

## LETTER

## Testing the energetic equivalence rule with helminth endoparasites of vertebrates

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### Abstract

As a general test of the energetic equivalence rule, we examined macroecological relationships among abundance, density and host body mass in a comparative analysis of the assemblages of trophically transmitted endoparasitic helminths of 131 species of vertebrate hosts. Both the numbers and total volume of parasites per gram of host decreased allometrically with host body mass, with slopes roughly consistent with those expected from the allometric relationship between host basal metabolic rate and body mass. From an evolutionary perspective, large body size may therefore allow hosts to escape from the deleterious effects of parasitism.

### Keywords

Chile, density, endoparasites, host body mass, macroecology, parasite body mass, trophically transmitted, vertebrates.

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### INTRODUCTION

The interspecific relationship between body size and population density has major implications for the structure of and energy flow in ecological communities (Damuth 1981, 1987; Brown 1995; Gaston & Blackburn 2000). The logarithmic relationship between body mass and population density for mammals has a slope of  $-0.75$  (Damuth 1981, 1987). Metabolic processes can explain the negative slope: larger animals should occur at lower population densities because they use more energy per capita per unit time (Peters 1983). Because the logarithmic relationship between the basal metabolic rate of mammals and their body mass has a slope of  $\approx 0.75$  (see Peters 1983), Damuth (1981, 1987) proposed the energetic equivalence rule, which states that the energy used by the local population of a species is independent of its body mass. Energetic constraints may thus influence the structure of communities of free-living organisms. However, the energetic equivalence rule also has important

ramifications for communities of parasites that live within host populations and derive all their energy from the host: given the relationship between body mass and metabolic rate, how should the average parasite density or biomass sustained by individual hosts scale with host body mass?

Individual hosts require energy to survive and reproduce such that abundance and total biomass are usually related to the amount of available energy (e.g. Wright *et al.* 1993; Turner *et al.* 1996; Crete 1999; Gaston & Blackburn 2000). Several key aspects of parasite populations and communities are thought to be determined by processes of energy flux (Arneberg 2002; Poulin *et al.* 2003). In this context, we hypothesize that larger hosts, with higher total energetic demands, by virtue of canalizing a higher amount of resources per unit time, should harbour a higher abundance of parasites (in terms of both numbers and biomass). Also, if both the parasite metabolic rate and the host metabolic rate scale with similar exponents of  $\approx 0.75$  (Von Brand 1979; Peters 1983), the number of parasites per unit host mass

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(numerical density) should decrease with increasing host body size. Quantitatively, we predict that total parasite biomass should scale with individual host mass with an exponent of 0.75 characterizing the body mass vs. metabolic rate relationship.

Here, we first provide empirical assessments of the relationships between host mass and parasite biomass and density across several species of vertebrate hosts. Second, we attempt to reconcile the observed slopes of the relationships with the predictions of the energetic equivalence rule. We consider the entire community of macro-parasites in a host as a unit, rather than focusing on particular parasite lineages as in earlier macroecological studies of parasites (Morand *et al.* 1996; Poulin 1996, 1999; Arneberg *et al.* 1998); the various species in a parasite community may or may not interact with each other, but they all combine to drain energy from the host.

Our analysis suggest that among host species, such communities vary in the total number of individuals, biovolume, and density of parasites is a function of the rate at which energy flows through the host.

## MATERIAL AND METHODS

Data on communities of helminth endoparasites of 131 vertebrate host species were compiled (a detailed list of host species can be found in Poulin *et al.* 2003). Between 1983 and 2000, 44 species of marine fish, two lizard (*Liolaemus* spp.), and one marine mammal (*Otaria flavescens*) were collected between 33° and 51° S along Chile, and examined for parasites. Data on the endoparasites of 84 additional species were obtained from the literature. Body dimensions of their parasites were retrieved from the taxonomic literature as described below. We analysed all helminth species found in these hosts, regardless of their location in the host's body. In all, 1014 different host-parasite associations were included. These included larval and adult nematodes, cestodes, acanthocephalans and adult digeneans.

