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International Journal for Parasitology 33 (2003) 799–805

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A comparative analysis of adult body size and its correlates in acanthocephalan parasites

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Received 3 March 2003; received in revised form 2 April 2003; accepted 9 April 2003

Abstract

Adult acanthocephalan body sizes vary interspecifically over more than two orders of magnitude; yet, despite its importance for our understanding of the coevolutionary links between hosts and parasites, this variation remains unexplained. Here, we used a comparative analysis to investigate how final adult sizes and relative increments in size following establishment in the definitive host are influenced by three potential determinants of acanthocephalan sizes: initial (cystacanth) size at infection, host body mass, and the thermal regime experienced during growth, i.e. whether the definitive host is an ectotherm or an endotherm. Relative growth from the cystacanth stage to the adult stage ranged from twofold to more than 10,000-fold across acanthocephalan species, averaging just over 100-fold. However, this relative increment in size did not correlate with host mass, and did not differ between acanthocephalan species using ectothermic hosts and those growing in endothermic hosts. In contrast, final acanthocephalan adult sizes correlated positively with host mass, and after correction for host mass, final adult sizes were higher in species parasitising endotherms than in those found in ectotherms. The relationship between host mass and acanthocephalan adult size practically disappears, however, once phylogenetic influences are taken into account. Positive relationships between adult acanthocephalan size, cystacanth size and egg size indicate that a given relative size is a feature of an acanthocephalan species at all stages of its life cycle. These relationships also suggest that adult size is to some extent determined by cystacanth size, and that the characteristics of the definitive host are not the sole determinants of parasite life history traits.

Keywords: Ectothermy; Egg size; Endothermy; Host body size; Phylogeny

1. Introduction

In most taxa of invertebrates, adult body size is the best predictor of fecundity in interspecific comparisons, as well as being a key determinant of other life history traits and fitness components (Blueweiss et al., 1978; Peters, 1983; Schmidt-Nielsen, 1984; Stearns, 1992). Yet the causes of the often considerable variation in body size among species within a taxon remain poorly understood. In animals with discrete life stages, assuming that evolution has optimised adult body size, the latter will depend on both the size of the previous life stage and on the available resources and environmental constraints shaping its growth. In other words, both the starting point and the relative increment in size achieved as the animal develops into an adult will determine the final adult size. Variations in these parameters among related species, along with trade-offs with other life history traits, may explain much of the observed variation in adult body sizes.

Gastrointestinal helminth parasites of vertebrates are good models with which to test the respective influences of pre-adult size and growth conditions on adult sizes. Helminths reach the gut of their vertebrate definitive host as juveniles, often inside an intermediate host ingested by the definitive host. These juvenile stages vary in size within a parasite species, but not nearly as much as between parasite species. Space constraints inside the definitive host may limit adult size, as can available nutrients, although these may be relatively abundant. Rearing temperature experienced by growing worms inside the definitive host can also select for given adult body sizes: as a rule for invertebrates, temperature modulates growth rates and maximum body size at any given developmental stage

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doi:10.1016/S0020-7519(03)00108-5

(Atkinson, 1994, 1995; Sibly and Atkinson, 1994). Many parasitic helminths exploit endothermic vertebrate definitive host, where the temperatures they experience are high (36–38 °C in placental mammals, 39–42 °C in birds) and constant. In contrast, the many other helminth species live in ectothermic vertebrates, at temperatures that fluctuate widely around much lower mean values. We might therefore expect selection to have favoured adult helminth body sizes that are a function of their larval size, the body size of their definitive host, and/or whether this host is ectothermic or endothermic.

