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Body size–density relationships and species diversity in parasitic nematodes: patterns and likely processes

S. Morand[1]* and R. Poulin[2]

[1]*Centre de Biologie et d'Ecologie Tropicale et Méditerranéenne, UMR 5555 CNRS, Université de Perpignan, 66860 Perpignan cedex, France and* [2]*Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand*

ABSTRACT

We examined the patterns of body size distribution in parasite nematodes in relation to species diversity and abundance. We hypothesized that parasite body size is optimized and we used the net transmission rate as a fitness function. The net transmission rate was derived from classical epidemiological models. We tested the predicted patterns emerging from the optimal model using observed patterns of nematode distribution and abundance of terrestrial mammals. Our model predicts a value for the slope of the relationship between parasite body size and host body size that is found for the oxyuroids, a highly host-specific group of nematodes with direct life cycles.

Keywords: abundance, body size, energetic equivalence rule, model, nematode.

INTRODUCTION

Two related research programmes in evolutionary ecology – life-history evolution and macroecology – are both founded on body size being the fundamentally most important feature of any organism. First, almost all life-traits, such as fecundity, basal metabolic rate and life span, covary with body size (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Charnov, 1993). Second, species diversification is related to body size diversification (May, 1978; Dial and Marzluff, 1988; Brown and Maurer, 1989; Maurer *et al.*, 1992), and body size is a predictor of animal abundance (Damuth, 1981, 1987). The patterns and the determinants of species diversity and abundance are a central theme in macroecology (Brown, 1995), although the cause of variations in abundance among related groups of organisms is still unclear (Damuth, 1981, 1987, 1991; Brown and Maurer, 1989; Lawton, 1990; Nee *et al.*, 1991; Brown, 1995).

With respect to body size, three empirical patterns have emerged from macroecological studies. First, frequency distributions of body size are usually log-normal in many groups of organisms (Brown and Maurer, 1989; Brown, 1995), including parasites (Kirchner *et al.*, 1980; Poulin and Morand, 1997) with the exception of marine bivalves (Roy *et al.*, 2000). These distributions are right skewed, even on a logarithmic scale, such that the smaller size

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* Author to whom all correspondence should be addressed. e-mail: morand@univ-perp.fr

classes include the most speciose taxa. However, the more diversified taxa are small but not the smallest (Dial and Marzluff, 1988).

Second, there is a negative interspecific relationship between population density and body size. The slope (or upper bounds) of about −0.75 for regressions of density versus body mass relationships in numerous groups confirms the energetic equivalence rule – that is, the energy used by the local population of a species in the community appears to be independent of body size (Damuth, 1981, 1991; Nee *et al.*, 1991). In the case of parasitic nematodes, Arneberg *et al.* (1998a) showed that the slope was around −0.20 and inconsistent with the energetic equivalence rule.

Third, the graphical distribution of data points in the above interspecific relationships is enclosed in a polygonal space. There is a small region where the upper bound declines as average body sizes decrease (Lawton, 1990; Brown, 1995), and below some critical density species disappear from the communities. For example, the threshold values where density starts to decrease when body size decreases are 100 g for mammals and 35 g for birds (Brown, 1995). Although the processes shaping body size distribution are not well understood, these processes invoke either ecological (predation, competition) or energetical (Bergman's rule) arguments (Roff, 1981; Charnov, 1993).

According to Naganuma and Roughgarden (1990), an optimally sized animal maximizes its rates of energy production throughout its life, and allocates its production energy towards growth and reproduction in a way that maximizes reproductive output (see also Kozlowski, 1992, 1996; Charnov, 1993). A similar energetic argument has been developed by Brown *et al.* (1993) in the case of mammalian species. Their model predicts an optimal body size for mammals, which fits the observed distribution. Moreover, the optimum mean body size of 100 g is the same as the mean observed mammalian body size.

Roff (1981), using a different approach, emphasized that the basic life-history parameters determining the rate of increase (r) are all known to be related to body size. Hence, r can be used as a fitness function that may be useful to investigate optimality in body size.

