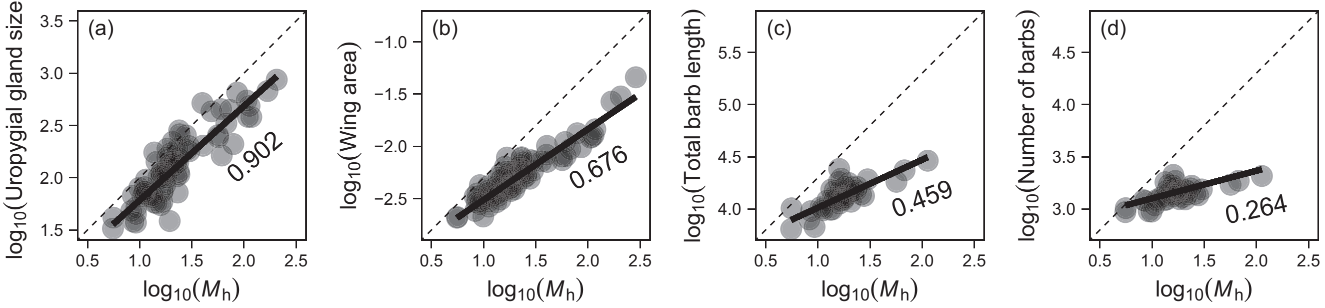

FIGURE 2 Relationships between potential energetic ([a] uropygial gland size) and spatial ([b] wing area, [c] total barb length, [d] number of barbs) constraints against bird species body size (in g). Dashed lines show slope = 1. Estimated slopes (solid lines) departed from 0 (p-value <0.05) in all cases.

