The scaling of total parasite biomass with host body mass

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Abstract

The selective pressure exerted by parasites on their hosts will to a large extent be influenced by the abundance or biomass of parasites supported by the hosts. Predicting how much parasite biomass can be supported by host individuals or populations should be straightforward: ultimately, parasite biomass must be controlled by resource supply, which is a direct function of host metabolism. Using comparative data sets on the biomass of metazoan parasites in vertebrate hosts, we determined how parasite biomass scales with host body mass. If the rate at which host resources are converted into parasite biomass is the same as that at which host resources are channelled toward host growth, then on a log–log plot parasite biomass should increase with host mass with a slope of 0.75 when corrected for operating temperature. Average parasite biomass per host scaled with host body mass at a lower rate than expected (across 131 vertebrate species, slope = 0.54); this was true independently of phylogenetic influences and also within the major vertebrate groups separately. Since most host individuals in a population harbour a parasite load well below that allowed by their metabolic rate, because of the stochastic nature of infection, it is maximum parasite biomass, and not average biomass, that is predicted to scale with metabolic rate among host species. We found that maximum parasite biomass scaled isometrically (i.e., slope = 1) with host body mass. Thus, larger host species can potentially support the same parasite biomass per gram of host tissues as small host species. The relationship found between maximum parasite biomass and host body mass, with its slope greater than 0.75, suggests that parasites are not like host tissues: they are able to appropriate more host resources than expected from metabolically derived host growth rates.
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1. Introduction

The growing recognition that parasitism is a major selective force in evolution and a key structuring force in ecosystems (e.g., Combes, 2001; Thomas et al., 2005) has fuelled much research on the determinants of parasite diversity and abundance. In particular, many studies over the past two decades have focused on patterns of parasite diversity and their underpinning mechanisms, mostly with respect to the interspecific variation in parasite species richness among host species (Poulin, 1997; Poulin and Morand, 2004). In contrast, there has been less attention paid to variation in parasite abundance among host species.

Parasite abundance, i.e., the number of parasite individuals per host, determines the importance of parasitism as a selective force or as an ecological process. As a rule, larger-bodied parasite species are less abundant than smaller-bodied species (Arneberg et al., 1998). From the host perspective, however, parasite biomass is a more relevant measure of parasite abundance than the total number of parasite individuals, simply because within a given parasite community, body sizes of individual parasites can vary over three or more orders of magnitude (e.g., tiny trematodes and large cestodes sharing the same host). The supply of energy and nutrients should ultimately determine how much biomass can be sustained; for parasites, therefore, host metabolic rate should be a key determinant of total biomass.

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Metabolism is the biological processing of energy and materials, determining the rate at which resources are taken up, transformed and allocated to various functions. Only George-Nascimento et al. (2004) have examined interspecific variation in total parasite biomass among different host species. They found that, among species of vertebrate hosts, the average total biomass of helminth parasites per host increased allometrically with host mass, with a slope close to but different from that expected from the relationship between basal metabolic rate and body mass. The log–log slope being less than 1, larger hosts appeared to harbour a lower parasite biomass per gram of host body than small hosts, that is, parasite 'density' scales negatively with host mass; however, host body mass explained only a small portion of the variance in parasite biomass. This applied to the *average* biomass supported by individual hosts in a population, and not to the *maximum* biomass that an individual host can support. Because of the stochastic nature of infection processes, most hosts harbour a parasite load well below that allowed by their metabolic rate; it is thus maximum parasite biomass, and not average biomass, that is predicted to scale with metabolic rate among host species. In addition, as emphasised in its latest formulation (Brown et al., 2004), the metabolic theory of ecology also accounts for the operating temperature of organisms. Metabolic rate increases exponentially with temperature, and many biological parameters, including individual and population growth rates, developmental time and lifespan, all show temperature dependence (Gillooly et al., 2001; Brown et al., 2004). This should also apply to the rate at which parasites process host materials and energy and convert them into parasite tissue.