Brown (1995) suggested that the pattern of abundance as a function of body mass would look the same for all organisms, including parasites. Indeed, parasites are good candidates for investigating evolutionary and ecological questions (Poulin, 1996, 1998; Poulin *et al.*, 2000). Although parasites appear to be the most abundant organisms on Earth (Price, 1980; Poulin and Morand, 2000), studies of their patterns of distribution and abundance remain scarce (Poulin and Morand, 1997; Arneberg *et al.*, 1998a,b; Morand and Guégan, 2000).

In this paper, we describe the distribution of abundance as a function of body size for the case of the intestinal parasitic nematodes of mammals and estimate the upper bounds of the density–body size relationship. We hypothesize that parasite body size is optimized and we use the net transmission rate as a fitness function (Frank, 1996; Morand and Poulin, 2000). The net transmission rate is derived from classical epidemiological models of Anderson and May's type (Anderson and May, 1978, 1985). We test the predicted patterns emerging from the optimal model using observed patterns of nematode distribution and abundance of terrestrial mammals.

METHODS

Data on the abundance and body size of nematodes come from 90 studies published over the last 30 years (the electronic data set is available from S.M. upon request). We compiled data for a total of 497 populations of adult monoxenous (i.e. with direct life cycles) nematode worms belonging to 180 distinct species, recorded from the gut of 66 different species of terrestrial mammals. Data on mean intensity of infection (mean number of conspecific worms per infected individual host) are available for only 396 populations (149 species), with at least 15 individual hosts sampled per population (42 mammal species). Each parasite population was considered individually. Hence, the same parasite species can be found in different host species. We calculated a measure of the density of each nematode population by using the ratio of abundance (mean intensity of infection) to host body mass (in grams); this does not correspond to a correction for host body mass but rather to a measure of density (mean number of worms per gram of host) similar to measures used with free-living organisms (mean number per m^2, for example). Ideally, comparative analyses across species should be based on phylogenetically independent contrasts, or should attempt in some other way to take into account the potential influences of shared ancestry. The phylogeny of nematode taxa is relatively well-resolved at the order level, but very poorly resolved at the within-family level. Based on current knowledge, it was not possible to derive more than a handful of contrasts from the species included in our analysis; we therefore used species values in our tests.

Net reproduction rate

According to Anderson and May (1978), a directly transmitted nematode can be modelled by a set of differential equations, which describe the host population dynamics (H) and the parasite population dynamics (P) according to time (t). Here, we assume that the dynamics of free-living stages is negligible:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \lambda\beta HP - \left(b + \mu + \left(\frac{(k+1)}{k}\right)P\right)P$$

where λ is the fecundity per capita of adult parasites, b is the mortality rate of the hosts, β is the rate of infection, μ is the mortality rate of parasites and k is the aggregation of parasites (coefficient of the negative binomial distribution).

The net reproductive rate R_0 corresponds to the number of female offspring produced by an adult female worm throughout her reproductive life span, which survive to reach sexual maturity. This very simple model does not capture all the complexity and the variability exhibited by the parasitic nematodes. However, this model captures all the common features of directly transmitted nematodes.

The expression of the net reproduction rate R_0 is then obtained by considering the growth rate of the parasite population when one parasite is introduced into a population of uninfected hosts. The value of R_0 is then derived from (Dietz, 1975):

$$\frac{1}{P}\frac{\mathrm{d}P}{\mathrm{d}t} > 0$$

This gives the following expression for the net reproduction rate:

$$R_0 = \frac{\lambda\beta H}{(\mu + b)} \tag{1}$$

All these parameters are linked with body size, either host body size or parasite body size. Hence, parasite fecundity is linked to parasite body length (S_P in mm) by the following allometric relation: $\lambda \approx S_P^a$ with $a = 1.89$ (Morand, 1996). Parasite fecundity is linked to parasite body volume (S_P in mm^3) by the following: $\lambda \approx S_P^a$ with $a = 0.54$ (Skorping *et al.*, 1991). A similar slope was found when re-analysing the data of Morand (1996) and using volume instead of body length: $a = 0.76 \pm 0.32$. Adult mortality rate is linked to parasite fecundity (mean number of eggs produced per adult female parasite per day) according to $\mu \approx \lambda^d$.