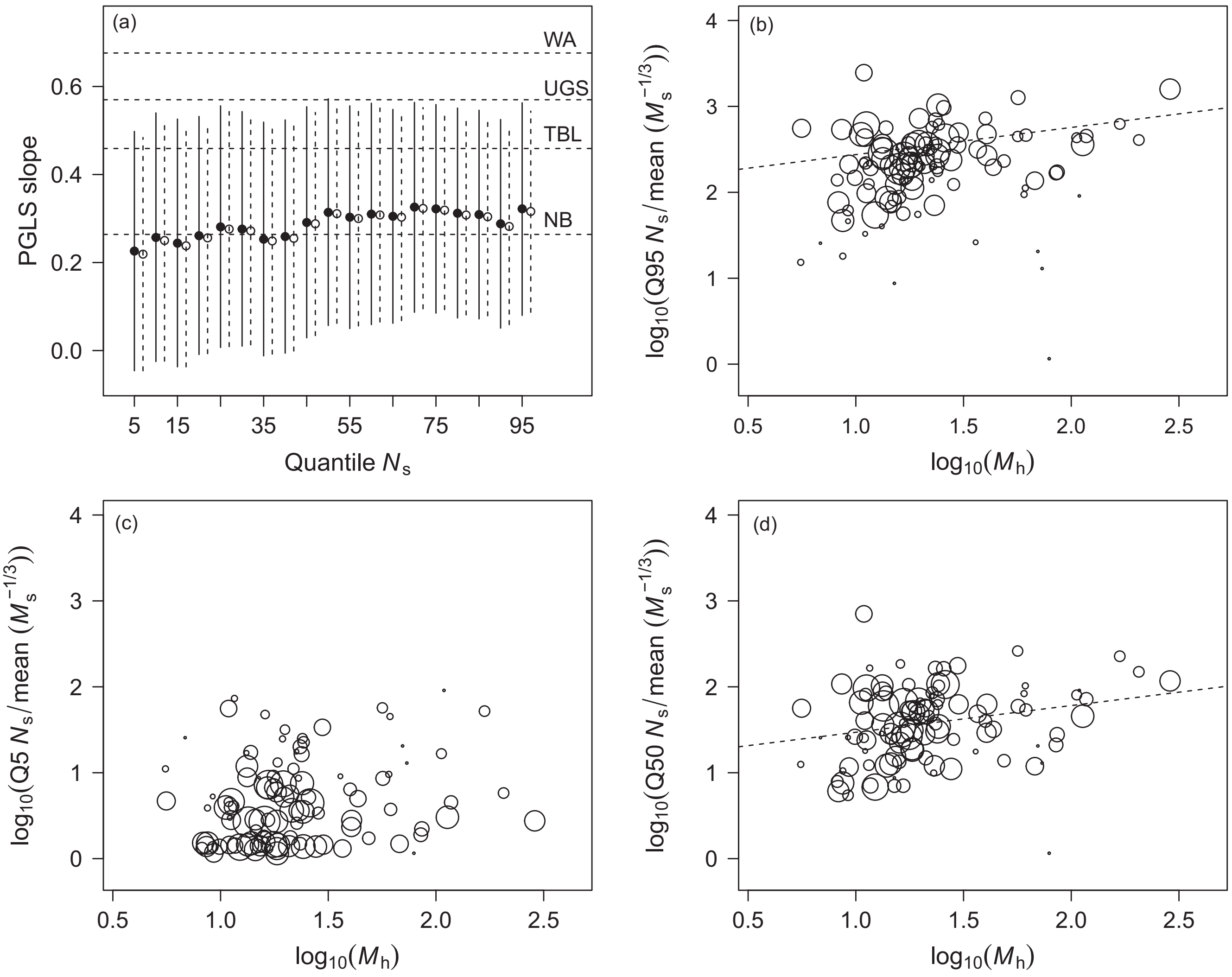

FIGURE 3 (a) Slopes (±95% CI) of the 38 PGLS models of the relationship between each of the equally spaced 19 quantiles (from Q5 to Q95) of $\log_{10}$(QX feather mite abundance/feather mite species' body mass^z) as dependent variable, and $\log_{10}$(bird species body size) as independent variable. Solid dots and error bars show slopes for $z=-3/4$, while empty dots and dashed bars show slopes for $z=-1/3$. Dashed horizontal lines show slope predictions according to Equation 3 (uropygial gland size, UGS), Equation 4 (wing area, WA), Equation 5 (total barb length, TBL) and Equation 6 (number of barbs, NB). (b–d) three example scatterplots for Q95, Q5 and Q50, respectively, for $z=-1/3$. Dot size is proportional to the $\log_{10}$(sample size) for each bird species. Only PGLS regression lines with slopes differing from 0 are shown.

length of barbs (Equation 5), and clearly departed from the ones predicted by the uropygial gland size (Equation 3), and wing area (Equation 4).

Quantile regression analyses showed a strong positive correlation between bird species body mass and feather mite Q95 abundance. Again, the number of barbs (Equation 6) showed the best fit to empirical data, particularly for higher τ values (Figure 4).

Feather mite body size was uncorrelated with host body size (Figure S1). Thus, larger birds carry larger numbers of mites, but this greater abundance is not achieved by carrying smaller mites.

When analysing only data from birds sampled in winter, the smaller sample size led to an increase in the uncertainty of the estimates, but similar qualitative results were found (Tables S4 and S5, Figures S2 and S3).

Dashed lines in Figure 4d and Figure S3d were drawn to cross the actual $\log_{10}\left(Q95\,N_s/M_s^{-1/3}\right)$ value for *Regulus ignicapilla*, the second smallest bird species in our sample (5.6 g). Thus, the dashed lines extrapolate this value for larger bird species, given the actual value for smaller ones. Given the M_s of mites of the largest bird species in our sample (*Pyrrhocorax pyrrhocorax*; 287.5 g), this species was predicted to have up to 5792 and 2465 feather mites according to the regressions fitted for wing area (Equation 4) and total length of barbs (Equation 5) respectively. These are markedly larger values than the 1155 Q95 feather mites found in this species. Interestingly, this empirical value is strikingly similar to the abundance of 1142 predicted by the number of barbs (Equation 6, Figure 4d). In summary, the rather flat slope of the quantile regression for the largest τ values (slope = 0.267, 95% CI = 0.265–0.495) shows the strong ceiling that the number of barbs imposes on feather mites' abundance, precluding larger birds from holding as many mites as expected based on other bird species' features.

