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Spatial scaling laws do not structure strongyloid nematode communities in macropodid hosts

Robert Poulin [a,*], Ian Beveridge [b], David M. Spratt [c]

[a] *Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand*
[b] *Veterinary Clinical Centre, University of Melbourne, Princes Highway, Werribee, Vic. 3030, Australia*
[c] *CSIRO Sustainable Ecosystems, G.P.O. Box 284, Canberra, ACT 2601, Australia*

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Abstract

The characteristics of species within a community can influence the number of species that can coexist within that community. In particular, body size can constrain how many individuals can ‘fit’ into a community, and overlap in resource use between species depends on differences in their body sizes. Here, using data from 18 communities of strongyloid nematodes living in the stomachs of macropodid marsupials, we test key predictions derived from spatial scaling laws regarding the minimum similarity in body size between coexisting species believed to control how many species can coexist in a community. These communities are ideal systems for such a test: they consist of huge numbers of individuals from numerous species, all belonging to the same family (Chabertiidae) and living in the same host organ. Within these communities, we found that mean abundance correlated negatively with body size across all nematode species, whether body size was measured as length or volume. However, we found no support for the predictions of spatial scaling laws. First, the size ratios of pairs of adjacent-sized species did not decrease as a function of the size of the largest species in a pair. The few significant relationships observed were all positive, suggesting that the relative difference in size between adjacent species in the size hierarchy may in fact increase toward the upper end of the size spectrum. Second, the frequency distributions of body sizes were predominantly right-skewed amongst the communities investigated: within the size spectrum observed in a nematode community, small-bodied species greatly outnumber large-bodied ones, in sharp contrast to the predictions of spatial scaling laws. Nematode body size may thus determine the abundance achieved by a species but not how many species can coexist; the limiting similarity between coexisting species must depend on other biological traits.

Keywords: Abundance; Body size; Fractal geometry; Species packing rule

1. Introduction

The search for universal determinants of species diversity in ecological communities has followed two main pathways (Ricklefs and Schluter, 1993; Rosenzweig, 1995). On the one hand, there have been numerous attempts to relate the species richness of a community to the environmental characteristics of the local habitat. For example, the species richness of parasite communities in different host species (i.e. different habitats) tends to covary with the ecological and life history characteristics of the hosts (Poulin, 1997; Poulin and Morand, 2004). On the other hand, the species richness of a community may instead be determined intrinsically, i.e. by the characteristics of the species it includes. The number of species that can coexist within a habitat should depend in large part on how finely the space and other resources can be divided. To a large extent, such resource partitioning must be constrained by the different body sizes of coexisting species (Morse et al., 1985; Siemann et al., 1996). Whether an additional species can ‘fit’ into a community may depend on its body size relative to those of species already established in the community.

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[*] Corresponding author. Tel.: +64 3 479 7983; fax: +64 3 479 7584.
E-mail address: robert.poulin@stonebow.otago.ac.nz (R. Poulin).

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The body sizes of species within a community can influence species richness in different ways. First, larger organisms apportion a greater amount of resources per capita: they consume more food, occupy more space, etc. Thus, in a habitat where resources are finite, larger-bodied species must occur at lower densities than smaller-bodied species. Negative relationships between body size and population density are indeed common amongst free-living animals (Damuth, 1981; Marquet et al., 1990; Blackburn and Gaston, 1997; Gaston and Blackburn, 2000), and they suggest that the different body sizes of the species in a community can determine how many individuals and species can coexist. Second, body size also determines the type of resources that can be used by an organism. The perception of habitat heterogeneity depends on scale: for example, what seems to be a smooth substrate to a large animal may appear grainy and highly textured to a much smaller one. Individuals experience a volume of space at a particular scale of resolution, and the latter is proportional to body size. Potential overlap in resource use between species increases as the difference in their body sizes decreases, and limits to the similarity in body size between any two species may determine how many species can coexist in a community. Ritchie and Olff (1999) have proposed a mathematical ‘species packing rule’, derived from fractal geometry, for the minimum similarity in size of species sharing resources and coexisting. Their spatial scaling law makes some simple predictions. One is that when species in a community are arranged by body size, the size ratio between species of adjacent size should decrease exponentially with increasing organism size. Another prediction of Ritchie and Olff’s (1999) scaling rule is that the distribution of species richness as a function of log-transformed body size should be unimodal and left-skewed, reflecting the larger size ratios and thus looser species packing of small species.

