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Body size vs abundance among parasite species: positive relationships?

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Across species, abundance usually correlates negatively with body size. This intuitive pattern may result from size-dependent resource requirements in habitats where only finite amounts of resources are available. Among parasite species, it is possible that some resource limitations are less severe than for free-living animals although this may depend on the type of parasites. The interspecific relationship between body size and abundance (measured as prevalence and intensity of infection) among parasites was tested in two groups of parasites. Among helminth endoparasites of fish, parasite body size correlated positively with prevalence and negatively with intensity of infection. Among copepod ectoparasites of fish, body size correlated positively with both prevalence and intensity. These trends were observed after controlling for the confounding influences of phylogeny and sampling effort. These contrasting patterns may result from the more intense link between body size and intensity-dependent regulation in endoparasites than in ectoparasites. The results of this comparative analysis suggest that parasite body size could be an important factor determining aspects of parasite abundance and distribution, including aggregation.

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The identification of the characteristics of organisms that are associated with their abundance and distribution is one of the central goals of ecology. Several interspecific patterns of abundance have been reported, and causal mechanisms have been proposed for most of them (Brown 1995). Of these interspecific patterns, one of the most extensively documented is the relationship between abundance and body size (Cotgreave 1993, Blackburn and Lawton 1994, Blackburn and Gaston 1997). Typically, the relationship is a negative one, with larger-bodied animal species occurring at lower abundance than smaller-bodied ones. The relationship can take other forms, however. For example, complex polygonal relationships are sometimes reported. The different patterns described in the literature are most likely the result of differences in study scale or in the type of data used (Blackburn and Gaston 1997). Positive relationships are occasionally observed between body size and abundance but these may sometimes be statistical artefacts (Blackburn and Gaston 1997). There are logical reasons to expect a negative correlation between body size and abundance. Fewer large-bodied animals can physically be packed in a given area, and resource requirements in general scale positively with body size. Thus the larger the animal, the more its maximum abundance will be constrained by available space and other resources. Although this explanation is plausible, it is unlikely to be the sole causal mechanism behind the many negative relationships reported (Currie 1993).

In some animal guilds, however, we might predict a positive relationship between size and abundance. Assuming that resource limitations can shape the relationship between body size and abundance, it might be informative to look at organisms for which resources are not limiting. For instance, nutrient limitations are unlikely to be as severe in most parasitic organisms as they are for free-living animals. Epidemiological models

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have highlighted the fundamental role of parasite fecundity in transmission success and the determination of abundance in metazoan parasites (Anderson and May 1978, May and Anderson 1979). Since the fecundity of metazoan parasites tends to correlate with body size across related species (Poulin 1996, 1998a), we might expect that, in the absence of resource limitations, larger-bodied parasite species achieve higher abundances than related, smaller-bodied species.

The situation is probably more complex, though. The abundance of a parasite species in a host population is the product of two parameters, prevalence (the percentage of hosts that are infected) and mean intensity (the mean number of parasite individuals per infected hosts). There is evidence that intensity-dependent regulation commonly takes place in intestinal helminth parasites of vertebrates (Keymer 1982, Shostak and Scott 1993). Because the intestinal tract of vertebrates has a finite size and nutrient content, larger-bodied parasitic helminths may be more prone to intensity-dependent regulation than small ones. In contrast, metazoan ectoparasites of vertebrates occur at intensities too low for intraspecific interactions to be important, at least in fish hosts (Rohde 1991, Rohde et al. 1995). Therefore, one might expect 1) among endoparasitic helminths, a positive relationship between body size and prevalence but a negative relationship between body size and intensity, because intensity-dependent regulation is likely to be more intense in large-bodied species, and 2) among ectoparasites, a positive relationship between body size and both prevalence or abundance.

The objective of this study is to quantify the relationship between body size and both prevalence and intensity of infection among parasite species, using two data sets: one on the endoparasitic helminths of freshwater fish, the other on the ectoparasitic copepods of marine and freshwater fish. These data sets include a random and most likely representative subset of existing species, i.e. all those for which data were available. Finding positive relationships between abundance and body size among these parasites would strengthen the case for resource limitation as a general causal mechanism (Currie 1993). The abundance of parasitic species is no doubt influenced by local environmental conditions, but there is evidence that it can be repeatable among populations of the same parasite species (Arneberg et al. 1997), making it a true species character like body size. The analysis thus controlled for phylogenetic influences, as well as two other potentially confounding variables: sampling effort and host body size. The latter variable may affect parasite abundance, in particular in the case of fish ectoparasites (Poulin and Rohde 1997, Grutter and Poulin 1998) but also in endoparasites (Shaw and Dobson 1995). Host body size may even correlate with parasite body size (Poulin 1997, 1998a). Despite the many published interspecific correlations between body size and abundance (see review in Cotgreave 1993, Blackburn and Gaston 1997), this is only the second test of the pattern among parasite species (see Arneberg et al. 1998).

