Biological Journal of the Linnean Society, 2007, **90**, 637–645. With 4 figures

Investing in attachment: evolution of anchoring structures in acanthocephalan parasites

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Received 10 October 2005; accepted for publication 20 June 2006

Secure attachment to host tissues is essential for survival and reproduction in parasitic organisms. The production of elaborate attachment structures must be costly, however, and investments in attachment should be approximately proportional to the likelihood that a parasite will be dislodged. In the present study, relative investments in attachment as a function of body size and the type of host used were examined across 138 species of acanthocephalans. These worms live anchored to the intestinal wall of a vertebrate host by inserting their hooked proboscis into host tissues. Taking proboscis volume into account, there is a negative interspecific relationship between the number of hooks borne on the proboscis and their mean length, reflecting a trade-off between hook number and hook length. This supports the assumption that hooks are costly to produce, because any given species cannot simultaneously maximize both the relative number and relative length of the hooks it produces. There is a positive relationship between total worm size and total hook length, but it is weak, with a slope indicating that, as total body volume increases, total hook length also increases but at a slower rate. Indeed, relative investments in attachment, measured as hook length per unit body volume, decrease as worm size increases. Independently of total body size, investments in hook production are higher in species exploiting endothermic hosts, especially birds, than in those living in ectothermic hosts. Given the greater amounts of food passing through the gut of endotherms, and the richer and denser communities of intestinal parasites that they harbour, they are likely to select for greater investments in attachment. These results support the prediction that investments in attachment are influenced by the probability of being dislodged, and allow comparisons with other groups of intestinal parasites such as cestodes or trematodes.

ADDITIONAL KEYWORDS: allometry – comparative analysis – definitive host – endothermy – hooks – proboscis – trade-off.

INTRODUCTION

Far from being degenerate and simplified organisms, as some textbooks still describe them, parasites display a wide range of superb adaptations to their lifestyle. Attachment organs (i.e. the structures responsible for anchoring the parasite to the external or internal surface of its host) offer remarkable examples of traits fine-tuned by natural selection. Monogeneans, small flatworms parasitic on the external surfaces of fish, use an array of mechanical clamps and chemical adhesives to remain attached to their hosts; their attachment organs often display an amazing level of complexity (Kearn, 2004). Parasitic worms living in the gastrointestinal tract of vertebrates rely mainly on suckers or hooked structures to maintain their position in the host gut, and these organs are also remarkably efficient and well-fitted to their function.

Producing these structures must be costly: any energy invested in the development of attachment organs will not be available for other functions, such as reproduction. It is therefore likely that investments in attachment made by parasites have been optimized by natural selection. In theory, we would expect that investments in attachment would be approximately proportional to the likelihood that a parasite can get dislodged. Thus, investments in attachment should covary with several variables associated with the

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probability of dislodgement. Surprisingly, despite many studies on variation in other parasite features, such as body size or egg output (Skorping, Read & Keymer, 1991; Morand, 1996; Morand *et al.*, 1996; Poulin, 1997; Trouvé *et al.*, 1998; Poulin, Wise & Moore, 2003), there have been no quantitative analyses of interspecific variation in the size of attachment structures among parasites.

The thorny-headed worms (phylum Acanthocephala) possess attachment structures that can be measured easily and that vary widely among species, making them an ideal group in which to study interspecific differences in investments in attachment and their potential causes. Adult acanthocephalans live in the gastrointestinal tract of their vertebrate definitive host, where they anchor themselves by inserting their hooked proboscis into the gut wall of the host, with the rest of the body floating freely in the gut lumen (Bush *et al.*, 2001; Taraschewski, 2000). Attachment is not necessarily permanent because, in some species, the proboscis can be retracted and invaginated into a receptacle at its base, and re-inserted elsewhere along the gut wall of the host. The proboscis is covered with rows of recurved, sclerotized hooks that secure the proboscis into the gut wall (Miller & Dunagan, 1985). Some acanthocephalan species also have small spines elsewhere on their bodies that may play a secondary role in attachment (Miller & Dunagan, 1985; Bush *et al.*, 2001), but the armed proboscis is the main anchoring structure. The shape, number, and distribution of hooks on the proboscis are important characters used in taxonomy and classification (Huffman & Bullock, 1975). Qualitative differences among acanthocephalan taxa in the arrangement of hooks on the proboscis, such as whether the hooks are aligned in longitudinal rows or in a spiral pattern, have long been recognized (Van Cleave, 1941). However, quantitative differences among species, in terms of the relative amount of energy and resources invested in the production of hooks, have never been investigated.