The expected scaling of parasite biomass with host body mass can be derived from theory. Body size and operating temperature are the key factors regulating host metabolic rate. Like other characteristics of organisms, whole-organism metabolic rate scales allometrically with body mass, as $H^{3/4}$; thus, on a log–log plot metabolic rate increases with increasing body mass, H, with a slope of 0.75 (Gillooly et al., 2001; Savage et al., 2004). At the same time, metabolic rate and other rates of biological activity also increase exponentially with temperature, as described by the Boltzmann factor $e^{-E/kT}$, where E is the activation energy (in electron volts), k is Boltzmann's constant, and T is absolute temperature in K (see Gillooly et al., 2001; Brown et al., 2004). The Boltzmann factor specifies the effect of temperature on reaction rates by determining the proportion of molecules with sufficient kinetic energy. It describes quite well the temperature dependence of whole-organism metabolic rate across all taxa and all sizes (Gillooly et al., 2001). Thus, the joint effect of body size and temperature on individual metabolic rate, I, can be described as:

$$I \propto H^{3/4}e^{-E/kT}$$

Using the value of $E = 0.63$ eV obtained by Brown et al. (2004), metabolic rate can be temperature-corrected to isolate the effect of body mass.

This relationship can be applied to other biological rates. Organisms devote some fraction of their metabolism to the production of new biomass for growth and reproduction. Empirically, rates of whole-organism biomass production should be proportional to $H^{3/4}e^{-E/kT}$, whereas rates of mass-specific biomass production should scale as $H^{-1/4}e^{-E/kT}$ (Brown et al., 2004). This suggests that a constant fraction of metabolism is allocated to biomass production. Brown et al. (2004) found that, across a wide range of eukaryotic plants and animals, the log–log relationship between temperature-corrected rates of whole-organism biomass production and body mass had a slope of almost exactly 0.75, with all values clustering tightly around the regression line.

Within the host organism, parasites 'steal' a portion of the metabolic products that would otherwise be allocated to host growth or other functions, and use it for the production of parasite biomass. Following infection, endo- and ectoparasitic metazoans either grow in or on their hosts, or transform host resources directly into parasite eggs or propagules. The combined parasites in or on a host can be viewed almost as a separate organ 'competing' for the available resources. The rate of conversion of host resources into parasite biomass may thus follow the same scaling rules and constraints that apply to the production of host biomass. The parasite biomass, P, supported by a host organism would therefore scale as:

$$P \propto H^{3/4}e^{-E/kT}$$

The mass-specific parasite biomass, P/H, or the parasite biomass per gram of host, would scale as:

$$\frac{P}{H} \propto H^{-1/4}e^{-E/kT}$$

When P and P/H are temperature-corrected, and plotted against host mass on a log–log plot, we would expect slopes of 0.75 and −0.25, respectively. These provide testable predictions and bases for comparisons should the observed relationships deviate from these values.

Here, we ask how much parasite biomass can be supported by host individuals and populations. We revisit the analysis of George-Nascimento et al. (2004) in two important ways. First, we account for the effect of operating temperature when scaling parasite biomass with host body mass. Second, we test whether *maximum* parasite biomass per host follows more closely the expectations of the metabolic theory than *average* parasite biomass.

2. Methods

We used the dataset of George-Nascimento et al. (2004), which is probably the most comprehensive comparative dataset on the biomass of larval and adult metazoan parasites in vertebrate hosts. The dataset includes average biomass of endoparasitic helminths (trematodes, cestodes, nematodes and acanthocephalans) from 131 species of vertebrates. To examine maximum parasite biomass per host

(see below), we used a separate dataset on the biomass of both ecto- and endoparasitic metazoans from 34 fish species, obtained by one of us (MGN) from direct measurements taken from commercially caught fish. The fact that this dataset includes ectoparasites as well might affect the intercept of the relationship with host body mass (by producing proportionally higher values of total parasite biomass), but not the slope, and it is the slope that is of interest here.

Biovolume was used as a surrogate for biomass, with 1 cm^3 representing 1 g of tissue. For parasites, biovolume was obtained either using body dimensions and simple formulae for the volume of regular shapes, such as a cylinder in the case of nematodes or most acanthocephalans, or by water displacement in a small beaker for large parasites with irregular shapes (see George-Nascimento et al., 2004). For each of the 131 host species in the first dataset, average parasite biomass, or P, was taken as the total combined biomass of all parasite species per individual host, averaged across all individuals examined for that particular host species. For the 34 fish species in the second dataset, maximum parasite biomass, or P_{max}, was the highest value for combined biomass of all parasite species found in an individual host. The number of individual hosts examined per fish species ranges from 15 to 923 among these 34 fish species. Given that one needs to look at many fish in a population in order to find the one harbouring the highest biomass of parasites, sampling effort may influence estimates of maximum parasite biomass. To account for this possibility, we performed a multiple regression across the 34 fish species, using ln-transformed data, with maximum parasite biomass as the dependent variable and both host mass and sample size as independent variables. There was no apparent effect of sample size on maximum parasite biomass (standardised regression coefficient = 0.053, $P = 0.546$); thus, our estimates of maximum parasite biomass for a given host mass are unbiased by sampling effort.

