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## Research



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# Metabolic theory of ecology successfully predicts distinct scaling of ectoparasite load on hosts

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The impacts of parasites on hosts and the role that parasites play in ecosystems must be underlain by the load of parasites in individual hosts. To help explain and predict parasite load across a broad range of species, quantitative theory has been developed based on fundamental relationships between organism size, temperature and metabolic rate. Here, we elaborate on an aspect of that ‘scaling theory for parasitism’, and test a previously unexplored prediction, using new data for total ectoparasite load from 263 wild birds of 42 species. We reveal that, despite the expected substantial variation in parasite load among individual hosts, (i) the theory successfully predicts the distinct increase of ectoparasite load with host body size, indicating the importance of geometric scaling constraints on access to host resources, (ii) ectoparasite load appears ultimately limited by access—not to host space—but to host energy, and (iii) there is a currency-dependent shift in taxonomic dominance of parasite load on larger birds. Hence, these results reveal a seemingly new macroecological pattern, underscore the utility of energy flux as a currency for parasitism and highlight the promise of using scaling theory to provide baseline expectations for parasite load for a diversity of host species.

## 1. Introduction

Intuition and general parasitological trends [1] indicate that larger hosts will harbour more parasites. But exactly how much more? Until recently, we lacked a quantitative theory that could help answer this basic question. This knowledge gap is unfortunate for several reasons, one being that parasites are increasingly recognized as being important for ecosystem structure and function [2–6]. The role of parasites in ecosystems must be underlain by the parasite load of individual hosts. Because ecosystems contain a diverse array of hosts, to better understand the role of parasites in ecosystems, an important step would be to generate and test theory that can explain and predict parasite load across a broad range of species.

To this end, following an earlier effort [7,8], Hechinger [9] developed a theory that predicts how total parasite load varies among hosts of different sizes. This ‘scaling theory for parasitism’ is derived from basic principles involving the relationships between organism size, temperature and metabolic rate of both hosts and parasites [10,11]. The theory makes distinct predictions for parasite load under contrasting conditions of parasites being limited by the supply of either host energy or space, and whether parasites access resources at host surface areas or from within host volumetric spaces (e.g. many ectoparasites versus many endoparasites). Initial testing showed that the load of endoparasitic worms in mammalian hosts met the specific theoretical predictions for host volume using parasites operating under energetic constraints [9]. Here, we elaborate on the host space use aspect of the theory, test previously unexplored theoretical predictions concerning the distinct scaling of ectoparasites, and assess whether these parasites are ultimately limited by host space or energy supply.

**Table 1.** Definitions of terms used in the paper.

term	definition
total host resources	The total energy or space possessed by an individual host within or on its body (or cell, for unicellular organisms).
parasite load	Parasite load. Total levels of parasitism on a host, often of a specific parasite assemblage under study. Can be expressed in different currencies: parasite numbers (or count), biomass, or energy flux. May also be expressed as 'load density' (e.g. the load per unit mass or surface area of the host).
maximum parasite load	The maximum load of parasites supported by a host as determined by resource supply limitation (i.e. barring 'top down' mechanisms such as host resistance mechanisms). Effectively, the 'carrying capacity' of the host for a parasite assemblage.
$e^{-E/KT}$	Arrhenius term, commonly used for the temperature dependence function, $f(T)$ .
$I$	Individual whole-organism metabolic rate (watts).
$F_p$	Parasite energy flux (watts). Equals 'parasite energetic load'. The aggregate energy flux of parasites of a host (i.e. the sum of individual parasite metabolic rates, $I_p$ ).
$f(T)$	Temperature effects. A dimensionless function that reflects the influence of temperature on metabolic rate. Often expressed with the Arrhenius term, $e^{-E/KT}$ .
$M$	Individual organism size (mass, g) of a host or a parasite (denoted by subscripts).
$N_p$	Parasite number or count. Equals 'parasite count load'. The total number of a host's parasites. Corresponds to the 'parasite abundance' term typically used in ecological parasitology [12].
$V$	Individual organism volume.
$W_p$	Parasite biomass (g). Equals 'parasite biomass load'. The aggregate biomass of parasites of a host (i.e. the sum of individual parasite body masses, $M_p$ ).
$W_p i e^{-E/KT} / \text{mean } M_p^{0.25}$	Metabolic-rate-adjusted parasite biomass. The aggregate biomass of parasites of a host, adjusted for parasite metabolic rates. Equal biomasses can flux different amounts of energy, depending on the size distribution of individuals comprising the biomass, given the sub-linear scaling of whole-organism metabolic rate with organism size.
$\alpha$	Scaling exponent for whole-organism metabolic rate with the body- or cell-size (mass); $\sim 3/4$ across a wide range of organisms.
$\rho$	Proportion of host resources available to parasites. The proportion of a host's total resources (energy or space) that parasites could possibly ingest, assimilate, convert to parasite tissue, and/or live within or on.