These predictions hold for assemblages ranging from mammalian herbivores to vascular plants (Ritchie and Olff, 1999). In contrast, in the only empirical test to date of these predictions on parasite communities, Rohde (2001) found no evidence that size ratios between species of adjacent size decreased with increasing size, or that the distributions of body size values were left-skewed, for metazoan parasite communities of marine fishes. However, these analyses combined parasites belonging to different phyla and inhabiting different organs within fish hosts. The species included by Rohde (2001) in his analyses are therefore not likely to represent assemblages capable of direct interactions and exploiting similar resources; in other words, they may not represent ‘real’ communities, and are not therefore expected to follow spatial scaling laws (see Ritchie and Olff, 1999).

Here, we test the predictions of Ritchie and Olff’s (1999) scaling law using communities of strongyloid nematodes from Australian macropodid marsupials (kangaroos and wallabies). They provide ideal model communities to test for a pivotal role of body size in determining community structure and species richness (see review by Beveridge and Spratt, 1996). All nematode species in these communities belong to the same family (Chabertiidae); in fact, with the exception of a single species of *Macropostrongyloides*, they all belong to the same subfamily (Cloacininae). They are thus highly similar in shape and resource use. They all live in the same host organ, the complex, sacculated forestomach (Hume, 1982). In this habitat, body size can determine the scale on which resources are available. With respect to space, for instance, large-bodied nematodes may be restricted to occupying the lumen, whereas small-bodied species can live in intimate association with the gastric mucosa; species of intermediate sizes may occupy positions somewhere between these two extremes. Finally, communities of gastric strongyloids in macropodid hosts are characterised by relatively high species richness and very high numbers of individual worms per host, a situation where resource partitioning, whether based on size or not, should play an important role.

Our specific objectives were: (i) to test for negative relationships between body size and mean abundance amongst all nematode species in a community, for each of the communities investigated; (ii) to determine whether the size ratio between species of adjacent sizes declines with increasing body size within a community, as expected from spatial scaling laws; and (iii) to determine whether the numbers of species in different size classes show a left-skewed unimodal distribution, again as predicted by spatial scaling laws. Overall, our analyses were replicated across several independent data sets, and they provide a robust test of the hypothesis that body size governs the richness and structure of parasite communities.

2. Materials and methods

2.1. Data on nematode communities

Data were obtained for 18 nematode communities in macropodid hosts (Table 1). A community was defined as all species found in a sample of one host species from one locality; the lack of physical barriers between different localities (in the case of *Macropus rufus*), or the parapatric occurrence of closely-related host species (genus *Petrogale*) sharing similar nematode faunas, could be used to justify pooling of data, but this was not done here. All communities were sampled in approximately the same manner. The stomach content of each individual host was fixed in formalin and later washed and sorted. All individual worms of large species (*Labiosimplex* or *Parazoniolaimus* spp.) were counted. Given their high intensities of infection, the numbers of worms from smaller species were estimated by dilution techniques. In brief, the total stomach sample of each host individual was well-mixed, after which subsamples corresponding to 5–10% of the total stomach sample were taken; worms from these samples were cleared in lactophenol for species identification and counts. The numbers of worms of each species in the whole stomach was then determined by extrapolation. Data on the mean body

Table 1
Communities of strongyloid nematodes from the stomachs of Australian macropodid hosts used in the analyses