Host mass, H, was obtained for each host species as the average mass of an individual, from various literature sources (George-Nascimento et al., 2004). Given that total parasite biomass is orders of magnitude smaller than host body mass, subtracting the former from the latter made no difference whatsoever to the analyses and in the analyses presented here we did not make the subtraction.

Values of parasite biomass, P and P_{max}, supported by a host and of mass-specific parasite biomass, P/H and P_{max}/H, i.e., the parasite biomass per gram of host, were temperature-corrected by the Boltzmann factor. We used the value of $E = 0.63$ eV obtained by Brown et al. (2004). For operating temperature, we used 37 °C for mammal hosts, 40 °C for bird hosts (Hoar, 1975) and 15 °C for ectothermic hosts, i.e., fish, amphibians and reptiles. This value of 15 °C for ectotherms is a rough median of the range that most ectothermic vertebrates would experience on a daily or seasonal basis, and is meant as a rough estimate of their average operating temperature. Using slightly different values had no major effect on the results: the intercept of the

relationship between temperature-corrected parasite biomass and host mass was pushed upward slightly by using a higher operating temperature for ectotherms, but the slope value did not change significantly.

Relationships between temperature-corrected parasite biomass and host mass were fitted using ordinary least squares (OLS) regression, as in Savage et al. (2004). It is possible that phylogenetic influences mask the true relationship between these variables. The standard way of controlling for potential phylogenetic influences is to use the phylogenetically independent contrast method (Felsenstein, 1985; Garland et al., 1992). Using a phylogeny of the 131 vertebrate taxa used here constructed from published studies (see George-Nascimento et al., 2004), we repeated our analyses using contrasts instead of species values, with the regression line forced through the origin.

3. Results

Temperature-corrected average parasite biomass, P, increased with increasing host mass ($F_{1,129} = 36.57$, $r^2 = 0.22$, $P = 0.0001$), though the relationship was not particularly strong (Fig. 1). The allometric exponent of the relationship, indicated by the slope, was 0.54 (95% confidence interval (CI): 0.36–0.71), lower than the expected value of 0.75. Similarly, the average mass-specific parasite biomass, P/H, decreased with increasing host mass ($F_{1,129} = 26.97$, $r^2 = 0.17$, $P = 0.0001$), again with much scatter in the data and with a slope (−0.46, 95% CI = −0.64 to −0.29) different from the expected slope value of −0.25. Following a correction for host phylogeny, the relationship between contrasts in temperature-corrected average parasite biomass, P, and contrasts in host mass again showed a slope (OLS regression forced through the
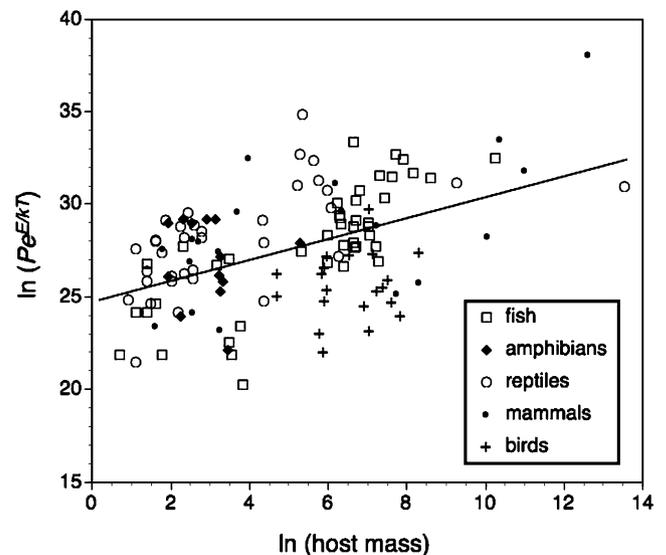

Fig. 1. Relationship between temperature-corrected average parasite biomass, P (in mg), and host mass (in g), across 131 species of vertebrate hosts.