Using the non-biased estimation of Gemmill *et al.* (1999), $\mu = \Pi/(g - \alpha M)$, where Π is assumed to be equal to the patent period – that is, the length of the reproductive period (Gemmill *et al.*, 1999) – and g and αM are constants ($g = 10$ and $\alpha M = 2$, according to Gemmill *et al.*, 1999), we obtained $d = -0.35$, in accordance with Morand (1996).

In the same way, host density (H) and host mortality (b) are both related to host body weight (W_H). In the case of mammals:

$$H \approx W_H^{-0.75}$$

$$b \approx 0.75\ W_H^{-0.25} \qquad \text{(Purvis and Harvey, 1995)}$$

Substituting λ, H, b and μ by their expressions in (1):

$$R_0 = \frac{\beta S_P^a W_H^{-0.75}}{((S_P^a)^d + W_H^{-0.25})} \tag{2}$$

Parasites may evolve in response to host density and host longevity (Sorci *et al.*, 1997; Morand and Sorci, 1998). Then, virulence and transmissibility will become evolutionary variables that may change to maximize the transmission of the disease, which is measured by the net reproduction rate.

The net reproduction rate has been repeatedly used as a fitness measure of mutant parasites, assuming that multiple infections do not occur (van Baalen and Sabelis, 1995; Frank, 1996; Morand and Poulin, 2000). The optimum parasite body size is obtained by solving

$$\frac{\delta R_0}{\delta S_P} = 0$$

$$\frac{\delta R_0}{\delta S_P} = 1 + \frac{d(S_P^a)^{-d}}{9(S_P^a)^{-d} + W_H^{-0.25})} = 0$$

This allows the following optimal parasite body size (calculated using MappleV®):

$$S_P^* = \mathrm{e}\left(-\frac{\ln(1/(W_H^{0.25})(1 + d))}{da}\right) \tag{3}$$

With the values of a and d given above, this leads to the following allometric relationships:

- log(S_P^* in mm) ≈ 0.38 log(host body size in grams)
- log(S_P^* in mm^3) ≈ 1.32 log(host body size in grams) using Skorping *et al.* (1991)
- log(S_P^* in mm^3) ≈ 0.94 log(host body size in grams) using Morand (1996) and the new estimates herein

TEST

Body size–density relationships in parasitic nematodes

The body size distribution of nematode species is log normal with a peak at 15 mm (Fig. 1). Nematode volume was calculated from measurements of body length and maximum width (in log mm^3) (Fig. 2a). The distribution of maximum intensity of infection as a function of body volume (in log mm^3) is enclosed in a polygonal space. There is a value of nematode body size, around 5 mm^3, corresponding to a body length of 15 mm, for which the maximum intensity of infection declines when body volume decreases. The estimated value of the slope is −1.77 (95% confidence interval of the slope −3.62 to −1.06) using major axis regression.

Two separate equations were fitted to the data on the maximal density observed for nematode species – that is, only one population per nematode species (Fig. 2b). The first was applied to nematode species for which volumes are greater than 1 (in log); this gave a negative slope of −1.19 (95% confidence interval of the slope −2.31 to −0.66) using major axis regression. The second was applied to nematode species for which volumes are less than 1 (in log); this gave a positive slope of 1.35 (95% confidence interval of the slope 1.01 to 1.84) using major axis regression.

Empirical relationship between host and parasite body size

An empirical relationship between host body size and parasite body size should be tested for in the case of highly host-specific nematodes only. The oxyuroids are one of these parasite groups that are highly specific to their mammalian hosts (Morand *et al.*, 1996; Hugot, 1999).