Parasites get all their energetic (food) and spatial resources from their hosts. Hence, a host's maximum parasite load (table 1) will be constrained to some proportion,  $\rho$ , of total host resources. Total host resources, whether energetic or spatial, are contained within the host's total body volume,  $V_h$ . Consequently, the way parasites use host space influences their access to host resources and, therefore, the magnitude of  $\rho$ . For instance, a parasite infection that uses numerous host tissues may access a much larger fraction of host resources (larger  $\rho$ ) than an infection restricted to a specific tissue type (smaller  $\rho$ ).

Furthermore, the way parasites use host space will also dictate whether the accessibility of host resources [9], and therefore  $\rho$ , scales with host body volume (i.e. whether  $\rho$  regularly changes among hosts of different total body volumes). For instance, many parasites access resources from within host volumes (e.g. part of the digestive tract, muscle tissue or the body cavity) that can increase roughly linearly with total host volume [13,14]. Therefore, both numerator and denominator of  $\rho$  will scale with  $V_h^1$ , as  $V_h^1/V_h^1 = V_h^0$ . The zero exponent reflects the independence from the host size of  $\rho$  for such volume-using parasites. In other words, all else being equal, we predict that the fraction of total host resources available to host volume using parasites (most endoparasites) will remain constant for small and large hosts.

By contrast, many parasites are restricted to accessing host resources at host external surfaces (e.g. many ectoparasites),

which scale with host body volume as  $V_h^{2/3}$  [13,15]. In such cases,  $\rho$  will therefore scale as  $V_h^{2/3}/V_h^1 = V_h^{-1/3}$ . The negative exponent reflects the ever-diminishing fraction ( $\rho$ ) of total host resources predicted to be available to such surface-resource using parasites on larger hosts.

Because host body volume generally scales linearly with host body mass [13],  $M_h$ , we can use host mass instead of volume for the geometric scaling of parasite use of host space, which has the advantage of providing a consistent size currency for subsequent equations.

The maximum parasite load can be limited by either the energy supply rate or the space provided by a host [9]. Factoring in the above geometric scaling of parasite use of space, we can readily derive predictions for the scaling of maximum parasite load with host body size under either energetic or spatial constraints [9]. For each constraint, there are predictions for parasite load expressed using three currencies (counts, biomass and energy flux) (table 1). Because the predictions are mathematically interrelated [9], for clarity, we focus on the simplest theoretical prediction for each constraint—where the currency for parasite load corresponds to the currency of the limiting resource (table 2).

Parasites under energetic constraints will be limited to some proportion of the host's total rate of ingestion, assimilation or new production of energetic resources. These whole-organism vital rates are proportional to the whole-organism

**Table 2.** Main theoretical predictions tested in this paper and general outcomes. Note: the + and × symbols indicate the matching or excluding of theoretical predictions for each of the three tests for each specific prediction depicted in figure 1 (namely, the scaling of maximum parasite load of individual hosts, the average load of individual hosts and the average load of species).

	parasites access host resources at		
	surfaces	versus	volumes
energetic constraints	$F_p \propto M_h^{5/12}$		$F_p \propto M_h^{3/4}$
versus	+++		xxx
spatial constraints	$W_p \propto M_h^{2/3}$		$W_p \propto M_h^1$
	+xx		xxx

metabolic rate,  $I$  [10,16–18]. In general,  $I$  increases with both individual mass,  $M$ , and temperature,  $T$ , as

$$I = iM^\alpha f(T), \quad (1.1)$$

where  $i$  is a normalization constant that differs for organisms of majorly different physiologies (e.g. unicells, invertebrates, endothermic vertebrates or plants),  $\alpha$  is an exponent reflecting how metabolic rate scales with organism size [10,16,19], which is often reported to be  $\sim 3/4$  across a wide range of organisms [15,16,20–22], and has theoretical justification [23]. The term  $f(T)$  is a dimensionless modifier function depicting the relationship of metabolic rate with temperature, which can be captured by a form of the Arrhenius term,  $e^{-E/kT}$ , where  $E$  is the activation energy,  $k$  is Boltzmann's constant and  $T$  is absolute temperature in degrees kelvin [10,19]. Hence, we can use host body size and temperature to estimate the host metabolic rate, which will be proportional to the total amount of host resources provided to parasites under energetic constraints [8,9].

Under energetic constraints, the parallel currency for parasite load is the aggregated energy flux of parasites,  $F_p$ , which can be calculated by multiplying the number of parasites by the average individual parasite metabolic rate (estimated by applying equation (1.1) to the parasites; see Methods) [9]. Maximum parasite energy flux,  $F_{p,\max}$ , is constrained by host whole-organism metabolic rate,  $I_h$ . Using the scaling of  $I_h$  with  $M_h^\alpha$  (equation (1.1); assuming  $\alpha = 3/4$  and ignoring the temperature function and coefficients for simplicity; see Methods), and considering the way  $\rho$  scales given parasite use of host space (see above), we can derive distinct predictions for how parasite energetic load scales with host body size for host-surface using versus host volume using parasites. Specifically, under energetic constraints, the maximum energetic load should scale as  $F_{p,\max} \propto \rho I_h \propto \rho M_h^\alpha \propto M_h^{-1/3} M_h^{3/4} \propto M_h^{5/12}$  for surface users, compared to  $F_{p,\max} \propto M_h^0 M_h^{3/4} \propto M_h^{3/4}$  for volume users.