Methods

The first data set, on endoparasitic helminths of freshwater fish, is a subset of a larger data set (Poulin 1998b) for which comparable data on body size were available. It consisted of data on adult digeneans and acanthocephalans parasitic in Canadian freshwater fish. Estimates of prevalence (percentage of hosts that are infected) and mean intensity (mean number of parasite individuals per infected host) were obtained from published records of occurrence listed in Margolis and Arthur (1979) and McDonald and Margolis (1995). To be included, data had to come from fish samples collected in the months of peak parasite abundance, since it varies seasonally (e.g., Chubb 1979, 1982), and including at least 20 fish of the same species. The number of hosts examined can influence measures of prevalence and intensity (Gregory and Woolhouse 1993). Therefore, for each parasite species, average prevalence and intensity values computed across all available records were weighted for the different sample sizes in each record. Data on parasite body size, i.e. total body length, were obtained from Arai (1989) and Gibson (1996). Host sizes (total length) were taken from Scott and Crossman (1973) and averaged across fish species for which occurrence records were available, to obtain an average host size for each parasite species.

The second data set, on ectoparasitic copepods of marine and freshwater fish, is also a subset of a larger data set (see Poulin 1995) for which data on either prevalence or intensity were available. It consisted of data on female copepods only (males are much smaller than females and often not found on fish) gathered from published records of occurrence. For each copepod species, estimates of prevalence and mean intensity were obtained from the same sample used to determine parasite body size; species were excluded if data were obtained from fewer than 20 fish. Host sizes were obtained from various fish guides (see Poulin 1995). Since latitude and water temperature may influence the abundance of ectoparasites on fish (Poulin and Rohde 1997), the latitude at which the samples were taken was also recorded and used in the analysis.

Phylogenetic information was obtained for digeneans (Appendix in Brooks and McLennan 1993), acanthocephalans (Amin 1985), and copepods (see Poulin 1995). I removed the confounding effect of parasite phylogeny by adopting the method of phylogenetically independent contrasts (Felsenstein 1985, Harvey and Pagel 1991), implemented with the widely-used CAIC 2.0 computer package (Purvis and Rambaut

1994). All analyses were performed on log-transformed data and adhered to the procedures outlined by Garland et al. (1992). Relationships between contrasts were determined using correlations forced through the origin (see Appendix 1 in Garland et al. 1992). Similarly, contrasts in a variable of interest were regressed against contrasts in a confounding variable, and the residuals were used as measures corrected for the confounding variable (see Appendix 2 in Garland et al. 1992), when a confounding variable was found to correlate with other variables.

Results

Endoparasitic helminths

Data were obtained for 43 species of endoparasitic helminths of fish (24 digenean species, 19 acanthocephalan species); data on intensity were not available for all species. Contrasts in sample size, i.e. the total number of fish examined per parasite species, correlated positively with contrasts in both prevalence ($r = 0.724$, $n = 21$, $p < 0.001$) and intensity ($r = 0.837$, $n = 15$, $p < 0.001$); the residuals of regressions of prevalence and intensity on sample size were thus used in subsequent analyses. Contrasts in host size did not correlate significantly with contrasts in either prevalence, intensity or parasite body size (all $p > 0.25$).

Contrasts in parasite body size correlated significantly with contrasts in both prevalence and intensity, but in opposite directions (Fig. 1). Contrasts in prevalence correlated positively with contrasts in body size ($r = 0.474$, $n = 21$, $p < 0.05$), whereas contrasts in intensity of infection correlated negatively with contrasts in body size ($r = -0.505$, $n = 15$, $p < 0.05$). The correlations remain significant following the removal of any outlier point.