Natural selection should optimize investments in hook production with respect to the probability of the worm being dislodged: the greater this probability, the more should be invested in attachment structures. This rests on the reasonable assumption that hook production is costly (i.e. it should be more costly to produce many or longer hooks than to produce few or shorter ones). Two factors are likely to influence the probability that a worm is dislodged from its site of attachment: (1) the size of the worm itself and (2) the type of vertebrate definitive host in which it lives. First, all else being equal, larger worms may be more likely to be dislodged, by passing food in the host gut, than small worms that can lie among the folds and villi lining the gut wall. We might even expect an allometric relationship between worm size and investment in attachment, with investment in hook production increasing faster than linearly with increasing worm body size. Second, the definitive hosts used by adult acanthocephalans are either ectotherms (fish, amphibians and reptiles) or endotherms (birds and mammals). The greater food intake required for endothermy (Karasov & Diamond, 1985), and the higher rates of peristalsis and other movements associated with the passage of more food along the gut, mean that intestinal worms in endotherms face a greater risk of being physically removed from their attachment site than their relatives in ectothermic hosts. In addition, bird and mammal hosts typically harbour communities of gastrointestinal parasites that are richer in species and denser in total individuals than those found in fish, amphibians or reptiles (Kennedy, Bush & Aho, 1986; Bush, Aho & Kennedy, 1990; Poulin, 1995; Poulin & Morand, 2004). This can only exacerbate competition for attachment sites. Thus, for all these reasons, we might expect that natural selection has favoured greater investments in hook production in acanthocephalans of endothermic hosts than in those parasitic in ectotherms.

The present study is the first to investigate relative investments in attachment structures by parasites to determine whether these investments are tailored to the conditions experienced by a parasite. Specifically, the analysis tests two predictions regarding relative investments in hook production (measured as the summed lengths of all hooks) by acanthocephalans: (1) hook production increases markedly with increasing parasite body size and (2) relative hook production is greater in species parasitic in endothermic hosts than in those living in ectothermic hosts.

MATERIAL AND METHODS

Data were obtained from acanthocephalan species descriptions published in the *Journal of Parasitology* subsequent to 1960, and from those available in the author's reprint collection. Although far from including all of the approximately 1100 species described to date (Bush *et al.*, 2001), this produced a large and random sample of known species.

There can be considerable intraspecific variability in morphometry in acanthocephalans, and two procedures were used to obtain standardized species values for comparative purposes. First, to account for any sexual size dimorphism, all measurements were taken exclusively from adult female worms. Second, when a range of values was given for any morphometric trait, the maximum value was always used. For each acanthocephalan species, the following traits were recorded: the length and maximum width of the trunk (here defined as the body excluding the proboscis but including the neck); the length and maximum width of the proboscis; the number of longitudinal rows of hooks on the proboscis; the number of hooks per row; and the mean hook length. If hooks were not arranged as longitudinal rows, then equivalent measures were used (e.g. the number of circles of hooks around the proboscis, and the number of hooks per circle). Mean hook length is a weighted mean taking into account variation in hook length with respect to their position on the proboscis (hook length typically varies slightly from the anterior end of the proboscis to its base, and/or between the ventral and dorsal surfaces of the proboscis). Here, 'hook' includes both hooks with a root and simple spines without roots. In addition, the identity of the definitive host (fish, amphibian, reptile, bird, or mammal) in which the acanthocephalans were found was recorded. The dataset includes only acanthocephalan species for which data are available for all the above morphometric traits.

From the above traits, the following five variables were calculated: (1) trunk volume, calculated as the volume of a cylinder, i.e. as $\pi L(W/2)^2$, where L is length and W is width; (2) proboscis volume, also calculated as the volume of a cylinder, even though in some species the proboscis is almost spherical; (3) total body volume, taken as the sum of trunk volume and proboscis volume; (4) the total number of hooks, which is the product of the number of rows of hooks and the number of hooks per row; and (5) total hook length, which is the product of the total number of hooks and mean hook length. All variables were $\log_{10}$-transformed prior to analysis, to meet the assumptions of normality.