We can similarly derive predictions for the scaling of maximum parasite load under spatial constraints. Here, the appropriate currency for parasite load and host resources is space, or, given relatively constant tissue densities, mass. Maximum parasite biomass on a host,  $W_{p,\max}$ , will be constrained by total host volume,  $V_h^1$  or body mass,  $M_h^1$ . Therefore, considering the way  $\rho$  scales given parasite space use, maximum parasite biomass load should scale under

spatial constraints as  $W_{p,\max} = \rho M_h^1 \propto M_h^{-1/3} M_h^1 \propto M_h^{2/3}$  for host surface-using parasites, and  $W_{p,\max} = \rho M_h^1 \propto M_h^0 M_h^1 \propto M_h^1$  for host volume users.

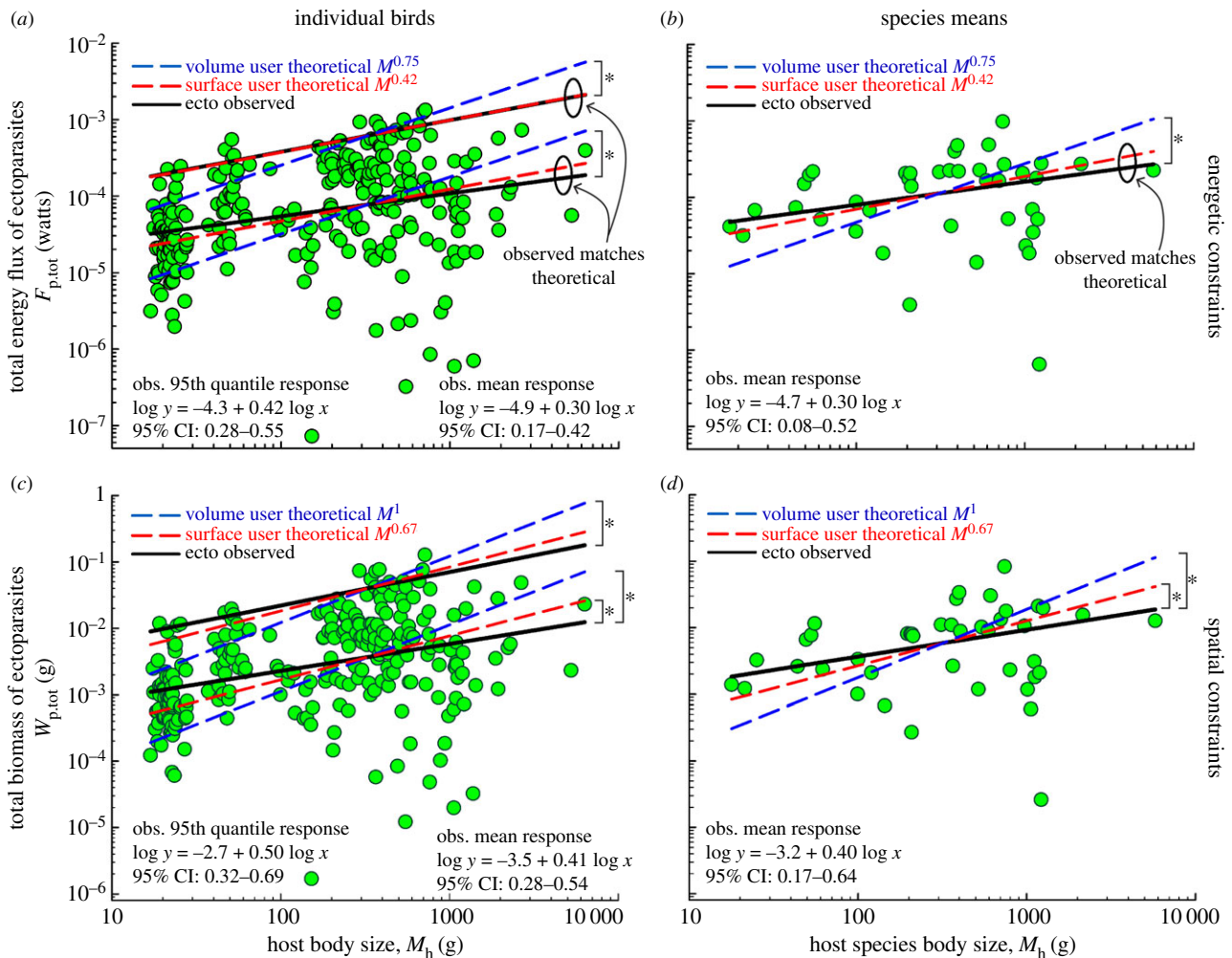
As stated, this theory provides baseline expectations for *maximum* parasite load. However, for various stochastic and mechanistic reasons, most hosts have parasite loads below the maximum [1,24,25]. Despite this, under conditions where average parasite load parallels maximum parasite load (or total available resources), the theory also predicts the scaling of *average* parasite load [9].