Host species	Location	No. of hosts examined	Strongyloid species richness	Source
Petrogale godmani	Queensland	13	13	Beveridge et al. (1989)
Petrogale assimilis	Queensland	36	16	Beveridge et al. (1989)
Petrogale inornata	Queensland	15	11	Beveridge et al. (1989)
Petrogale herberti	Queensland	11	8	Beveridge et al. (1989)
Petrogale persephone	Queensland	20	11	Begg et al. (1996)
Petrogale purpureicollis	Queensland	12	10	Bradley et al. (2000)
Macropus rufus	Western New South Wales	34	9	I. Beveridge, unpublished data
M. rufus	South Australia	9	7	I. Beveridge, unpublished data
Macropus fuliginosus fuliginosus	Kangaroo Island	25	8	Webley et al. (2004)
Macropus fuliginosus melanops	Victoria	10	9	Pamment et al. (1994)
Macropus rufogriseus banksianus	Coastal New South Wales	9	13	D. Spratt, unpublished data
M. rufogriseus banksianus	montane New South Wales	22	14	D. Spratt, unpublished data
Macropus rufogriseus rufogriseus	Tasmania	4	15	D. Spratt, unpublished data
Macropus giganteus	Coastal New South Wales	10	14	D. Spratt, unpublished data
M. giganteus	montane New South Wales	10	13	D. Spratt, unpublished data
M. giganteus	Tasmania	2	12	D. Spratt, unpublished data
Wallabia bicolor	Coastal New South Wales	10	14	D. Spratt, unpublished data
W. bicolor	Australian Capital Territory	3	11	D. Spratt, unpublished data

length and mean maximum body width, averaged across males and females, were usually obtained from 10 individuals for each nematode species; apart from a few data taken from unpublished sources, most measurements were obtained from published descriptions (Beveridge, 1982, 1983, 1998, 2002; Beveridge and Chilton, 1999; Smales, 1995).

The following three variables were used for each nematode species in each community: (1) body length; (2) body volume, calculated using mean body length and mean maximum body width and assuming that the worms are cylindrical; and (3) mean abundance, or the mean number of worms of the same species per host in the community, computed including uninfected hosts. The two different measures of body size, length and volume, were used to determine whether the linear dimensions of an organism or its mass (equivalent to volume) were most relevant to spatial scaling laws derived from fractal geometry.

2.2. Data analyses

For each community, we fitted linear regressions between mean abundance and either body length or body volume, across all species in the community. Data were log-transformed prior to these analyses; in log–log space, abundance generally decreases as a linear function of body size in most taxa where body size is related to resource use (Gaston and Blackburn, 2000).

Secondly, we arranged all species in a community from smallest to largest based on body length, and computed size ratios for all pairs of adjacent species. These ratios were then plotted against the log-transformed size of the larger species in a pair, as in Ritchie and Olff (1999). We then determined whether a negative relationship (either a linear or exponential decay function) could be fitted to those data, as expected from theory. Each community often included a single species (either of the genus *Labiosimplex* or *Parazoniolaimus*) that was several times larger, sometimes by about one order of magnitude, than other community members. Including this unusually large species created a size ratio that was a clear outlier on scatterplots, and which by itself generated spurious positive associations between size ratios and body size; in these communities, the analyses were performed after excluding the outlier. The same analyses were then repeated using body volume instead of body length as a measure of parasite size.

Finally, we tested for significant skewness in the distribution of log-transformed body length values within each community. This was achieved using the g_1 moment statistic, with the latter's significance assessed with a *t*-test (Sokal and Rohlf, 1995). If a body size distribution is right-skewed, that is small-bodied species outnumber large ones even on a logarithmic scale, the value of g_1 should be significantly greater than zero, whereas if the distribution is left-skewed, i.e. large species outnumber small ones, g_1 should be significantly less than zero. The analysis was then repeated for each community using body volume values instead of body length.