Table 1
Results of log–log ordinary least squares regressions between temperature-corrected average parasite biomass, P, and host mass, in different host taxa

Host taxon	df	F ratio	r^2	P-value	Slope (95% CI)
Fish	1, 41	68.45	0.63	0.0001	1.10 (0.83, 1.37)
Amphibians	1, 11	0.11	0.01	0.7526	−0.25 (−1.96, 1.46)
Reptiles	1, 33	18.86	0.36	0.0001	0.63 (0.34, 0.93)
Mammals	1, 18	10.36	0.37	0.0048	0.63 (0.22, 1.04)
Birds	1, 18	0.34	0.02	0.5683	0.25 (−0.64, 1.13)

95% CI, 95% confidence interval.

origin: slope = 0.59, 95% CI 0.45–0.73) lower than the expected one. Another way of dealing with potential phylogenetic effects is to repeat the analysis within each host taxon separately. When this is done, the slope of the regression between temperature-corrected average parasite biomass and host mass only approximates the predicted value of 0.75 in two host taxa, the reptiles and mammals (Table 1).

Among fish hosts, temperature-corrected maximum parasite biomass, P_{max}, increased with increasing host mass ($F_{1,32} = 113.12$, $r^2 = 0.78$, $P = 0.0001$). This clear linear relationship (Fig. 2) had a slope of approximately 1, i.e., 0.97 (95% CI: 0.80–1.14), clearly higher than the value of 0.75 expected if parasites behaved merely as host tissues. The maximum mass-specific parasite biomass, P_{max}/H, did not change with increasing host mass ($F_{1,32} = 0.06$, $r^2 = 0.03$, $P = 0.822$; slope = −0.02, 95% CI = −0.20 to 0.17). These relationships are essentially unchanged when the analyses are performed on phylogenetically independent contrasts (P_{max} versus host mass: slope = 0.99). These log–log slopes indicate that maximum parasite biomass per gram of host is independent of host mass, i.e., larger hosts can potentially support the same parasite biomass per gram as small hosts.
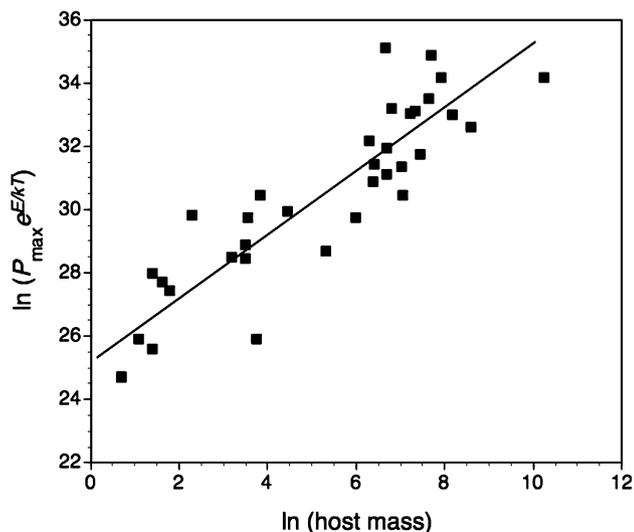

Fig. 2. Relationship between temperature-corrected maximum parasite biomass, P_{max} (in mg), and host mass (in g), across 34 species of fish hosts.

4. Discussion

Biomass production within an organism includes that of the organism itself and also that of its parasites. The latter divert a portion of the metabolic products of the host and use it for the production of parasite biomass. We might expect that parasite biomass would scale with host body mass just as host biomass production, as though the combined parasites in a host were like a separate organ competing for the available resources. However, the empirical evidence suggests that the *maximum* rate of conversion of host resources into parasite biomass can exceed (slope > 0.75) the predicted value that applies to the production of host biomass. In contrast, when computed across all individual hosts in a population, the *average* parasite biomass does not increase as markedly (slope < 0.75) with host mass as expected from the predictions of the metabolic theory, after correcting for the host's operating temperature. Many potential confounding variables, not taken into account in our analysis, may mask the true relationship between parasite biomass and host mass. Nevertheless, assuming that the scaling factors we obtained here are approximately correct, physiological, epidemiological and evolutionary arguments can explain why they differ from the one expected for host biomass production and derived from the metabolic theory of ecology.

First, the rate at which host energy and resources are taken up by parasites may depend more on parasite body sizes than on host mass. Since metabolism scales with body size for parasites as well as for hosts, small parasites should require more resources, per unit body mass, than large parasites (Brown et al., 2004). Here, we considered the entire parasite community in a host as a pooled mass. As there can be hundreds of individual parasites, of different species and of vastly different sizes, inside a single host, taking parasite body size into account is problematic. Their small size relative to the host might explain why the slope of the relationship between maximum parasite biomass and host body mass was higher than the 0.75 expected if this parasite biomass were merely behaving like host tissue.