Acanthocephalans display the sort of interspecific body size variation that requires explanation: among the approximately 1100 described species, adult body lengths vary from 1 mm to more than 60 cm (Bush et al., 2001). The life cycle of acanthocephalans includes two hosts, an arthropod intermediate host (either an insect or a crustacean) and a vertebrate definitive host; a paratenic, or transport, host in which no development occurs may also be used in some species (Crompton and Nickol, 1985). There is some growth inside the intermediate host, and it is thus the size of the last juvenile stage, the cystacanth, which corresponds to the starting size of the parasite when it arrives in the vertebrate host. The final size of the adult worm will depend not only on cystacanth size, but also on the increment in size achieved within the definitive host. In turn, the dimensions of eggs produced by adult worms in the definitive host may be related to adult worm size. These eggs are released in host faeces and infect intermediate hosts via ingestion, although the likelihood of any single egg being ingested by a suitable intermediate host must be very low. Larger eggs may have greater success, their greater energy stores and their thicker eggshells allowing the larvae they contain to survive for longer. Surely, qualitative features of the eggs may be just as important, if not more so, than egg size in determining transmission success; still, larger eggs tend to be more successful than small ones in many other animal taxa (Stearns, 1992). There is probably a trade-off between the numbers of eggs produced and their average size (Stearns, 1992); the relative investment made by acanthocephalan into each egg may be influenced by the type of definitive host they exploit, which determines nutrient availability as well as the thermal regime under which they live.

The objectives of this study were (1) to compare the adult body sizes, and relative increments in size from the cystacanth to the adult stage, of acanthocephalans in ectothermic and endothermic hosts, and to evaluate the effect of host body mass on these variables; (2) to determine whether the initial (cystacanth) size of an acanthocephalan has any bearing on its final adult body size; and (3) to determine how adult size and egg size covary, and whether relative egg size is influenced by the type of definitive host used by a parasite. The results shed new light on the evolution of acanthocephalan life history strategies, in particular on the determinants of adult sizes.

2. Methods

Data were obtained from life cycle studies and new species descriptions found in a comprehensive survey of the parasitology literature. These sources should provide a random sample of acanthocephalan species currently known for which some life history data are available. Although thousands of acanthocephalan species have been described, most are known only from their adult stage. We cross-checked our species list with the complete list of known acanthocephalan species compiled by Golvan (1994), to resolve cases of synonymy. Measurements were only taken from naturally-infected host species, and not from experimental infections of laboratory hosts. This is important because commonly used laboratory hosts are often immunosuppressed and thus provide unnatural growing conditions for parasites. For each acanthocephalan species included in our data set, we recorded whether the definitive host was an endotherm or an ectotherm. If available, we also recorded host body mass; information on this variable was obtained from a range of sources, mainly from Grzimek (1990); Dunning (1993); Scott and Crossman (1973), and Fishbase (www.fishbase.org). When an acanthocephalan species was recorded from more than one host species, we averaged their body masses to obtain an average host body mass for each acanthocephalan species. This procedure may occasionally have resulted in the inclusion of host species that are not optimal for acanthocephalan development; however, averaging across host species, and the fact that the differences among acanthocephalan species with respect to host mass cover several orders of magnitude, should negate the effects of any such error factors.

Acanthocephalan measurements recorded were either means or the mid-points of ranges based on the examination of several individuals. The length and width (or diameter), in mm, of the cystacanth and adult worm were recorded for each species, if available; in cases where data were given separately for female and male worms, they were recorded separately and later averaged to obtain a species value. We also recorded the length and width of the eggs (these latter two dimensions are the same in the few species where the egg is spherical). Given that the worms are tubular in shape, the best measure of their body size is their volume. This was obtained separately for cystacanths and adult worms using the formula for the volume of a cylinder, $\pi L(W/2)^2$, where L and W are, respectively, the length and width of the worms. Similarly, the volume of the egg was calculated as the volume of an ellipsoid, $(\pi LW^2)/6$, with L and W being the length and width of the egg. Volumes were $\log_{10}$-transformed for all analyses described below.

Relative growth from the cystacanth stage, t_1, to the adult stage, t_2, was calculated as (log volume at t_2) $-$ (log volume at t_1). The use of log-transformed data on volume of acanthocephalans at different stages allows for comparisons across species without spurious scaling effects. Relative growth computed this way measures the proportional increase in size, not the absolute growth, and can thus be compared among species that differ widely in actual cystacanth or adult sizes. Negative values indicate a reduction in size, values of zero indicate no growth, values of one indicate a 10-fold increase in size, values of two a 100-fold increase, etc.