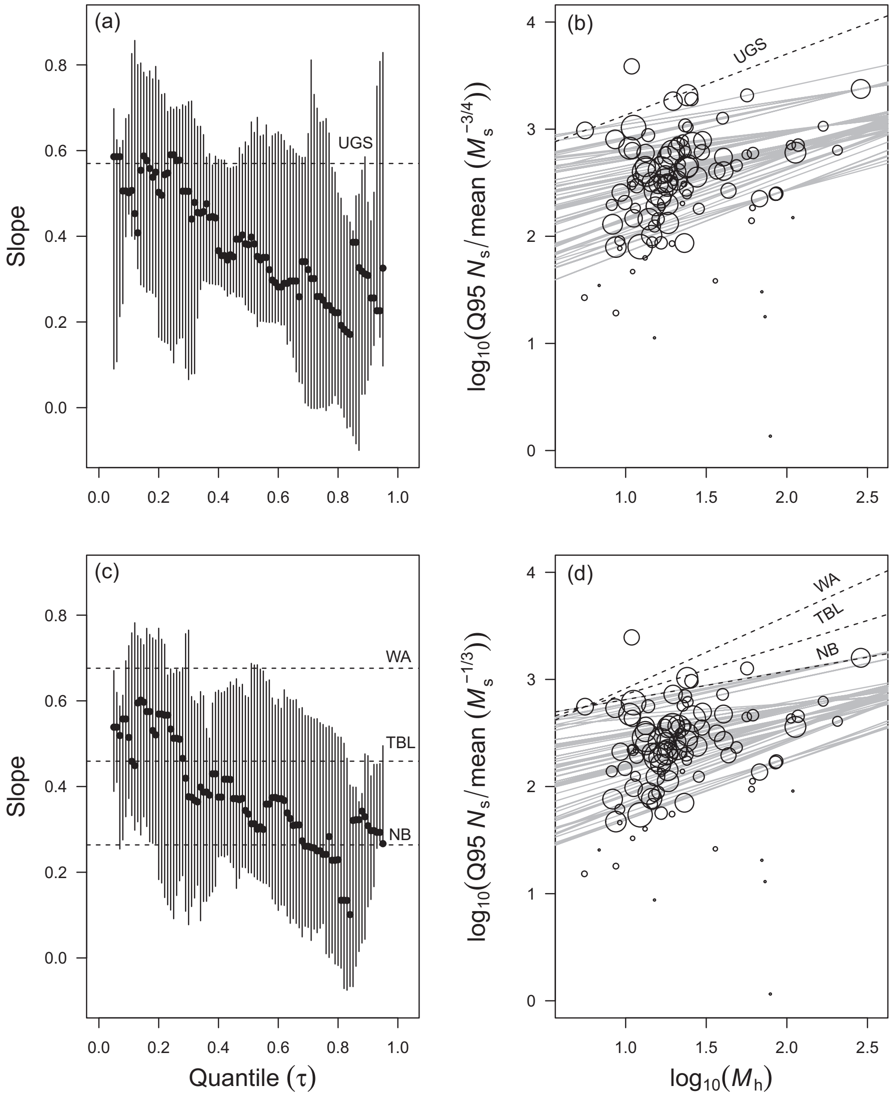

FIGURE 4 (a, b) Quantile regression on $\log_{10}$(Q95 feather mite abundance/feather mite species' body size$^{-3/4}$) as dependent variable and $\log_{10}$(bird species' body mass) as independent variable. Dashed lines show slope predictions according to Equation 3 for the uropygial gland size (UGS). (c, d) Quantile regression on $\log_{10}$(Q95 feather mite abundance/mite species body size$^{-1/3}$) as dependent variable and $\log_{10}$(bird species' body mass) as independent variable. Dashed lines show slope predictions according to Equation 4 (wing area, WA), Equation 5 (total barb length, TBL) and Equation 6 (number of barbs, NB). (a, c) Error bars show ±95% CI for each tau (τ) value. (b, d) Dot size is proportional to the $\log_{10}$(sample size) for each bird species.

4 | DISCUSSION

The carrying capacity of birds to hold feather mite populations increases with bird species' body size, with a scaling exponent close to that predicted by space (but not energy) constraints. Specifically, the empirical scaling we found fitted closely the scaling exponents predicted by the equation involving the number of feather barbs, and less so by total length of barbs, wing area or uropygial gland size. Moreover, feather mite size was not correlated with the size of their hosts.

An exploration (see Section 1) on the allometry of the abundance of feather microorganisms (a potential food resource for feather mites; Doña, Proctor, et al., 2019) showed no apparent correlation with bird body mass, suggesting that this variable is not involved in the allometry of feather mite abundance (Figure S5). However, this aspect would benefit from further research given the small sample size used here and the snapshot (instead of rate) nature of the variable.