We tested the above predictions using new data on bird ectoparasites. We collected 263 individual estuarine birds belonging to 42 species spanning several taxonomic families and orders (electronic supplementary material, table S1). We processed each host for all animal parasites living on the skin and feathers (retrieving mites, ticks and lice), obtaining data on parasite body sizes and total parasite load in terms of numbers, biomass and energy flux (Methods). Bird ectoparasite assemblages are unusual for ectoparasites in that their habitat (feathers + skin) does not scale as a surface area (as  $M_h^{2/3}$ ), but as a volume, because the total mass of bird plumage scales as  $\sim M_h^1$  [26,27]. Hence, under spatial constraints, bird ectoparasites should scale following the above predictions for host volume using parasites (i.e.  $W_{p,\max} \propto M_h^1$ ). However, bird plumage is predominantly non-living tissue, the entirety of which originates from the metabolic activity at the host's skin. Hence, under energetic constraints, bird ectoparasites should scale following the above predictions for host-surface using parasites (i.e.  $F_{p,\max} \propto M_h^{5/12}$ ).

## 2. Results and discussion

As expected, although each bird was infected, there was a large variation in the parasite energetic load of birds of any given body size (figure 1). Despite this variation, the *maximum* energetic load increased with host body size exactly as predicted for parasites constrained by energy supply at host surfaces (figure 1a). Furthermore, the 95% confidence intervals (CIs) for the scaling slope excluded the prediction for volume-using parasites (figure 1a). Similarly, the CIs for the scaling slope of *average* parasite energetic load, among both host individuals and species means, also consistently included the theoretical prediction for host-surface using parasites under energetic constraints and excluded the prediction for volume users (figure 1a,b). We further validated these results with an analysis that factored in the bird taxonomic hierarchy (electronic supplementary material, tables S2 and S3). Hence, larger birds tended to harbour greater energetic loads of ectoparasites than smaller birds, and did so as theoretically predicted for parasites limited by the supply of energetic resources to host surface areas.

By contrast, the theoretical predictions for parasites operating under *spatial* constraints were not consistently met (figure 1c,d). The 95% CIs for the slopes of parasite biomass-load consistently *excluded* the predictions for parasites using host volumes. These predictions would appear to be appropriate for this bird ectoparasite assemblage, which probably uses much of the plumage volume [28,29]. However, even if we assume that these parasites were limited to the host-surface areas, the CIs still *excluded* predictions for spatial constraints in two of the three regressions. These results were also consistent with the analysis that factored in the bird taxonomic



**Figure 1.** Tests of theoretical predictions for the scaling of parasite load with host body size. (a,b) Data represent tests for parasites operating under energetic constraints, with total parasite energy flux as the parasite load currency. Under energetic constraints, the bird ectoparasites would operate as ‘surface users’. (c,d) Data represent tests for parasites operating under spatial constraints, with total parasite biomass as the parasite load currency. Under spatial constraints, the bird ectoparasites would operate as ‘volume users’. (a,c) Data represent 263 individual birds. The top sets of theoretical and best-fit lines are based on 95th quantile regressions, which reflect the scaling of maximum parasite load. The bottom sets of lines are based on ordinary least-squares regressions, reflecting the mean response. (b,d) Data represent means for the 42 included species. Here, the fitted lines are from ordinary least-squares regressions, weighted by host species sample size. The asterisked brackets indicate cases where an observed slope’s 95% confidence interval excludes a specific theoretical slope. The data consistently match theoretical predictions for ectoparasites operating under energetic constraints.

hierarchy (electronic supplementary material, tables S2 and S3). Hence, although larger birds did tend to harbour greater ectoparasite biomass, the rate of increase was much less than expected if space constrained parasite load.