In the first instance, interspecific relationships among life history traits, and comparisons of life history traits between acanthocephalans with ectothermic hosts and those with endothermic hosts, were assessed across species values using standard parametric tests (linear regressions, product-moment correlations, two-tailed *t*-tests). These statistical procedures assume that acanthocephalan species are independent, which might be true if host effects (i.e. developmental temperature) outweigh phylogenetic influences. However, similarities among acanthocephalan species due to common ancestry should make them non-independent in a statistical sense, and the analyses were thus repeated while controlling for potential phylogenetic influences. The phylogenetically independent contrasts method (see Felsenstein, 1985; Harvey and Pagel, 1991) was used. The phylogeny of acanthocephalans is still not fully resolved. Here, we constructed a working phylogeny using proposed relationships among families and higher taxa from Near et al. (1998) and Garcia-Varela et al. (2000, 2002), with additional information from the taxonomic classification of Amin (1985). Independent contrasts were computed between sister taxa in the acanthocephalan phylogeny, using the program CAIC, version 2.0 (Purvis and Rambaut, 1994). The only variation in type of definitive host used by acanthocephalans occurs between, and not within, acanthocephalan classes; thus, contrasts between sister taxa that differed with respect to whether the definitive host is an ectotherm or an endotherm were too few (i.e. three) for us to assess the impact of host thermal physiology on acanthocephalan life history traits while controlling for phylogenetic influences. Relationships between contrasts in the other variables (volume of adult worm, volume of cystacanth, egg volume, relative cystacanth-to-adult growth, host body mass) were assessed using correlations forced through the origin (see Garland et al., 1992).

3. Results

3.1. Analyses across species values

Data were obtained for 181 acanthocephalan species from 57 genera; of these, 52 species used ectothermic definitive hosts and 123 used endotherms (the identity of the definitive hosts of the remaining six species could not be ascertained). Data on all variables were not available for all species, and the sample sizes therefore vary from one analysis to the next. The full data set is available upon request. Relative growth from cystacanth to adult varied widely across species ($N = 22$ species, mean $= 2.031$, range 0.257–4.03). Using back-transformation of the log-based values, the volume of worms increased from less than twofold to more than 10,000-fold from the cystacanth stage to the adult stage, with an average of more than 100-fold. Relative growth from cystacanth to adult did not differ between species using ectothermic or endothermic definitive hosts ($t = 0.683$, d.f. $= 20$, $P = 0.5023$), nor did it correlate with host body mass ($r = -0.022$, $N = 21$, $P = 0.9261$). It must be pointed out that although hosts ranged in body size from very small birds and fish to whales, there was no difference between the average mass of ectothermic hosts and that of endotherms in our data set (based on log-transformed values, $t = 0.021$, d.f. $= 138$, $P = 0.9834$).

Adult acanthocephalan body volume correlated positively with host body mass ($r = 0.275$, $N = 117$, $P = 0.0026$). In addition, adult acanthocephalans tended to be larger than expected based on the mass of their host if their host was an endotherm, and smaller if the host was an ectotherm. This is seen in Fig. 1, where points for parasites of ectotherms tend to fall below the regression line, and those for parasites of endotherms tend to lie above the line. Indeed, using the residuals from the regression in Fig. 1, there was a difference in adult acanthocephalan volume standardized for host mass between species in ectotherms and species in endotherms ($t = 4.421$, d.f. $= 115$, $P = 0.0001$).