Initially, relationships among morphometric variables, and differences in morphometry among acanthocephalan species exploiting different types of hosts, were assessed using standard parametric tests on species values. This procedure assumes that acanthocephalan species are statistically independent of each other, which might be true if host effects outweigh phylogenetic influences. However, potential similarity among species due to common ancestry must be taken into account and, to this end, the phylogenetically independent contrast method (Harvey & Pagel, 1991) was used. A working phylogeny of the acanthocephalan species in the dataset was constructed based on published phylogenies derived from molecular data (Near, Garey & Nadler, 1998; Garcia-Varela *et al.*, 2000, 2002). Independent contrasts were calculated between sister taxa in the phylogeny using the program CAIC, version 2.0 (Purvis & Rambaut, 1994). Relationships between contrasts in continuous variables were assessed using correlations forced through the origin (Garland, Harvey & Ives, 1992). All of these produced results very similar to and fully consistent with those obtained by conventional analyses on species values; for the sake of brevity, only the latter are presented here. Differences in the type of definitive host used occur between, and not within, higher taxa of acanthocephalans; thus, phylogenetic contrasts between sister taxa that differ with respect to the type of vertebrate host used were too few (i.e. three) to determine the impact of host type on investment in hook production while controlling for phylogenetic influences. This could only be assessed using standard statistical tests on species values.

RESULTS

Data were obtained for 138 acanthocephalan species, representing 50 genera, and 19 families, based on the classification of acanthocephalans by Amin (1985). The full dataset is available from the author upon request.

Across all species, proboscis volume correlated strongly and positively with mean hook length (product-moment correlation: $r = 0.493$, $P = 0.0001$), with the total number of hooks ($r = 0.703$, $P = 0.0001$), and with total hook length ($r = 0.814$, $P = 0.0001$; Fig. 1). The size of the proboscis is thus proportional to the overall number and size of sclerotized hooks that it bears. The apparent outlier in Figure 1 corresponds to *Plagiorhynchus* (*Prosthorhynchus*) *formosus*, although nothing that is known of this species can explain why it falls away from other species. These relationships hold when the data are analysed separately for species that use ectothermic definitive hosts and those that use endothermic hosts (all $P \leq 0.0007$), except that for the latter species the total number of hooks does not covary with proboscis volume ($r = 0.204$, $N = 56$, $P = 0.1311$). The total number of hooks varied greatly among acanthocephalan species, from fewer than 20 in some genera (e.g. *Neoechinorhynchus*) to well over 1000 in other genera (e.g. *Centrorhynchus*). Mean hook length also varied across species, although not as extensively, from about 20 to 180 μm. Across all species, after correction for variation in proboscis volume, there was a significant negative relationship between the total number of hooks and mean hook length ($r = -0.486$, $P = 0.0001$; Fig. 2); there were also negative relationships between these variables when the data were analysed separately for species that use ectothermic definitive hosts and those that use endothermic hosts (both $P \leq 0.0025$).

Across all species, trunk volume and proboscis volume are correlated ($r = 0.394$, $P = 0.0001$): the larger the worm, the larger the proboscis. However, this trend was weaker when the data were analysed separately for species that use ectothermic definitive hosts ($r = 0.236$, $N = 82$, $P = 0.0331$), and absent among species that use endothermic hosts ($r = 0.176$, $N = 56$, $P = 0.1957$). Across all acanthocephalan species, total body volume correlated positively, although not