Ectoparasitic copepods

A total of 46 species of parasitic copepods could be included in the data set; again, data on both prevalence and intensity were not available for all species. Of the three confounding variables analysed (sample size, host size and latitude), only contrasts in sample size correlated significantly with both contrasts in prevalence ($r = 0.564$, $n = 30$, $p < 0.01$) and contrasts in intensity of infection ($r = 0.459$, $n = 33$, $p < 0.01$). Except for the relationship between host size and intensity ($r = 0.329$, $n = 33$, $p < 0.10$), none of the correlations between contrasts in host size and in latitude and contrasts in either measure of parasite abundance approached significance (all $p > 0.25$). As above, the residuals of regressions of prevalence and intensity on sample size were used in subsequent analyses.

Contrasts in parasite body size correlated positively with contrasts in both prevalence and intensity (Fig. 2). Both relationships were significant (prevalence: $r = 0.372$, $n = 30$, $p < 0.05$; intensity: $r = 0.413$, $n = 33$, $p < 0.05$). Again, the correlations are not reduced below significance following the removal of any outlier point.

Discussion

The negative interspecific relationships between body size and abundance commonly reported in the literature are possibly the result of size-dependent resource requirements in habitats where only finite amounts of resources are available (Cotgreave 1993, Blackburn and Lawton 1994, Blackburn and Gaston 1997). The results of this study indicate that among parasite species, some resource limitations may be less severe than for free-liv-

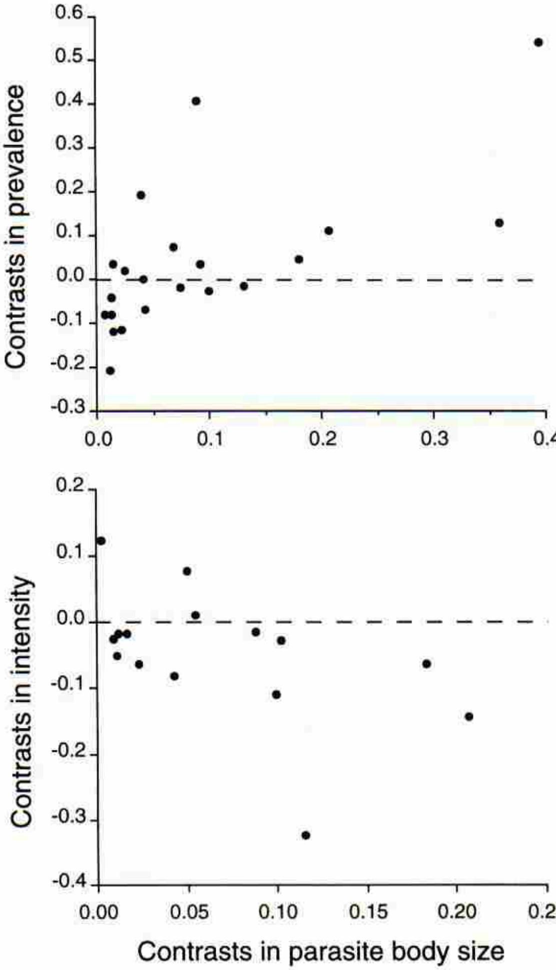

Fig. 1. Interspecific relationships between parasite body size and both prevalence and intensity of infection among endoparasitic helminths of freshwater fish, using phylogenetically independent contrasts. Contrasts in prevalence and intensity have been corrected for sampling effort.