3. Results

The species richness of the 18 communities investigated ranged from seven to 16 strongyloid species (Table 1), and the combined mean abundances of all species in a community ranged from 1975 to 274,840 individual worms per host. The genera *Cloacina* and *Rugopharynx* were well represented in most of these communities. Although the different communities shared some common nematode species, each can be considered as a distinct assemblage when searching for rules determining which species can coexist. The complete lists of nematode species found in each host, as well as their body sizes, are available (Supplementary data).

In all but one of the communities, mean abundance was correlated negatively with body length across all nematode species, though only seven of the linear regressions were statistically significant (Table 2). Essentially the same pattern was observed when body volume was used as a measure of body size instead of length (Table 2). The relatively low number of species in some communities limited the power of the analyses; nevertheless, the general trend was for the abundance of a species to decrease with increasing body size (see examples in Fig. 1).

There was no such general trend when size ratios of pairs of adjacent-sized species were plotted against the size of the largest species in a pair. In 12 of the 18 communities analysed, the largest species was always strikingly larger than the rest, and including this species invariably produced positive relationships between size ratios and body size; these communities were therefore analysed after exclusion of the largest species. Whether body length or volume was used as a measure of body size, the negative relationships predicted by spatial scaling laws were not observed, whether exponential or linear (Table 2) functions were used. The few significant relationships observed were all positive (see examples in Fig. 2), suggesting that, if anything, the relative difference in size between adjacent species in the size hierarchy increases toward the upper end of the size spectrum.

Finally, the frequency distributions of both body length and body volume values were predominantly right-skewed, many significantly so, amongst the communities investigated (Table 2). In other words, within the size spectrum observed in a given nematode community, small-bodied species tend to be more numerous than large-bodied ones, even on a logarithmic scale, in sharp contrast to the predictions derived from spatial scaling laws.

4. Discussion

Many parasite communities are characterised by the co-existence of numerous closely-related species, in some cases representing true species flocks. Well-documented examples include the oxyuroid nematodes of tortoises (Schad, 1963; Petter, 1966), the strongyloid nematodes of horses and elephants (Inglis, 1971; Matthee et al., 2004) and the dactylogyrid monogeneans of freshwater fishes (Kennedy and Bush, 1992). The communities of strongyloid nematodes inhabiting the stomachs of macropodid marsupials are also composed of species flocks typified by the co-occurrence of many species from the genus *Cloacina* (Beveridge et al., 2002). Groups of closely-related species using the same host can originate via two types of processes. First, they may be the product of an evolutionary radiation, whereby an ancestral species splits and gives rise to two or more daughter species in a rapid sequence of intra-host speciation events. Second, they may arise following several successive host-switching events, consisting of related species from other hosts col-

Table 2
Analyses on the importance of body size as a structuring force in 18 communities of strongyloid nematodes from macropodid hosts