We found a positive relationship between parasite body length and host body size in oxyuroids (Fig. 3a): $\log(S_P \text{ in mm}) \approx 0.33 \log(W_H \text{ in grams})$ using major axis regression (95% confidence interval of the slope 0.28 to 0.39). A value of 0.33 for the observed slope is similar to the estimated slope of 0.38 (equation 3). Using volume, we found (Fig. 3b; note the smaller number of oxyuroid species for which we could estimate body volume): $\log(S_P \text{ in mm}^3) \approx 0.80 \log(W_H \text{ in grams})$ using major axis regression (95% confidence interval of the slope 0.63 to 1.03). The value of 0.80 for the observed slope tends towards the estimated slope of 0.94 (the estimated slope is within the 95% confidence interval of the observed slope).

We should point out that there was a good relationship between body length and body volume of oxyuroids ($R = 0.94$, $P < 0.0001$). A similar relationship between nematode body length and body volume was also found for the whole data set ($R = 0.78$, $P < 0.0001$), suggesting that either volume or body length can be used as measures of size of nematodes.

Simulating the distribution of nematode body size

The distribution of body masses of North American land mammals was obtained from Brown and Nicoletto (1991) (Fig. 4a). Using equation (3), we generated the predicted distribution of parasitic nematode body sizes (Fig. 4b) by substituting W_H in the equation for actual masses of North American mammals; this procedure produces one optimal nematode body size per host species for which a mass is known. Thus, our approach constrained the distribution of parasite body sizes to reflect that expected from the distribution

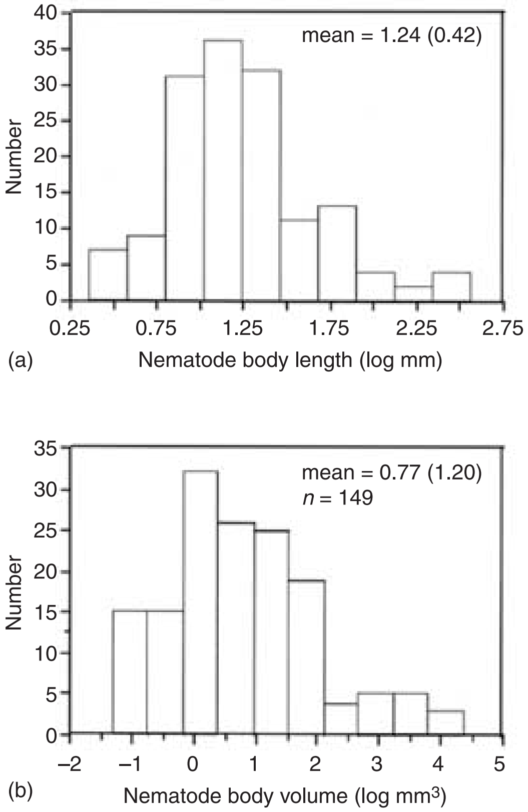

Fig. 1. Frequency distribution of body sizes (a) and body volumes (b) of parasitic nematodes of mammals.

of mammalian body sizes if each mammal species harbours one optimally sized nematode species. The simulated distribution has the same mean (1.05 ± 0.41) as the observed distribution of parasitic nematode sizes (1.24 ± 0.42; Fig. 1). However, the shapes of the two distributions did not fit each other (Kolmogorov-Smirnov's test, $P < 0.01$).

Despite being statistically significantly different, the observed and simulated distributions of nematode body sizes have the same mode and are slightly right-skewed. The only difference in shape between these distributions is that the simulated values are more tightly clustered around the mean than the observed values. This is probably because simulated values are generated using a single parameter, host body mass, whereas in nature other confounding factors influence nematode body sizes and will produce more variability around the mean optimal value.

DISCUSSION

Studies of macroecological patterns in parasitic organisms such as nematodes can serve to validate general hypotheses and processes proposed for free-living animals. We found that the frequency distribution of nematode body sizes is unimodal in log with a peak at