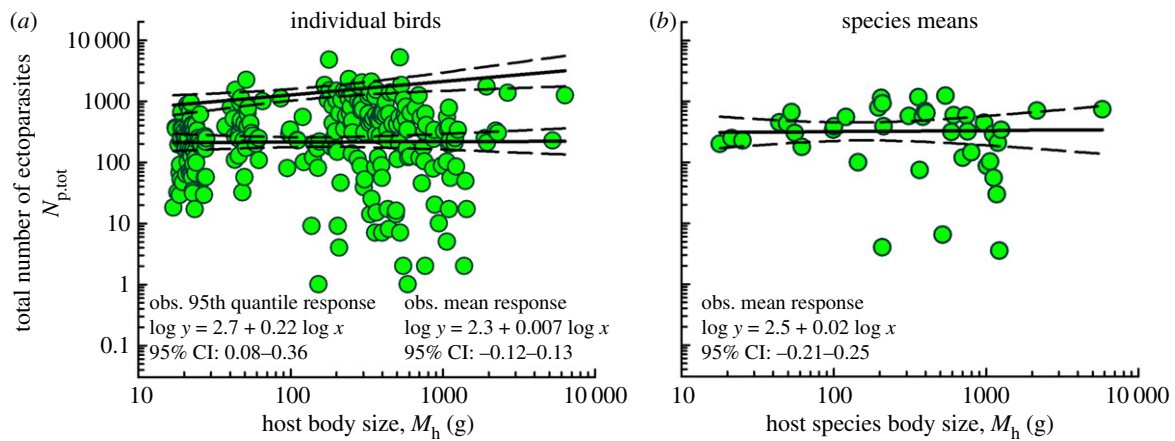
An analysis of the scaling of ‘metabolic-rate adjusted’ parasite biomass (table 1) further indicates that the primary limiting resource for parasites is not host space, but host energy—even for parasites living outside the bodies of their hosts. Under *energetic* constraints, theory predicts that parasite biomass, if adjusted for parasite metabolic rate, will scale parallel to energetic load (i.e. as  $\propto M_h^{5/12}$  for surface users, and  $\propto M_h^{3/4}$  for volume users; see Methods [9]). Here too, the data consistently met the specific predictions for ectoparasites under *energetic* constraints when using either individual birds or species means as data (electronic supplementary material, figure S1). This result helps clarify the inadequacy of using simple biomass as a currency for parasite load, relative to using energy flux or metabolic-rate-adjusted biomass, each of which consistently scales as theoretically predicted under energetic constraints.

Counts of all individual parasites on hosts (count load) are the most widely used currency for parasite load, despite

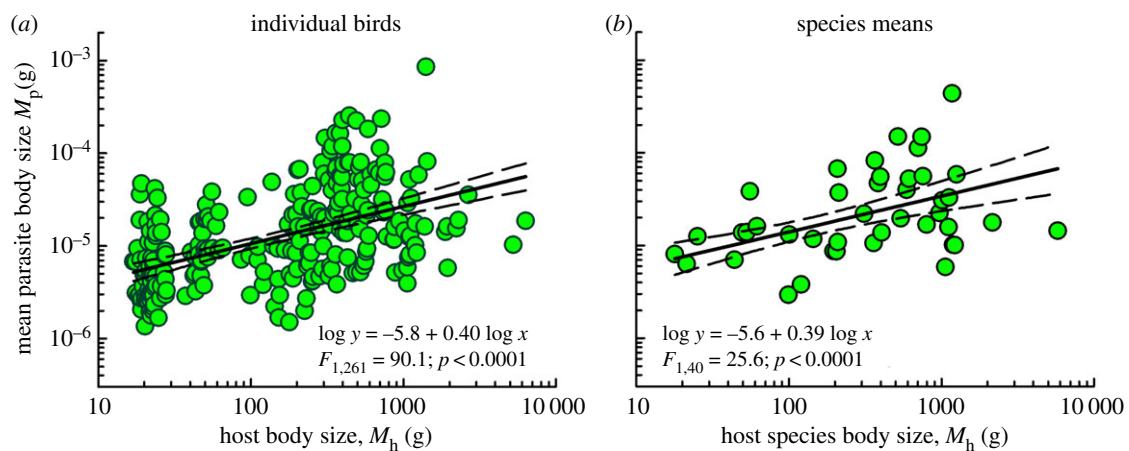
lacking a theoretical prediction that does not factor in their body size or metabolic scaling [9]. Interestingly, parasite *maximum* count load only weakly increased with host size (figure 2a). Furthermore, the *average* count load showed no hint of a relationship with host body size, with the average large or small bird harbouring equal numbers of ectoparasites (figure 2b). The lack of a clear increase in parasite count load with increasing host size, despite the increases in energetic- and biomass-loads, further indicates the utility of moving away from simple counts as currency for parasite load. This is particularly important when dealing with diverse communities of parasites where count load patterns may greatly differ from energetic- and biomass-load patterns [9,30,31].

The lack of a clear increase in parasite numbers on larger hosts contrasts with the increases in parasite biomass and energy flux. However, this pattern is readily explained by parasite body size increasing with increasing host body size (figure 3). This finding fits in with a well-known macroecological pattern in parasitology known as ‘Harrison’s rule’, wherein larger hosts tend to have larger-bodied parasites [1,32–34]. Harrison’s rule is normally examined for specific taxa of parasites





**Figure 2.** The lack of, or weak, increase of total ectoparasite count load with host body size for the (a) 263 individual bird hosts and (b) 42 host-species means. In (a) the top solid-line comes from a 95th quantile regression and represents the weak scaling of maximum numeric loads. The bottom solid lines come from ordinary least-squares regressions and represent the lack of scaling of mean count loads. Dashed lines indicate 95% confidence curves. (Online version in colour.)