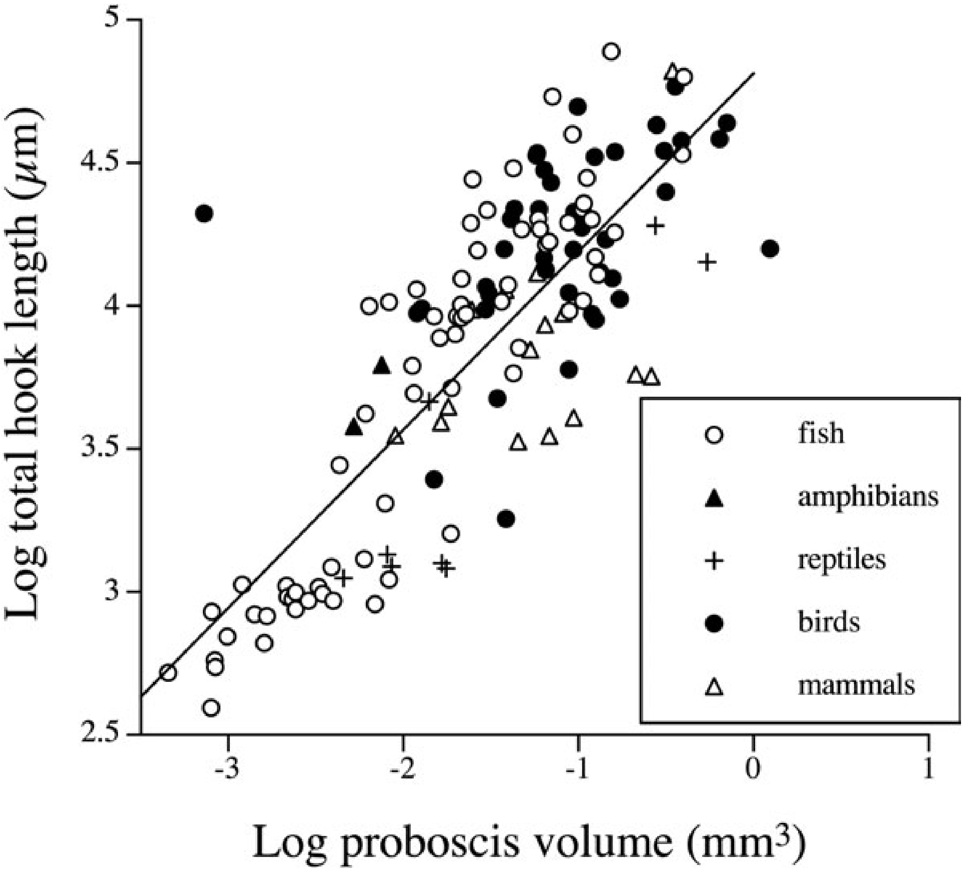

Figure 1. Relationship between proboscis volume and the total length of all hooks borne by the proboscis, across 138 acanthocephalan species using different taxa of definitive hosts (indicated by different symbols). The line is the best-fit line from a simple linear regression.

strongly, with total hook length ($r = 0.191$, $P = 0.0251$; Fig. 3A). The slope of this relationship, on a log-log plot, is less than unity (slope = 0.146, 95% confidence intervals 0.019–0.273), which indicates that as total body volume increases, total hook length also increases but at a slower rate. This can be seen when the ratio of total hook length to total body volume is plotted against total body volume: the relationship is clearly negative ($r = -0.751$, $P = 0.0001$; Fig. 3B), showing that, per unit body volume, large species have shorter total hook lengths. Nevertheless, the relationship between total body volume and total hook length is not a strong one because it disappears when species parasitic in ectothermic and endothermic hosts are analysed separately (parasites of ectotherms: $r = 0.059$, $N = 82$, $P = 0.5993$; parasites of endotherms: $r = -0.123$, $N = 56$, $P = 0.3548$).

Even if the relationship between total body volume and total hook length is weak, total body volume differs significantly between species parasitic in ectothermic hosts and those parasitic in endothermic hosts (two-tailed t-test: $t = 6.661$, d.f. = 136, $P = 0.0001$). Acanthocephalans in ectothermic hosts tend to be smaller (mean ± SE of raw data: 30.2 ± 7.9 mm^3, $N = 82$) than those living in endothermic hosts (192.4 ± 54.6 mm^3, $N = 56$). Thus, total body volume was taken into account as a covariate in an analysis of covariance comparing total hook length among acanthocephalan species living in different taxa (fish, amphibians, reptiles, birds, and mammals) of vertebrate hosts. Independently of total body volume, total hook length differed significantly among acanthocephalans living in different types of vertebrate hosts ($F_{4,132} = 6.472$, $P = 0.0001$), with those in mammals and especially birds having greater total hook length than those in fish, amphibians, or reptiles (Fig. 4). The same result was obtained when acanthocephalan species were separated into two groups (i.e. those from ectothermic and endothermic hosts), rather than being separated into five groups based on the host taxon they use as definitive host ($F_{1,135} = 16.817$, $P = 0.0001$).