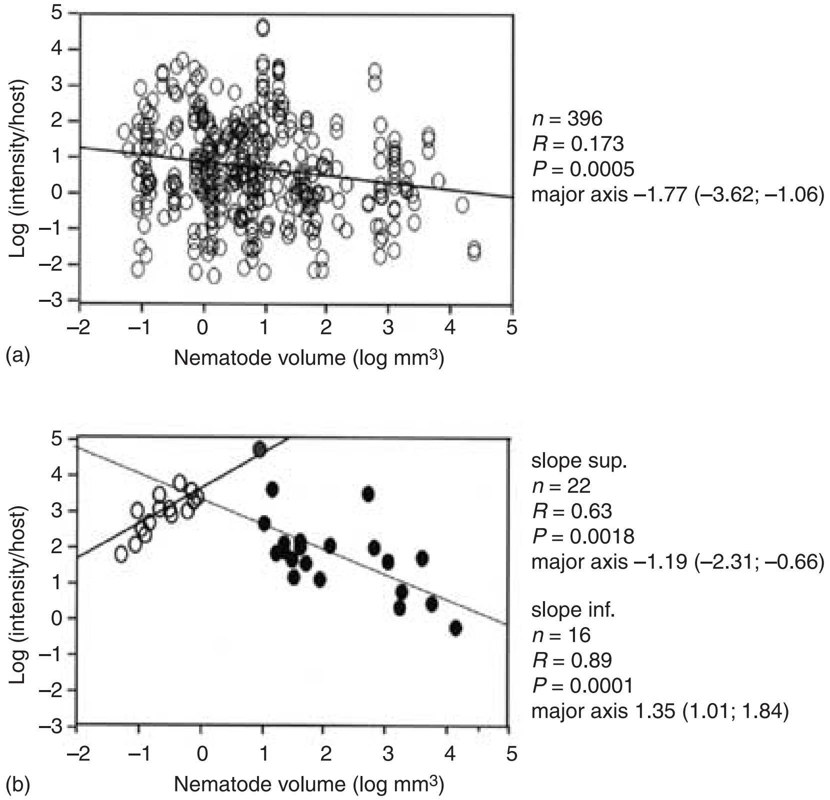

Fig. 2. (a) Distribution of nematode population density (log mean intensity of infection/host body mass) as a function of nematode volume (log mm^3). (b) Distribution of maximum nematode population density as a function of nematode volume. Two separate regressions were fitted for nematode species with volume (log mm^3) greater than 0 (black and grey dots) and less than 0 (white and grey dots). Only maximal density has been kept and with only one population per nematode species.

approximately 15 mm. The distribution is also right-skewed (see Poulin and Morand, 1997), a pattern similar to that of many other taxonomic groups, including the mammal hosts of nematodes (Brown and Maurer, 1989).

The highest nematode population abundance is reached by small species, but not the smallest. The maximum abundance is found for nematode body lengths around 15 mm. Hence, the maximum population abundance is observed for the highly diversified taxa of this body size class. Minimum abundance appears to be independent of body size – that is, there is no region below some critical density where species disappear. This supports Brown's (1995) hypothesis, that because parasites are proportionally more abundant than their hosts, their minimum abundance should decrease moderately with decreasing body size. He also suggested that the greatest variation in abundances should occur in small-sized species, as we found here.

Two questions arise from a triangular scatter of species values in abundance versus body size plots (Lawton, 1990; Brown, 1995; Blackburn and Gaston, 1997). First, what is the

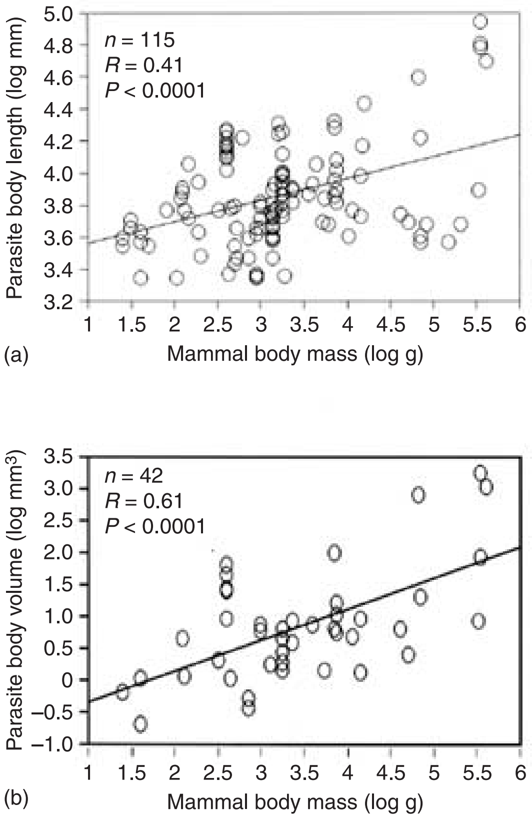

Fig. 3. Relationship between oxyuroid body length (a) and body volume (b) and body mass of their mammal hosts.

slope of the upper limit in abundance as a function of body size? Second, what determines the threshold value below which the small-bodied species decrease in density?