Adult worm volume, egg volume and cystacanth volume all correlated positively with one another (Fig. 2). Acanthocephalan species with larger adults produce larger eggs ($r = 0.414$, $N = 114$, $P = 0.0001$); species with larger eggs have larger cystacanths ($r = 0.364$, $N = 26$, $P = 0.0679$);

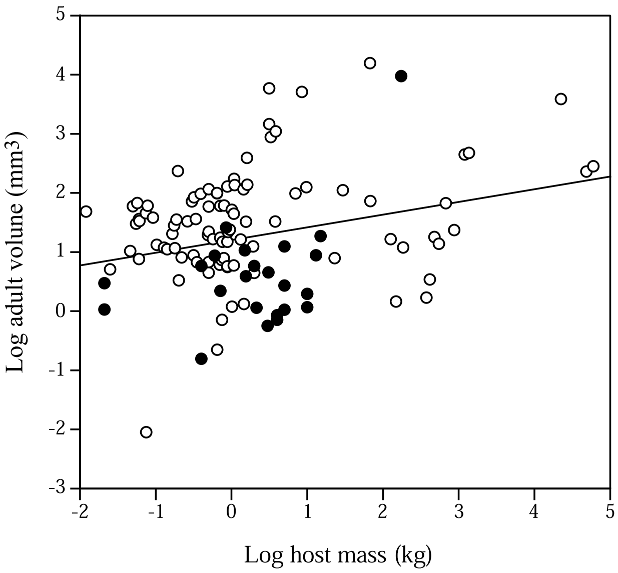

Fig. 1. Relationship between the body mass of the definitive host and the body volume of adult worms across 117 acanthocephalan species. Filled circles, acanthocephalans with ectothermic hosts; open circles, acanthocephalans with endothermic hosts.

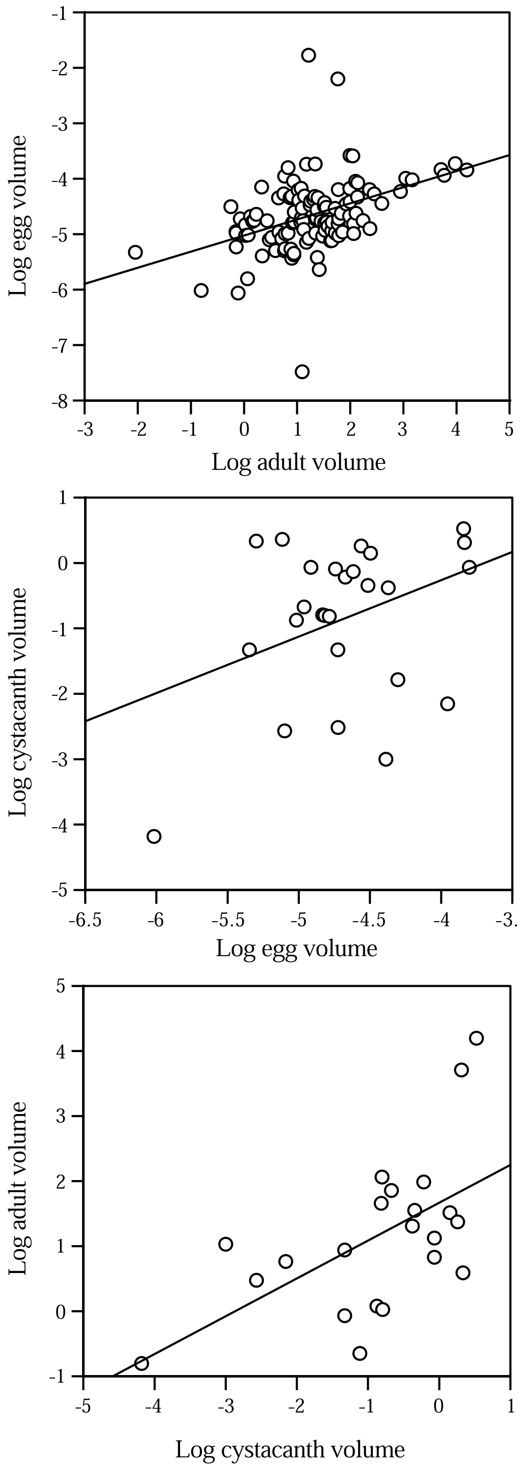

Fig. 2. Pairwise relationships between adult body volume, cystacanth volume and egg volume, across species of acanthocephalans. Volumes are in mm^3 in all cases.

and species with larger cystacanths end up with larger adults ($r = 0.576$, $N = 22$, $P = 0.0051$).