Second, unlike host tissues, which grow from cells already present in the host's body, parasites must first be recruited from the external environment before they can grow using host resources. In the case of endoparasitic helminths, infection usually occurs when the host ingests food containing the parasite's infective stages. Differences among individual hosts in past acquisition of parasites will generate differences among them in parasite biomass currently harboured. Because of the stochasticity of infection processes, even conspecifics of similar age, sex and body size often differ greatly in how many parasites they harbour (Shaw and Dobson, 1995; Wilson et al., 2002). Among the naturally infected animals that contributed to the dataset, many were probably far from harbouring the maximum number of parasite species or individuals that they can support in principle, resulting in a scaling factor between average parasite biomass, P, and host mass well below 0.75.

Thus, at the host population level, predictions from the metabolic theory of ecology are confounded by epidemiological processes that cause some host individuals to harbour only a partial load of parasites. Host mass and metabolism may well place an upper limit on the parasite biomass that can be supported, however; maximum parasite biomass, P_{max}, representing host individuals saturated with parasites, does indeed relate strongly to host mass, though the maximum parasite biomass per gram of host is independent of host mass.

Third, some parasite species may have evolved rates of resource uptake approaching the maximum that host metabolism allows, even if these rates are not sustainable in the long term. In many of the fish species analysed here, when an individual host harbours a high parasite biomass, this is normally due to one or a few dominant parasite species accounting for most of the biomass (Mouillot et al., 2005). Helminth parasites are often rather benign to their vertebrate definitive host, and deleterious effects of infection are sometimes difficult to detect under natural conditions (Ewald, 1995; Poulin, 1998). Nevertheless, flexible growth strategies may allow some parasite species to build up a biomass close to the upper ceiling that their host can support; low virulence may ensure the survival of the host and extend resource use by the parasites to make this growth possible.

It is likely that our data slightly underestimated parasite biomass for two reasons. First, part of the parasite production derived from host energy and nutrients is manifested not as parasite growth, but as parasite reproductive output. This component of parasite biomass could not be estimated here, but it can be substantial. Second, we included only data on metazoan parasites in our computation of total parasite biomass; although much smaller, protozoans, fungi and other taxa of pathogens could also make a small contribution to parasite biomass in some extreme cases. Our data set did not happen to include fish species harbouring the unusually large larval (plerocercoid) stages of certain cestode taxa, such as *Schistocephalus* or *Ligula*, which can achieve up to 50% of their host's mass (Arme and Owen, 1967; Sweeting, 1977). These occur in small-bodied fish, and their inclusion would greatly lower our slope values. However, these cestodes are truly exceptions among helminth parasites and in a search for general patterns it may be best to exclude them.

Our results on maximum parasite biomass are based on data for fish hosts only. In fish, average parasite biomass also scales with host body mass with a slope of about 1 (Table 1), just like maximum parasite biomass. It would therefore be important to verify whether the relationship is unique to fish or more broadly applicable to vertebrates. Also, different parasite taxa feed on host resources in different ways: some absorb digested food in the host gut, others browse on host tissues, etc. It would be interesting to see whether the biomass of these different feeding guilds scales differently with host body mass. Nevertheless, based on the results presented here, parasites as a whole do not appear to behave like host tissues: they apportion a greater amount of host resources than their 'fair' share.

Host metabolism determines the availability of resources for parasites and it is not surprising that maximum parasite biomass scales strongly with host metabolism. For the same reasons, parasite diversity should also depend on host metabolism. In the only study of its kind, Morand and Harvey (2000) found that the basic metabolic rate of mammals correlated positively with the species richness of their fauna of endoparasitic helminths. Two alternative explanations exist for this finding. On the one hand, host species suffering from infection by many parasite species may have been selected to evolve a higher metabolic rate to compensate for the cost of stronger immune responses. On the other hand, host species with a high metabolic rate would consume food at a higher rate and thus be exposed to more parasite infective stages, leading to higher colonization rates by new parasites over time. The lack of a quantitative prediction for the slope of the relationship between metabolic rate and parasite species richness makes it difficult to distinguish between these two causal pathways.

Just as predicting the quantitative relationship between host traits and parasite species richness has proven difficult (see Poulin and Morand, 2004), predicting parasite biomass is apparently not as simple as extending the expectations of the metabolic theory of ecology regarding biomass production. The *maximum* parasite biomass per gram of host appears to be mass-independent, at least among fish hosts; it is the *average* parasite biomass across the host population that remains difficult to predict. A theoretical synthesis of metabolic and epidemiological processes may be necessary to achieve this ultimate prediction.

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