Host species	Location	Abundance vs body size[a]		Size ratio vs body size[a]		Skewness of body sizes[b]	
		Length	Volume	Length	Volume	Length	Volume
Petrogale godmani	Queensland	-2.68^{*}	-0.94^{*}	−0.08	−0.06	1.38^{*}	0.75
Petrogale assimilis	Queensland	−0.28	0.02	−0.29	−0.87	1.22^{*}	0.45
Petrogale inornata	Queensland	-2.11^{*}	-0.76^{*}	−0.05	−0.66	1.28	0.70
Petrogale herberti	Queensland	−2.34	−0.83	−0.02	0.27	−0.42	0.05
Petrogale persephone	Queensland	−1.99	−0.79	0.36	1.35	0.44	0.39
Petrogale purpureicollis	Queensland	-3.37^{***}	-1.23^{**}	0.09	0.52	0.01	0.43
Macropus rufus	New South Wales	−0.22	−0.12	0.73^{*}	0.62	2.29^{**}	2.22^{**}
M. rufus	South Australia	−2.49	−0.99	0.42	0.48	2.07^{**}	2.08^{**}
Macropus fuliginosus fuliginosus	Kangaroo Island	−2.72	−1.28	0.20	0.62	0.35	0.74
Macropus fuliginosus melanops	Victoria	−1.34	−0.53	−0.57	0.14	1.71^{*}	1.83^{**}
Macropus rufogriseus banksianus	Coastal NSW	−1.68	−0.70	−0.17	0.17	2.62^{***}	2.76^{***}
M. rufogriseus banksianus	Montane NSW	−0.52	−0.28	−0.24	−0.04	2.58^{***}	2.72^{***}
Macropus rufogriseus rufogriseus	Tasmania	−0.92	−0.42	−0.23	−0.10	2.82^{***}	2.82^{***}
Macropus giganteus	Coastal NSW	-3.36^{***}	-0.83^{*}	0.39	0.33	1.70^{**}	1.40^{*}
M. giganteus	Montane NSW	-1.69^{*}	−0.38	0.69^{***}	0.50^{*}	2.34^{***}	1.77^{**}
M. giganteus	Tasmania	-2.71^{*}	-0.98^{*}	0.09	0.05	0.13	−0.16
Wallabia bicolor	Coastal NSW	-2.01^{*}	-0.77^{*}	0.46^{*}	0.88^{*}	0.99	1.05
W. bicolor	Australian Capital Territory	0.77	0.51	0.09	0.11	2.19^{**}	1.08

[a] Slope of regression line.
[b] Value of the g_1 moment statistic.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.005$.

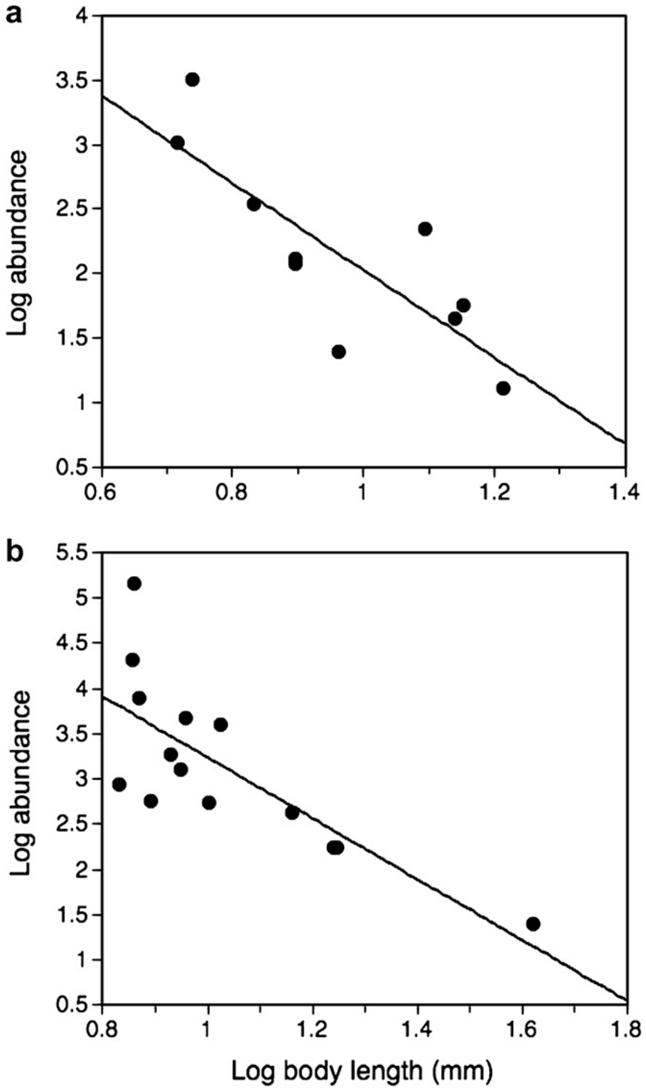

Fig. 1. Relationship between mean abundance (number of individuals per host) and body size across species from the nematode communities living in the stomachs of the macropodid hosts (a) *Petrogale purpureicollis* from Queensland and (b) *Macropus giganteus* from coastal New South Wales.