There was no evidence that the type of definitive host used influences the reproductive strategies of acanthocephalans as measured by the volume of the eggs they produce. Using the residuals of the regression between egg volume and adult volume (Fig. 2) as measures of egg volume corrected for adult worm size, we found no correlation between egg volume and host body mass ($r = 0.134$, $N = 99$, $P = 0.1871$), and no difference between the egg volume of species with ectothermic hosts and those with endothermic hosts ($t = 0.054$, d.f. = 107, $P = 0.9573$).

3.2. Analyses of phylogenetically independent contrasts

The analyses controlling for acanthocephalan phylogeny could not verify the apparent influence of host thermal physiology on adult worm volume because of a lack of valid contrasts between sister taxa that differ with respect to whether the host is an ectotherm or an endotherm. Phylogenetic contrasts, however, could be used to assess the effect of another host feature, i.e. host body mass, on adult worm volume, and produced results that do not support those of the analyses across species values. Among contrasts, there was no significant relationship between host body mass and acanthocephalan adult size ($r = 0.237$, $N =$ 49 sets of contrasts, $P = 0.1006$; Fig. 3). There was a weak tendency for both variables to covary: in 28 of the 47 sets of contrasts for which the difference in host mass between sister acanthocephalan taxa was not zero, the taxon with the larger host also had the larger adult worm (see Fig. 3), but it was not significant ($\chi^2 = 1.723$, d.f. = 1, $P > 0.10$). Still, as seen in Fig. 3, when adult worm size was much larger in one acanthocephalan taxon than in its sister taxon, the larger of the two was likely to be in the larger-bodied host. As with the analyses across species values, host body mass also did not correlate with the relative cystacanth-to-adult growth

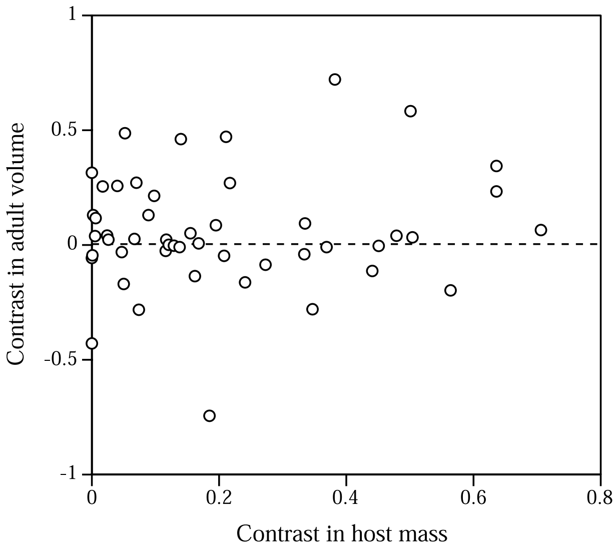

Fig. 3. Relationship between the body mass of the definitive host and the body volume of adult worms across acanthocephalan species. Each point represents an independent phylogenetic contrast between sister taxa in the acanthocephalan phylogeny.

among phylogenetic contrasts ($r = 0.090$, $N = 19$, $P = 0.7144$).

As with the analyses using species values, analyses of contrasts also revealed positive covariation between adult worm volume, egg volume, and cystacanth volume (Fig. 4). Acanthocephalan taxa with larger adults produce larger eggs than their sister taxa with smaller adults ($r = 0.427$, $N = 55$, $P = 0.0012$); larger egg volumes are associated with larger cystacanths ($r = 0.452$, $N = 22$, $P = 0.0347$); and larger cystacanths tend to lead to larger adults ($r = 0.411$, $N = 20$, $P = 0.0715$). These relationships are not very strong, but it is clear that large positive phylogenetic contrasts in one of these variables are more likely to be associated with large positive contrasts in another, than with negative contrasts (Fig. 4).