The identified space constraint seems to be in conflict with the observation that birds harbouring many feather mites often show large sections of each flight feather, or even entire feathers, devoid of feather mites (e.g. Jovani & Serrano, 2004). However, feather mites show strong preferences for certain feathers and feather sections (e.g. Figure 1), and these preferences differ among feather mite species (Bridge, 2003; Fernández-González et al., 2015; Jovani & Serrano, 2004; Mestre et al., 2011; Stefan et al., 2015), feather mite life stages (Labrador et al., 2022), and according to environmental conditions (Wiles et al., 2000) or even to time of the day (Labrador et al., 2022). Moreover, there is no evidence that feather mite abundance is top-down regulated by bird preening (Blanco et al., 1997) as it happens for feather lice (Bush & Clayton, 2023). Indeed, feather mite abundance is often found to be positively correlated with bird body condition (Blanco et al., 1997; Galván et al., 2012). Therefore, our results, complemented with previous knowledge about the bird–feather mite system, show that feather mite populations are spatially limited, likely because of some negative density dependence (i.e. intra- or interspecific competition for space) acting well before the entire feather surfaces are fully occupied.

Our results showed also a strong ceiling for the maximum feather mite abundance, and manifold differences in the abundance of feather mites among bird species with similar body sizes (note the logarithmic scale of the *y*-axis of Figures 3 and 4). For instance, in the Q95 abundance of feather mites of well-sampled bird species under 10 g there was an eightfold difference between *P. collybita* and *A. caudatus* (Q95 abundance of mites per species 47.9 vs. 389.5 respectively). Further comparative studies (as the one by Galván et al., 2008) are needed to understand which traits of birds and traits of feather mites are responsible for these large differences in feather mite abundance across bird species (Díaz-Real et al., 2014). According to our results, the uropygial gland size did not constrain feather mite populations, suggesting that preen waxes are not an important food resource for feather mites, as previous studies have found (e.g. Doña, Proctor, et al., 2019; Pap et al., 2010).

Our findings disagree with those of Hechinger et al. (2019), who also studied the allometry of bird ectosymbionts' abundance. While they found that energetic constraints were more relevant for arthropod ectosymbionts of birds, we have not found this energetic constraint. This discrepancy may be because Hechinger et al. (2019) mainly studied non-passerine birds, and here we studied only passerines. Moreover, Hechinger et al. (2019) studied a more complete arthropod ectosymbiont community (lice and mites, including a few ticks), while we focused on a more taxonomically and ecologically restricted group (only feather mites). While there may be constraints shaping the whole community of ectosymbionts (thus supporting the approach of Hechinger et al. (2019)), it is also likely that different symbiont groups are constrained by different host traits, or by the same host traits but in different ways. Thus, this would demand a different parameterization of the metabolic theory equations. Interestingly, our findings concurred with Hechinger (2013) finding that space constraints may be more relevant than energy in metabolically inactive symbiont stages that do not use the energy resources provided by their hosts (e.g. cyst). Our results support this view as feather mite abundance was found to be constrained by space, but not by host energy resources. Definitely, it is necessary to nurture the framework proposed by Hechinger (2013) and Hechinger et al. (2019) with more knowledge about the ecology and biology of the symbionts studied, and to integrate this with interspecific comparative analyses to understand the relevant processes regulating symbiont abundances and energy fluxes in host–symbiont systems.

Contrary to Harrison's rule (Harrison, 1915), we did not find a significant correlation between the body size of the bird species studied here and the size of their feather mites. This may be because feather mite species show a complex co-evolutionary history with their hosts, with host-switching being as frequent as cospeciation (Doña, Serrano, et al., 2019; Doña, Sweet, et al., 2017), and relevant at both micro- and macroevolutionary scales (Doña, Sweet, et al., 2017; Matthews et al., 2023). In other words, mites currently found on one bird species may have speciated on another host species (typically from the same genus or family). That may involve the evolution of their body sizes to the previous bird species, followed by a recent host-switching and no time to have reached an optimal feather mite body size on the new host species. This may partly explain why the smallest (*Regulus regulus*; 5.6 g) and the largest (*P. pyrrhocorax*; 287.5 g) bird species in our study have different mites of similar size (i.e. similar weighted mean size of their mite species): 3.82 and 2.61 μg respectively (Figure 3).