Arneberg *et al.* (1998a) tried to answer the first question with respect to parasitic nematodes. They found a value of the slope around −0.20, which is not consistent with the energetic equivalence rule, although they did not estimate the slope of the upper bound. However, when using only upper bounds of the polygonal distribution, we found a slope of −1.16. The estimate obtained from major axis regression is higher than the expected value (− 0.75) of the energetic equivalence rule (Damuth, 1981) for nematode volumes above the threshold value (i.e. greater than 10 mm long). Moreover, we found a decrease in density with decreasing body size for nematode volumes less than the threshold value, with a slope of 1.35. The estimated values of the slope are higher than, but close to, those found in birds and mammals (about 1.0 in Brown, 1995). Our analyses did not take phylogenetic influences into account; however, data points from related species were not markedly clumped on the plots, and these influences are thus unlikely to have affected our results.

The fitness model developed by Brown *et al.* (1993) assumes that resource acquisition and conversion determine an optimal body size for a given assemblage. They defined fitness as reproductive power – that is, the rate of conversion of energy into offspring. The model

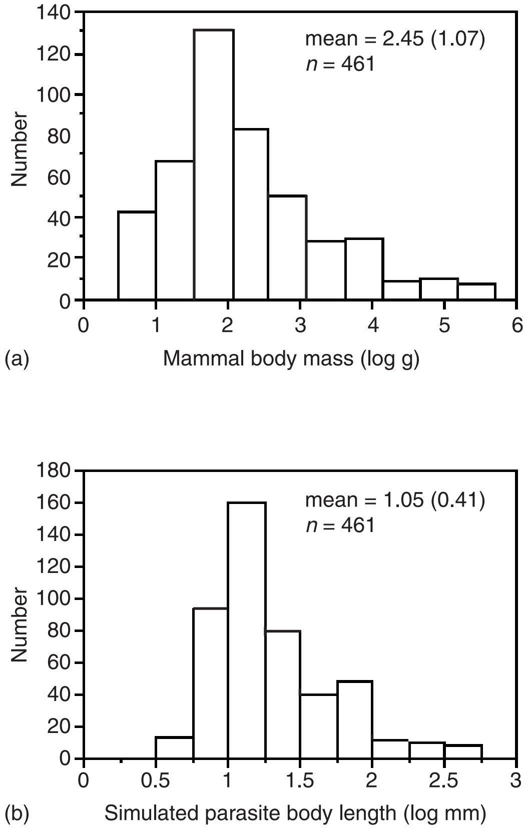

Fig. 4. (a) Body size distribution of mammals (based on data of Brown and Nicoletto; 1991). (b) Simulated distribution of optimal body size of parasitic nematodes (see Methods and compare with the observed distribution in Fig. 1).

we develop here is also a fitness model, where the optimal body size is derived from an epidemiological model using the net transmission rate. Our model is oversimplified for the following reasons:

1. The model does not take into account the survival of the parasite in the outside environment, and thus applies only to directly transmitted parasites. However, it applies to oxyuroid nematodes and other parasites that are directly transmitted and have low life expectancy of eggs in the outside environment.
2. Interspecific competition is not considered. Models of multi-infection show, however, that there is more interaction between each parasite species and the host than among parasite species (Dobson and Roberts, 1995).
3. The optimal body size can be derived only for specific parasite species, for which we know the body size of their unique host species.

In spite of this oversimplification, our model predicts a value for the slope of the relationship between parasite body size and host body size that is found for the oxyuroids, a highly host-specific group of nematodes with direct life cycles.

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