Finally, among phylogenetic contrasts, there was no evidence that host body mass influences the relative volume of eggs produced by acanthocephalans. Using residuals of the regression of contrasts in egg volume against contrasts in adult worm volume as egg size values standardized for worm size, we found no relationship between contrasts in egg volume and contrasts in host mass ($r = -0.118$, $N = 47$, $P = 0.4313$).

4. Discussion

Adult acanthocephalan body sizes vary across species by several orders of magnitude. Our results suggest that the final (adult) body size of acanthocephalans is determined to some extent by their starting (cystacanth) size, independently of the type of host in which they develop. Cystacanth size only explains approximately 33% of the variation in adult size, and there are most likely other influential factors involved. Host mass appears also to influence acanthocephalan adult body size, but this trend weakens considerably once phylogenetic influences are removed. Whether the host is ectothermic or endothermic appears important too, although this effect could not be evaluated in a phylogenetic context. In the future, it may be desirable to examine acanthocephalan size variation within a range of ectotherms, to determine whether acanthocephalan sizes vary with ectotherm temperature preferences and/or habitats. An interesting feature of our results, however, is that only final adult size, and not the magnitude of the size increment achieved following the infection of the definitive host, appears related to host characteristics. Overall, positive correlations between the sizes of adults, eggs and cystacanths, irrespective of host features, suggest that acanthocephalan life histories are not too constrained by host influences. These relationships also indicate that acanthocephalan species that are relatively large at one stage of their life cycle are relatively large at other stages as well: if the adult body is large, so are the eggs and cystacanths. These results add weight to the view that the biology of parasites is not necessarily strictly determined by that of their hosts (Brooks and McLennan, 1993).

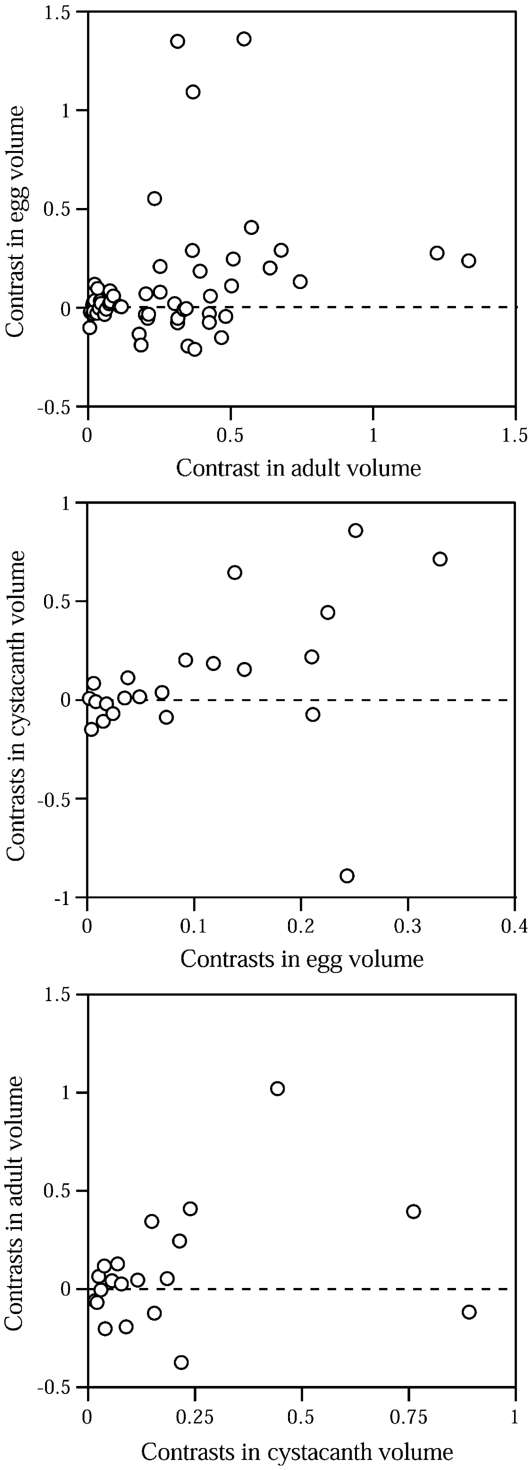

Fig. 4. Pairwise relationships between adult body volume, cystacanth volume and egg volume, across species of acanthocephalans. Each point represents an independent phylogenetic contrast between sister taxa in the acanthocephalan phylogeny.