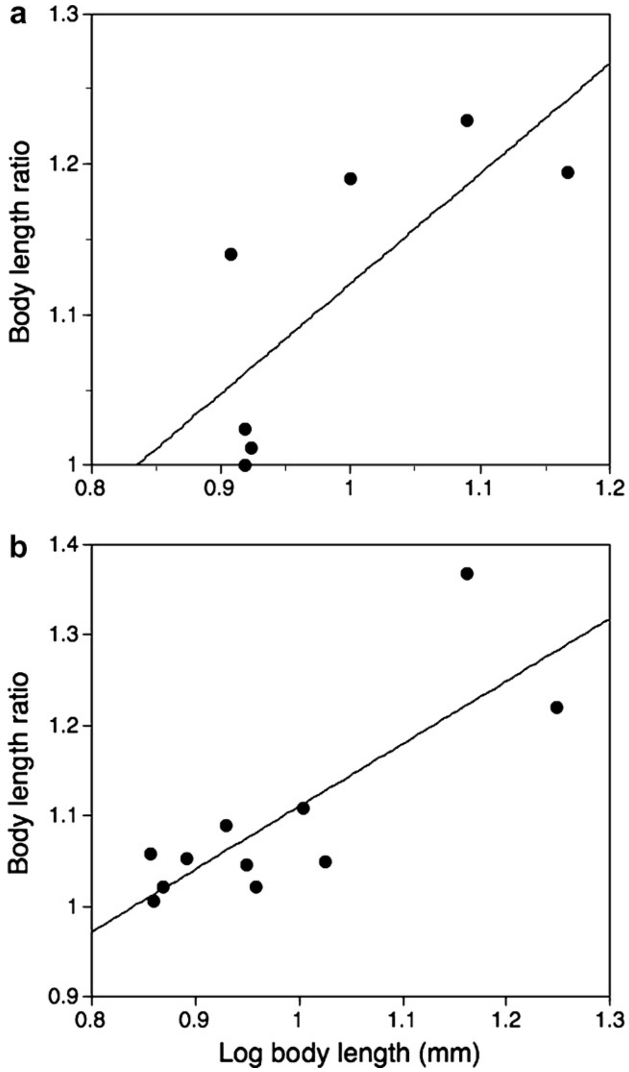

Fig. 2. Observed size ratios (larger/smaller species) between all pairs of adjacent species in the body size hierarchy as a function of the size of the larger species of the pair, for the nematode communities living in the stomachs of the macropodid hosts (a) *Macropus rufus* from New South Wales and (b) *Macropus giganteus* from montane New South Wales. In both cases, a species of *Labiosimplex* is excluded from the analysis, since this large-bodied nematode represents an outlier greatly strengthening the positive relationships shown here.

onising the same host species. Either way, the question that begs an answer is how numerous congeneric species, or species from related genera, all having very similar if not identical resource requirements, can successfully coexist within the same habitat. Ritchie and Olff (1999) provided a simple and elegant solution by proposing that resources can be apportioned purely based on scale. The spatial scaling laws they suggested revolved around the reasonable assumption that potential overlap in resource use between species increases as the difference in their body sizes decreases. According to this hypothesis, limits to the similarity in body size between any two species determine how many species can coexist in a community, and the body size of colonising species also determines their likely success of establishment by determining whether they can 'fit' into gaps along the body size continuum of the community. Spatial scaling laws therefore seem a priori to be a promising explanation for the coexistence of diverse species flocks of parasites.

