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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.

Keywords: Helminths; Metabolic rate; Operating temperature; Vertebrate hosts; Virulence

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