**Figure 3.** Average ectoparasite body size increases with host body size across the (a) 263 sampled individual bird hosts and (b) 41 host-species means. Both fitted lines represent ordinary least-square regressions (weighted for sample size in (b)), with dashed lines indicating 95% confidence curves. (Online version in colour.)

(including bird lice; e.g. [34,35]), not for mixed-taxon assemblages like those we examined. Indeed, consistent with previous taxon-specific analyses, the increase in parasite body size with increasing host size also occurred separately *within* each major taxonomic group collected in our study: lice and mites (electronic supplementary material, figure S2).

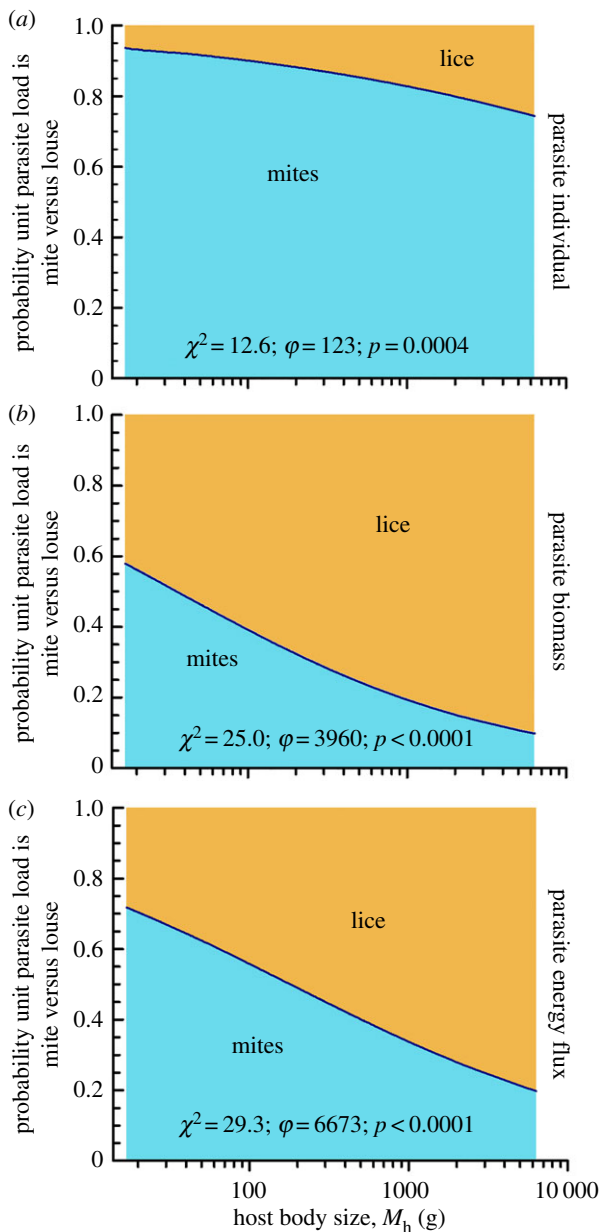
However, the positive relationship between parasite and host body size was not only explained by an increase in the mean size of both mites and lice, but also by a decrease in the dominance of mites relative to lice with increasing host body size (figure 4). The probability that an individual parasite was a mite decreased approximately 20% going from the smallest to largest birds (figure 4a). Despite this decrease, mites were consistently numerically dominant. However, the situation was very different using alternative currencies. With biomass-load, there was a transition from roughly equal importance of mites and lice on the smallest hosts, to dominance by lice in the largest hosts (figure 4b). With energetic load, there was nearly a complete switch from mite dominance on the smallest birds to louse dominance on the largest birds (figure 4c). The substantial difference in the appearance of the shift in dominance when using alternative currencies further underscores the importance of identifying and using appropriate currencies for parasite load.

The shift in relative dominance from mites to lice in larger birds represents a seemingly novel macroecological pattern, perhaps previously undetected because these taxa are rarely

studied together. This pattern's generality, and its causes and consequences, require further investigation. The explanation may lie in mechanical issues involving parasite body size, host feather morphology (e.g. barb size or spacing) and the parasite's ability to escape host preening. These factors often vary with bird body size [36,37], and are known to influence the optimal body sizes of lice (e.g. [36]). Such issues could therefore influence the relative performance of mites and lice, which vary in body size by an order of magnitude. Whatever the explanation, the shifts in parasite body size and taxon appear to have occurred within the constraints on total parasite load set by energy supply from the host, given that parasite load increased with host size exactly as predicted by scaling theory for ectoparasites limited by energy supply.