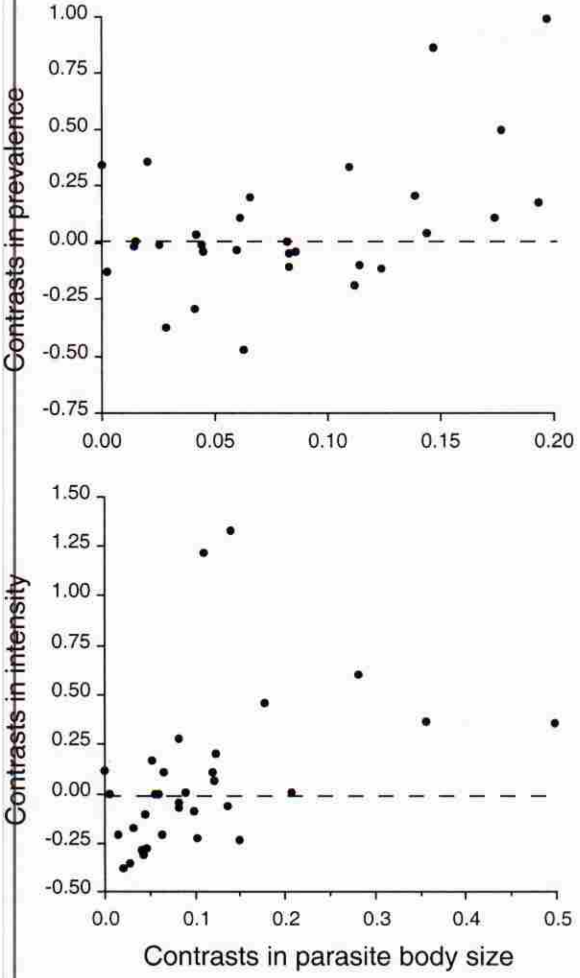

Fig. 2. Interspecific relationships between parasite body size and both prevalence and intensity of infection among copepods ectoparasitic on fish, using phylogenetically independent contrasts. Contrasts in prevalence and intensity have been corrected for sampling effort.

ing animals, at least for some types of parasites. Among helminth endoparasites of fish, parasite body size correlated positively with prevalence and negatively with intensity of infection. Among copepod ectoparasites of fish, body size correlated positively with both prevalence and intensity. These trends are not artefacts of phylogeny or sampling effort. The contrasting patterns observed in endoparasites and ectoparasites may result from the more intense link between body size and intensity-dependent regulation in endoparasites. The patterns presented here are among the first ones reported for parasites (see Arneberg et al. 1998), and they suggest that the negative relationship between body size and abundance can break down when resource limitations are not tightly dependent on body size.

The results obtained here may not apply universally to all parasites. Arneberg et al. (1998) also found that intensity of infection correlated negatively with body size among nematodes parasitic in mammals. However, Sasal et al. (in press) found no relationship between parasite body size and prevalence, among monogeneans parasitic on fish. Like copepods, monogeneans are external parasites of fish with direct life cycles. The ecological pressures and constraints acting on copepods should be similar to those acting on monogeneans, and yet the pattern of abundance of monogeneans with respect to body size does not mirror that of copepods. Monogeneans often make use of the small spaces between the gill filaments of their hosts. However, if the finite space available for attachments places constraints on the abundance of large-bodied monogenean species, these should affect the relationship between body size and intensity of infection, not prevalence.

Relationships between abundance and body size are influenced by the scale of the study and the abundance measures used (Blackburn and Gaston 1997). The definition of abundance used in a study is crucial. Ecological parasitologists usually define mean abundance of a parasite species as the product of prevalence and mean intensity (Bush et al. 1997). This is simply the mean number of parasites per host, when uninfected hosts are included in the computation. In this study, an analysis using mean abundance showed that it was not correlated in any way to parasite body size among endoparasitic helminths. Obviously, the positive correlation between prevalence and body size was offset by the negative correlation between intensity and body size when the composite measure of abundance was used. Splitting parasite abundance into its two components proved more informative, and illustrates how the choice of abundance measures can determine the outcome of a study. Prevalence, however, can be viewed as a measure of distribution rather than abundance, and distribution is expected to covary positively with body size (Gaston and Blackburn 1996). The results obtained here with intensity of infection as a measure of parasite abundance may thus be more directly comparable with results obtained for free-living animals.

The results (obtained for endoparasitic helminths) have implications for the patterns of parasite distribution among hosts in a population. Parasites are typically aggregated, with most hosts harbouring few or no parasites and a few hosts each harbouring many parasites; however, levels of aggregation vary among host-parasite systems, and the biological processes determining aggregation are not clear (Shaw and Dobson 1995). The results presented here suggest that large endoparasites tend to occur at higher prevalence and lower mean intensity than their smaller-bodied relatives. This could generate size-dependent distribution patterns. Large worms produce eggs at a higher rate than small worms (Poulin 1996, 1998a) and may be successful at transmitting their offspring to a relatively high proportion of the host population. They might not attain high numbers per host because of the greater density-dependent, or more precisely intensity-dependent regulation resulting from their large size. Small worms, on the other hand, have a lower daily rate of egg production and may only be capable of disseminating their propagules to a small fraction of available hosts. However, if heterogeneity in exposure or susceptibility makes certain hosts more likely to accumulate parasites, small worms may achieve high intensities since they are less likely to be under strong intensity-dependent regulation. The resulting interspecific pattern would be a decrease in aggregation associated with an increase in parasite body size among related parasite species. This idea could be tested using comparative data on aggregation levels in given taxa of parasites. If correct, then size-dependent distribution patterns may explain some of the variability observed in aggregation levels in natural systems.

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