Numerical abundance (total number of parasites per host), volumetric abundance (total volume of parasites per host), numerical density (numerical abundance divided by the host body volume or mass), volumetric density (volumetric abundance divided by the host body volume or mass), and sample size (number of individual hosts examined) were recorded for each component community. Biovolume is used here as a surrogate for biomass. Host body size for each fish host species is the average volume of individual fish (cm<sup>3</sup>), based on measurements of total body length, width and depth (volume = length × width × depth). Similar data were obtained from the literature for the host body volume (reptiles and amphibians) or body mass (birds and mammals, in grams) of the other vertebrate

groups. Parasite body sizes of all metazoan parasites inhabiting each fish were quantified for each taxon separately. The body mass of each parasite taxon was expressed as the volume (mm<sup>3</sup>) of a cylinder (nematodes and some acanthocephalans), an ellipsoid (digeneans, monogeneans and some cestodes), or a cylinder with an ovoid base (most cestodes). For taxa with large bodies or irregular forms, we measured the volume of displaced water in a beaker. In common and abundant taxa, the number of parasites measured consisted of at least 30 specimens. In parasites with more than one host, body size was measured in each host species. Body size of parasites in hosts other than fish was determined using body dimensions of these parasites obtained from the literature.

To account for potential host phylogenetic influences on the various relationships, we analysed the data using the phylogenetically independent contrasts method (Felsenstein 1985). Phylogenies were constructed from the literature for species of fishes (Lauder & Liem 1983; Nelson 1994; Bargelloni *et al.* 2000), amphibians (Hillis & Davis 1986; Ruvinsky & Maxson 1996; Graybeal 1997), reptiles (Estes *et al.* 1988; Densmore *et al.* 1992; Butler & Losos 1997; Wiens & Reeder 1997; Bonine & Garland 1999; Jackman *et al.* 1999; Giannasi *et al.* 2000), birds (Sibley & Ahlquist 1990) and mammals (Cooper & Fortey 1998; Bininda-Emonds *et al.* 1999; DeBry & Sagel 2001; Jones *et al.* 2002) in our data set. Contrasts were computed on log-transformed data and all regression analyses were forced through the origin (Garland *et al.* 1992; Purvis & Rambaut 1994). Additional corrections for other confounding variables such as sample size were based on residuals of ordinary least squares (OLS) regressions before and after phylogenetic corrections.

## RESULTS

The analysis for the pooled data across all host taxa shows that the total number of parasite individuals per host and the total volume of parasites per host, increased with host body size. Allometric exponents were less than 1, both before and after corrections for sampling effort and phylogenetic influences (Table 1). Consequently, numerical and volumetric density of parasites decreased with host body mass. This negative trend was steeper, and stronger for numerical density than for the volumetric density (Fig. 1, Tables 1 and 2). Within taxa, parasite biomass per unit host biomass also decreased, but the exponents did not differ significantly from 0.0, perhaps reflecting smaller sample sizes.

## DISCUSSION

As predicted by the energetic equivalence rule, parasite biomass (estimated here as volumetric abundance  $A_v = M_p \times N_p$ ; see Table 1) should increase with host mass ( $M_h$ ) as

$$M_p \times N_p \propto M_h^{0.75}, \tag{1}$$

where *M* stands for mass, *N* for abundance or number of individuals, *h* for host and *p* for parasite. Equation 1 implies that parasite biomass is in a steady state with available energy, which is a function of the host body size and metabolic demands. The existence of this steady state between energy use and energy availability underpins the allometric scaling of most of the other quantities as we show below. Our results indicate that

$$N_p \propto M_h^{0.274}. \tag{2}$$

Hence, replacing eqn 2 in eqn 1 we obtain

$$M_p \propto M_h^{0.476}. \tag{3}$$

Using the above assumptions and equations we can derive the scaling of the following quantities with host body mass:

Parasite volumetric density

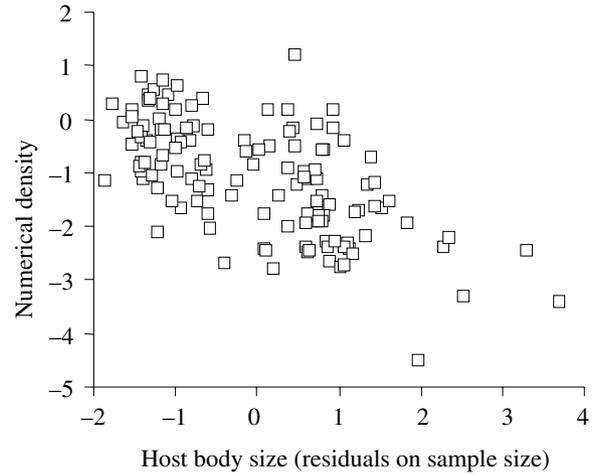
$$\frac{M_p \times N_p}{M_h} \propto M_h^{-0.25}. \tag{4}$$

Parasite numerical density (replacing eqn 3 in eqn 4),

$$\frac{N_p}{M_h} \propto M_h^{-0.726}. \tag{5}$$

Both of these exponents are close to the estimated slopes we obtained when all host taxa are combined (Table 1, Fig. 1).

Our first conclusion is that parasite communities inhabiting large hosts have more individuals but attain lower numerical density than those in small hosts; the latter relationship shows a good quantitative fit to the predictions of the energetic equivalence rule. Small hosts might thus evade the deleterious effects of parasitism on a per capita basis, while in large hosts the harmful effects of parasites might be diluted when considered on a per-unit-mass basis.



**Figure 1** Numerical density of parasites decreases with the host body size at a rate of  $-0.71$  ( $SE = 0.10$ , after correction for sampling effort) accounting for  $c. 32\%$  of the variance. Each data point is an independent phylogenetic contrast.

When the allometric relationships are calculated separately for the different host taxa, that data on fish and mammals provide the best match with theoretical expectations (Table 2), probably because they are of better and more consistent quality. For most other taxa, the relationships are not statistically significant. Interestingly, the relationship between numerical density and host body mass is strong and significant (or close to significant) for most taxa. In part, this may be explained by the simple fact that counting parasite individuals provides more accurate results than evaluating their weight or volume. In addition, biomass estimates are based on the average size of parasites in each assemblage, a procedure that may introduce additional noise in the relationship. Still, our second main conclusion is that, if the patterns in Table 2 are not influenced by other confounding variables, the allometric exponent relating the

**Table 1** Slope (*b*), standard error (SE) and coefficient of determination ( $r^2$ ) of OLS log–log linear regressions on the raw data ( $n = 131$  communities) and on log–log linear regressions through the origin between independent contrasts of the residuals of all the variables ( $n = 108$  contrasts) corrected for sample size, vs. the independent contrasts in vertebrate host body size, also corrected for sample size

	$N_p$	$A_v$	$M_p$	$D_n$	$D_v$
<b>Raw data</b>					
<i>b</i> ± SE	0.418 ± 0.061	0.819 ± 0.089	0.390 ± 0.064	-0.570 ± 0.060	-0.187 ± 0.088
$r^2$	0.268	0.398	0.224	0.409	0.031
<i>P</i> -value	<0.001	<0.001	<0.001	<0.001	0.044
<b>Independent contrasts corrected for sample size</b>					
<i>b</i> ± SE	0.274 ± 0.111	0.663 ± 0.156	0.376 ± 0.117	-0.713 ± 0.100	-0.336 ± 0.157
$r^2$	0.054	0.144	0.087	0.321	0.041
<i>P</i> -value	0.015	<0.001	0.002	<0.001	0.035

$N_p$ , numerical abundance;  $A_v$ , volumetric abundance;  $M_p$ , average parasite volume ( $\text{mm}^3$ );  $D_n$ , numerical density (number of parasites  $\text{cm}^{-3}$  host);  $D_v$ , volumetric density ( $\text{mm}^3$  parasite  $\text{cm}^{-3}$  host).