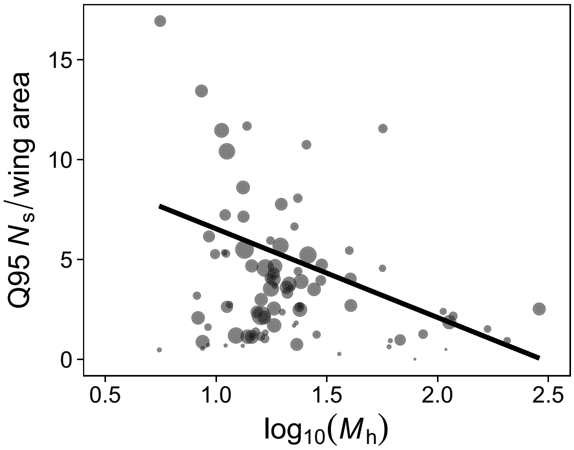

FIGURE 5 Relationship between $\log_{10}$(bird species body size) (in g) and the maximum density of their feather mites (Q95 feather mite abundance/cm^2 of wing area). Dot size is proportional to the $\log_{10}$(sample size) for each bird species.

Besides the relevance of the number of barbs for mite abundance, the allometry of other host traits may also have interesting implications for our understanding of the entire symbiont community composed of all organisms living on bird feathers, the so-called pterosphere (sensu Labrador et al., 2021). For instance, we showed that feather mite abundance scaled with bird species' body size with a much shallower slope than the wing area did (Figures 3 and 4, Tables S2 and S3). Consequently, although absolute feather mite abundance increased with host body size, the maximum density of feather mites (i.e. Q95 feather mite abundance/cm^2 wing area) decreased sharply with increasing bird species body size (PGLS: $t = -3.083$, $df = 86$, $p = 0.003$; Figure 5 and Figure S4). This raises the question of (1) whether a lower density of feather mites in larger bird species implies a lower microbe-removing efficiency of feather mites of large hosts; and (2) whether this lower density is the result of a potential competition between feather mites and feather lice, as numeric dominance of lice relative to mites has been observed in larger-bodied bird species (Hechinger et al., 2019).

Overall, our study shows the potential of the theoretical and quantitative framework proposed by Hechinger (2013) using the metabolic theory of ecology to disentangle the mechanisms behind symbiont abundance across host species. It also shows the necessity to fully integrate the biology of the studied species to make accurate predictions on the factors limiting symbiont populations.

AUTHOR CONTRIBUTIONS

María del Mar Labrador, David Serrano, Roger Jovani and Miriam Gurpegui conceptualized the study. All authors except for Miriam Gurpegui, László Z. Garamszegi and Jorge Doña collected the data. María del Mar Labrador and Roger Jovani performed analyses with support from Jorge Doña and László Z. Garamszegi. María del Mar Labrador and Roger Jovani wrote the first draft of the manuscript, and all authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code used in this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cjsxksn9r (Labrador et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. PGLS model coefficients of the relationship between potential energy and space constraints against bird species body size (in g).

Table S2. Coefficients of the 19 PGLS models. .$\log_{10}\left(N_s/M_s^{-\frac{3}{4}}\right)\sim\text{intercept}+\text{slope}\times\log_{10}(M_h)$

Table S3. Coefficients of the 19 PGLSs models. .$\log_{10}\left(N_s/M_s^{-\frac{1}{3}}\right)\sim\text{intercept}+\text{slope}\times\log_{10}(M_h)$

Table S4. As Table S2 but only analysing bird individuals captured in winter.

Table S5. As Table S3 but only analysing bird individuals captured in winter.

Figure S1. Relationship between the weighted mean of feather mite species body size (in µg) and the body size (in g) of their bird host species.

Figure S2. As Figure 3 in the main text, but only analysing data from birds sampled in winter.

Figure S3. As in Figure 4 in the main text, but only data from birds sampled in winter were used.

Figure S4. As Figure 5 in the main text, but only data from birds sampled in winter were used.

Figure S5. Relationship between microbial abundance in feathers against bird species body size (in g).

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