Our findings can be compared with the results of similar studies on trematodes (Loker, 1983; Poulin and Latham, 2003). In trematodes, the size of the juvenile stage arriving in the definitive host (metacercaria) also correlates well with the size of the adult worm, suggesting that, as in acanthocephalans, initial worm size determines to some extent final worm size (Poulin and Latham, 2003). Increments in body size from the metacercarial stage to the adult are also not influenced by host size or thermal regime (Poulin and Latham, 2003). In addition, the sizes of trematode eggs and their different life stages tend to covary significantly (Loker, 1983).

Unlike what appears to be the case in acanthocephalans, however, the final adult size of trematodes does not correlate with host body mass (Poulin, 1997). A significant influence of host body size on the size of adult parasites has been demonstrated for other helminths (see Poulin, 1998). All else being equal, larger hosts should provide more space and nutrients for parasite growth, and with helminth fecundity generally a function of their size (Poulin, 1998), natural selection should have favoured the evolution of the largest parasite sizes that a host can sustain. For instance, host body mass covaries positively with the adult size achieved by parasitic nematodes (Morand et al., 1996) and taeniid cestodes (Moore, 1981), although in the latter case the relationship is tempered by the extent of asexual reproduction achieved by taeniids in their intermediate hosts. It is likely that the space and nutrients available in the parasite's microhabitat are more important determinants of parasite body size than host mass; data on the diameter of the host's intestine or other similar measures are generally unavailable, however. Our results indicate that host body size and host thermal physiology can both affect adult acanthocephalan body sizes, although phylogenetic influences confound this pattern. It may thus be that acanthocephalan adult sizes are traits optimised by selection to fit the conditions experienced in the host. What is clear, however, is that the growth achieved by an acanthocephalan in its definitive host has nothing to do with the characteristics of the host: final adult size of an acanthocephalan is instead a direct extension of the size it had when it arrived in the host, as a cystacanth.

Cystacanth size may relate well with adult size across acanthocephalan species, but within species, as in any other organism, it is influenced by many factors. In insects and small crustaceans (amphipods, isopods, ostracods) that serve as intermediate hosts, the number of cystacanths per host is often quite low, often only one or two per host. In these situations, where the space available for growth is restricted, cystacanth size may correlate positively with the size of the intermediate host (see Dezfuli et al., 2001). Some acanthocephalans use larger intermediate hosts, such as crabs (see review in Nickol et al., 2002). In such hosts space is not a constraint and cystacanth size may not relate with host size. However, these large hosts can harbour large numbers of cystacanths (e.g. *Profilicollis* spp. in shore crabs, mean >10 cystacanths per infected crab, maximum number in a single crab >100; Latham and Poulin, 2001, 2002). At high intensities like these, cystacanth size is decreased (Poulin et al., 2003); intensity-dependent effects on cystacanth size are also apparent in small intermediate hosts with lower infection intensities (Dezfuli et al., 2001). Recent theoretical arguments suggest that reductions in cystacanth sizes at higher intensities of infection may reflect adaptive life history strategies, and not merely an adjustment to resource limitations (Parker et al., 2003). Whatever the reason for the variation in cystacanth sizes within acanthocephalan species, it may generate within-species variation in adult acanthocephalan sizes, just as we find at the interspecific level. It should be possible to manipulate cystacanth sizes within an acanthocephalan species, for instance by experimentally restricting growth in the intermediate host, and then see whether cystacanths of different sizes produce adults of different sizes when growing under identical conditions in a definitive host. This would allow a test of one our main findings, i.e. that adult acanthocephalan size is mainly determined by cystacanth size.

Acknowledgements

RP is supported by a James Cook Research Fellowship from the Royal Society of New Zealand.

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