On the whole, the scaling results clearly better meet theoretical predictions for energetic over spatial constraints (table 2). Thus, these findings combine with previous results for endoparasites [9], and with the substantial difference in perspective when using different currencies to depict parasite load and dominance (figure 4), to suggest that our understanding of parasitism can be enhanced by a shift to use energy flux as a fundamental currency for host–parasite relationships.

The scaling theory for parasitism is derived from underlying principles involving the relationships of metabolic rate, temperature, space use and individual size of hosts and parasites. Because the theory provides baseline expectations for the parasite load of a wide range of organisms, it has promise



**Figure 4.** Shift in the relative dominance of ectoparasite load by mites and lice among hosts of different sizes using three currencies for parasite load: (a) counts, (b) biomass and (c) energy flux. Results are from quasi-binomial regressions on parasite loads of the 263 sampled individual bird hosts. (Online version in colour.)

for being used in two general ways. First, it can be applied to a great diversity of species to predict and understand the role of parasitism in ecosystems. Second, it can provide the starting point to understand the substantial variation in parasitism among hosts that has long been studied in parasitology and infectious disease ecology (e.g. variation due to host resistance, exposure levels and phylogeny). This variation itself can be informed by scaling theory [38–42], further highlighting the possibility of generating a unified, thorough and efficient [43] scaling theory for parasitism.

### 3. Methods

#### (a) Bird and parasite collections

From March 2014 through April 2016, we collected estuarine birds throughout CA, USA. Sample sites included seven

estuaries: from Tomales Bay (Marin County) in the North to Mission Bay (San Diego County) in the South. Birds were taken using mist nets, shotgun and air-rifle. After euthanizing, all specimens were immediately placed into sealed plastic bags, chilled and frozen for later laboratory processing.

To remove ectoparasites, we washed each bird (modifying the technique of Clayton & Drown [44]), followed by direct visual assessment. We manually washed each host with dish detergent and room-temperature water in a bucket for a minimum of 3 min and until all skin was wetted. The bucket contents were strained through 50  $\mu\text{m}$  mesh and preserved in 90% ethanol. To protect host internal areas from the wash, we taped shut the bill (mouth and nares) and cloaca prior to washing. After subsequent endoparasite processing (not reported here), we removed the bill and cloacal tape and examined it for ectoparasites. The skin and feathers of the carcass were then thoroughly visually assessed under the stereomicroscope to collect any ectoparasites not removed during the washing process.

Because the scaling theory most directly applies to entire parasite assemblages, our sampling included all animal ectoparasites that live on the birds' skin and feathers. The encountered parasites were entirely mites (Arachnida: 'Acari') and lice (Insecta: Phthiraptera), which are perhaps the major ectoparasites of birds [28,45]. As a group, bird mites and lice feed on a wide range of host resources, including blood, skin, feathers, host secretions, fungi and bacteria that themselves feed on the host material, and some non-host items that stick to feathers, such as pollen grains [28,46]. Because the host is the ultimate source of most of the energetic resources and all of the spatial resources, one can reasonably test hypotheses concerning whether host energetic or spatial constraints limit the total size of ectoparasite infracommunities.

#### (b) Parasite processing, energy flux, biomass and host metabolic rate

With the assistance of 15 trained interns, involving a minimum of 4000 worker-hours over a period of 3 years, we counted and sorted all collected parasites. Parasites from each bird were first placed into a major taxonomic group. Lice and mites (including a few ticks) were all we encountered. We then grouped the ectoparasites into morphologically distinct size–shape categories (morphospecies), and counted them using gridded transparent trays and stereomicroscopes at 8.6–40 $\times$  magnification. Parasites were exhaustively counted, with the exception of six instances (out of 2013) where we extrapolated mite numerical load from counts of at least one-sixth of the gridded area. We photographed five individuals of each morphospecies on every host and measured the median-sized individual of the five photographs. We estimated the height-to-width ratio of each of these individuals at the microscope, and quantified their body length, width and area using the photographs and IMAGEJ software (Fiji: v. 2) [47]. Body volume (body height  $\times$  body area) was converted to parasite body mass by multiplying the volume by 1.1  $\text{g ml}^{-1}$  [16].

To calculate total ectoparasite energetic load on a host, we first calculated individual whole-body metabolic rate for each ectoparasite morphospecies, by plugging their body size into equation (1.1), using the normalization constant for invertebrates of Brown *et al.* [10] ( $\ln i = 17.17$ ) and the theoretical scaling exponent of 0.75, which matches or is close to empirical estimates (e.g. [48,49]). We used the Arrhenius term for temperature dependence, and plugged in expected order-specific skin temperatures of the host birds by subtracting 5 $^{\circ}\text{C}$  [50] from the body temperatures reported in Prinzing *et al.* [51]. Using host skin temperatures would more accurately reflect the environmental temperature for ectoparasites than would using the hosts' internal body temperatures (but we note that simply using the average bird body temperature of 40.8 $^{\circ}\text{C}$  provided energy flux estimates that strongly

correlated with the more precise estimates:  $R^2 > 0.999$ ,  $p < 0.0001$ ,  $n = 263$ ). The morphospecies's individual metabolic rate (in watts) was then multiplied by its numeric abundance on that host to provide the energy flux for that morphospecies on the host. Summing the energy flux for all morphospecies provided the total ectoparasite energy flux for each host.