**Table 2** Slope ( $b$ ), standard error (SE) and coefficient of determination ( $r^2$ ) of log–log linear regressions through the origin between the independent contrasts of all the variables vs. the independent contrasts in vertebrate host species body size (separate for each vertebrate class) corrected for sample size

	$N_p$	$A_v$	$M_p$	$D_n$	$D_v$
Fishes ( $n = 30$ )					
$b \pm SE$	$0.363 \pm 0.149$	$0.943 \pm 0.256$	$0.580 \pm 0.171$	$-0.637 \pm 0.149$	$-0.057 \pm 0.256$
$r^2$	0.169	0.319	0.284	0.385	0.002
$P$ -value	0.022	0.001	0.002	0.001	0.825
Amphibians ( $n = 12$ )					
$b \pm SE$	$-0.226 \pm 0.372$	$-0.147 \pm 0.758$	$0.080 \pm 0.492$	$-1.227 \pm 0.363$	$-1.147 \pm 0.745$
$r^2$	0.033	0.003	0.002	0.509	0.176
$P$ -value	0.555	0.850	0.874	0.006	0.153
Reptiles ( $n = 31$ )					
$b \pm SE$	$0.428 \pm 0.275$	$0.172 \pm 0.415$	$-0.256 \pm 0.442$	$-0.571 \pm 0.273$	$-0.828 \pm 0.416$
$r^2$	0.075	0.005	0.011	0.128	0.116
$P$ -value	0.130	0.681	0.567	0.045	0.056
Birds ( $n = 17$ )					
$b \pm SE$	$0.219 \pm 0.772$	$0.481 \pm 0.569$	$0.400 \pm 0.365$	$-0.837 \pm 0.447$	$-0.518 \pm 0.583$
$r^2$	0.005	0.043	0.046	0.180	0.047
$P$ -value	0.780	0.410	0.494	0.079	0.387
Mammals ( $n = 14$ )					
$b \pm SE$	$0.302 \pm 0.271$	$0.714 \pm 0.348$	$0.412 \pm 0.215$	$-0.698 \pm 0.303$	$-0.286 \pm 0.384$
$r^2$	0.087	0.244	0.220	0.289	0.041
$P$ -value	0.285	0.061	0.078	0.039	0.470

$N_p$ , numerical abundance;  $A_v$ , volumetric abundance;  $M_p$ , average parasite volume ( $\text{mm}^3$ );  $D_n$ , numerical density (number of parasites  $\text{cm}^{-3}$  host);  $D_v$ , volumetric density ( $\text{mm}^3$  parasite  $\text{cm}^{-3}$  host);  $n$ , number of contrasts.

total parasite biomass per  $\text{cm}^3$  of host to host body mass (i.e. including all species within a parasite community;  $D_v$  in Table 2) is not different from 0, implying that the parasite community as a whole uses a fixed proportion of the available host energy, and that each gram of host can support a more or less constant amount of parasite biomass (see Carbone & Gittleman 2002). While the idea is seductive, this result differs from the predicted exponent of  $-0.25$  (eqn 4). This discrepancy may reflect the absence of a relationship between  $N_p$  and  $M_p$  in our data (among host species in our data set,  $r^2 = 0.01$ ,  $b \pm SE = 0.10 \pm 0.89$ ,  $P < 0.26$ ), as well as a lower expected slope when the analyses are made within host taxa (Pagel & Harvey 1988).

Our results indicate that parasite communities scale in both numbers and biomass with host body mass, in a way that fits some predictions of the energetic equivalence rule. The rule was developed as an explanation for interspecific variation in population density (Damuth 1981, 1987); when applied to entire communities, however, its predictions do not always prove accurate (e.g. Russo *et al.* 2003). There are no analogous study units such as hosts in communities of free-living organisms, and there is no parallel to host metabolic rate in free-living communities inhabiting non-living environments; nevertheless, our results indicate that energy availability may play the same fundamental role in all

kinds of ecological communities. Our results also have evolutionary implications, as they suggest that, on average, the selective pressures exerted by parasites on small-bodied hosts are greater, per gram of host, than those placed on large-bodied host species.

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