Here, we have tested two key predictions of Ritchie and Olff's (1999) hypothesis on 18 communities of strongyloids from macropodid hosts, and found no evidence in its favour. Firstly, the size ratios of pairs of adjacent-sized species did not decrease as a function of the size of the largest species in a pair. There was even some suggestion that, in certain communities, the relative difference in size between adjacent species in the size hierarchy increased toward the upper end of the size spectrum, in sharp contrast to the predictions of Ritchie and Olff's (1999) model. This could indicate that there are vacant niches in these communities for new species to be 'squeezed in' toward the higher end of the size continuum. Alternatively, since this relationship was only found in very few of the 18 communities investigated, it may be that body size is not a relevant predictor of species richness and structure in nematode communities. The limiting similarity between coexisting species, i.e. the most similar they can be whilst stile coexisting successfully on the same resources, may depend on a broader range of variables than just body size, as suggested by a recent study of species flocks of dactylogyrid monogeneans on fish (Mouillot et al., 2005). In the case of nematodes, differences in functional traits relating to mode of feeding, for instance, could overshadow any similarities in body sizes to determine whether species can coexist or not.

Second, frequency distributions of body size values were predominantly right-skewed, many significantly so, amongst the 18 nematode communities investigated. In fact, this is exactly the pattern commonly reported in the literature, for a wide range of animal taxa (Blackburn and Gaston, 1994; Gaston and Blackburn, 2000), including parasites (Poulin and Morand, 1997). Therefore, within the size spectrum observed in a given assemblage, small-bodied species tend to be more numerous than large-bodied ones, even on a logarithmic scale. Ritchie and Olff (1999) argue that most of these right-skewed distributions are based on data from species pooled from widely different taxa or biogeographical regions, and thus not representing true communities where interactions are at least possible. Their own data from interacting communities of free-living organisms indicated that body size distributions should be left-skewed. Our data fail to confirm this hypothesis, although they come from taxonomically-constrained assemblages all co-occurring within the same host organ. The findings of our study confirm the widely-held view that more small species can be accommodated in a particular habitat simply because their resource requirements are lower than those of larger species. It is interesting to note that right-skewed distributions were more pronounced in hosts of the large-bodied genus *Macropus* than in the smaller *Petrogale* or *Wallabia*; this may indicate that factors associated with the host can influence the assembly of nematode communities.

In most of the nematode communities investigated here, we observed a general trend for the abundance of a species to decrease with increasing body size. This negative abundance-versus-body size relationship is one of the most common macroecological patterns in the literature on free-living animals (Damuth, 1981; Marquet et al., 1990; Blackburn and Gaston, 1997; Gaston and Blackburn, 2000), and has also been reported for parasites (Arneberg et al., 1998; but see Poulin, 1999). With finite resources available to a species supporting only a limited biomass, this biomass must be partitioned into either many small individuals or few large ones. Limiting resources thus impose a trade-off between body size and the abundance or density of a population. The evidence presented here indicates that strongyloid nematodes living in the stomachs of wallabies and kangaroos are subject to that trade-off. Body size therefore does play a role in structuring nematode communities, but not in the sense proposed by Ritchie and Olff (1999): it determines the abundance achieved by a species but apparently not how many species can coexist.

With the failure of spatial scaling laws to account for the variation in body size amongst nematode species from the same community, we are left seeking alternative explanations for parasite species richness. Coexisting species cannot infinitely partition space and other resources, and what places an upper limit on diversity in parasite communities remains unclear. It may be that interactions amongst nematode species are generally weak and play only a very minor role in determining the richness of component communities (see Behnke et al., 2001). Thus possibly the ecological and life history characteristics of the host remain the best determinants of parasite species richness (Poulin, 1997; Poulin and Morand, 2004). If there are intrinsic factors, i.e. properties of the parasites themselves and not of the host that place limits on species richness, we may have to look at a broader range of functional traits (see Mouillot et al., 2005) than just body size.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ijpara.2008.01.006.

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