To calculate total ectoparasite biomass on a host, we first multiplied the mean body size (g) of each morphospecies by its numeric abundance to provide infrapopulation biomass. Infrapopulation biomass was summed for all morphospecies infecting a host to provide total ectoparasite infracommunity standing-stock biomass.

Given the sub-linear scaling of whole-organism metabolic rate with organism size, equal biomasses can flux different amounts of energy, depending on the size distribution of individuals comprising the biomass [9,10]. Therefore, under energetic constraints, both host and parasite metabolic scaling should influence total parasite biomass,  $W_{p,tot}$  [9]. We can divide  $W_{p,tot}$  by the average  $M_p^{0.25}$  characterizing the parasites on a host ( $\times ie^{-E/kT}$ , to be most precise) to create a metabolic-rate-adjusted parasite biomass, which should have parallel scaling as parasite energy flux has with host body size. Hence,  $W_{p,tot} ie^{-E/kT} / \text{mean } M_p^{0.25} \propto M_h^{5/12}$  for ectoparasites, and  $\propto M_h^{3/4}$  for endoparasites [9]. We calculated metabolic-rate-adjusted parasite biomass using the same parameters for temperature effects as described above and in the main text. Ignoring the metabolic scaling coefficient,  $i$ , and temperature effects provided nearly identical results to those reported here.

To estimate the host metabolic rate, we used equation (1.1), plugging in their measured body sizes, the endotherm normalization constant from Brown *et al.* [10] ( $\ln i = 19.5$ ), the order-specific body temperatures from Prinzinger *et al.* [51], and the theoretical exponent  $\alpha = 0.75$ , which matches or is close to empirical estimates (e.g. [52]).

### (c) Primary statistical analyses

We first performed analyses using the parasite load of individual birds as the response variable, considering each individual bird to harbour a separately assembled community of parasites for analysis. We also performed analyses using means for each host species, which ensured that uneven sampling among host species did not bias results (for instance, if a particularly well-sampled host deviated from the mean expectation).

In log-log space, power-scaling relationships are linearized and scaling exponents are represented by slopes [53]. We focused on 95% CIs (which are 'two-sided') for slope estimates to test theoretical predictions. We fit lines to the data using ordinary least-squares regression (OLS) [54] to estimate the scaling of mean parasite loads, and 95th percentile quantile regression [55–57] to reflect the scaling of maximum parasite loads. We did not use quantile regression on the species-mean data, as estimating the 95th quantile regression line requires a sample size of

100–200, which was exceeded by the individual bird data, but not by species-mean data. OLS analyses of host-species means were weighted by host species sample sizes. For visualization, we plotted lines with theoretically predicted slopes that intersected the fitted lines at the mid-point of the x-data.

We inspected residual versus predicted and normal quantile plots to ensure the data met parametric OLS assumptions of normality and homogeneity of variance [54], using Studentized residuals for the weighted regressions.

To examine the relative change in dominance of mites versus lice, we used quasi-binomial regression with a logit link and an overdispersion scaling-parameter,  $\phi$  [58], using parasite load currencies that provided count data appropriate for the binomial regression (i.e. simple numbers, micrograms and 100  $\mu W$ ).

All analyses were implemented with JMP PRO 13 (SAS Institute Inc.).

### (d) Statistical analyses factoring in the taxonomic hierarchy

Bird taxa may have different maximal and average parasite loads and it is possible that this could confound relationships with host size in our primary analyses. We therefore examined whether analyses factoring in bird taxonomy provided results that statistically varied from our primary analyses (those depicted in figure 1).

We included the bird taxonomic hierarchy (order, family, genus, species) as a series of nested random effects in general linear mixed models [58] to examine the scaling of parasite load with host body size using the individual-level data. We assessed model adequacy as described above. These analyses were also implemented with JMP PRO 13 (SAS Institute Inc.).

**Ethics.** We collected animals in the field with the following permissions: UCSD Institutional Animal Care and Use Committee Protocol no. S15102, California Department of Wildlife Permit no. SC-7273 and US Fish and Wildlife Permit no. MB74895A-0.

**Data accessibility.** Data available from the Dryad Digital Repository: <https://doi.org/10.6075/JOP55KVH> [59].

**Authors' contributions.** R.F.H. conceived of the study; K.L.S. and R.F.H. designed the methodology; K.L.S., A.V.T. and R.F.H. obtained and managed the data; R.F.H. performed the analyses; R.F.H. and K.L.S. interpreted the data. R.F.H. drafted the paper, while K.L.S. and A.V.T. critically edited the paper.

**Competing interests.** We declare we have no competing interests.

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