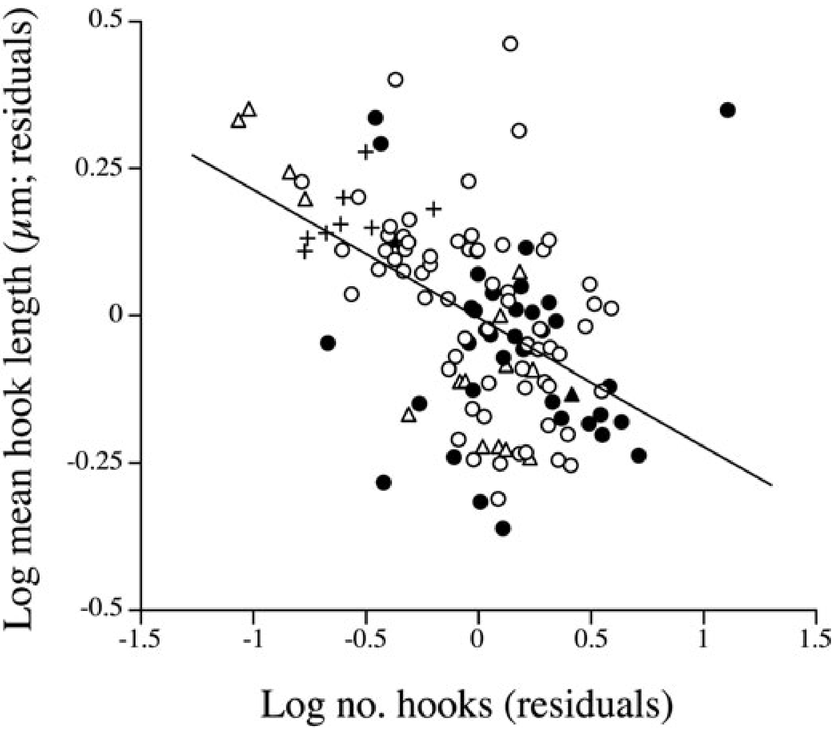

Figure 2. Relationship between the total number and the mean length of hooks on the proboscis, across 138 acanthocephalan species using different taxa of definitive hosts (symbols are as indicated in Figure 1). Both variables are corrected for proboscis volume (i.e. the data are residuals of log-log regressions against proboscis volume). The line is the best-fit line from a simple linear regression.

DISCUSSION

The attachment structures of parasites show strong evidence of having been fine-tuned by natural selection. For example, among chewing lice parasitic on mammals, there is a strong relationship between the diameter of host hair shafts and the width of the groove on the head of lice used for attachment (Morand *et al*., 2000). Lice grasp host hair with this groove, and selection has favoured a slightly different groove width in different lice species, each well-matched to the diameter of the hairs of its host species. Tetraphyllid cestodes provide another example. Among distantly related genera of tetraphyllids, it appears that the scolex (i.e. the complex anterior structure used for anchoring the worm) has converged in species inhabiting hosts with similar intestinal surfaces, such that scolex morphology sometimes reflects selective pressures more than phylogenetic constraints (Williams, 1960, 1966). Whether living on the inside or the outside surfaces of their host, parasites that become dislodged are likely to leave the host and die. Investing in secure attachment is thus important, but only to the extent that the investment matches the likely risk of detachment. The results of the present analyses indicate that among acanthocephalan species, investments in the production of attachment structures are on average higher when the definitive host is an endothermic vertebrate than when it is an ectotherm. Because the results also suggest that the production of hooks is costly, this shows that acanthocephalans make relatively greater investments in attachment structures in hosts where they are more likely to be dislodged.

Evidence that producing hooks for attachment is costly comes from the negative relationship between the number and mean length of hooks, once the effect of proboscis length is taken into account. The negative relationship reflects a trade-off between hook number and hook length, with various species located at different positions along a continuum between the ‘many-short-hooks’ and the ‘few-long-hooks’ extremes. It appears that a given species does not simultaneously maximize both the relative number and the relative length of hooks. This is a strong indication that producing hooks must entail a cost, otherwise there should be no constraints preventing a worm from achieving both relatively many and relatively long hooks (Stearns, 1989). Energy and materials drawn from finite reserves and allocated to the

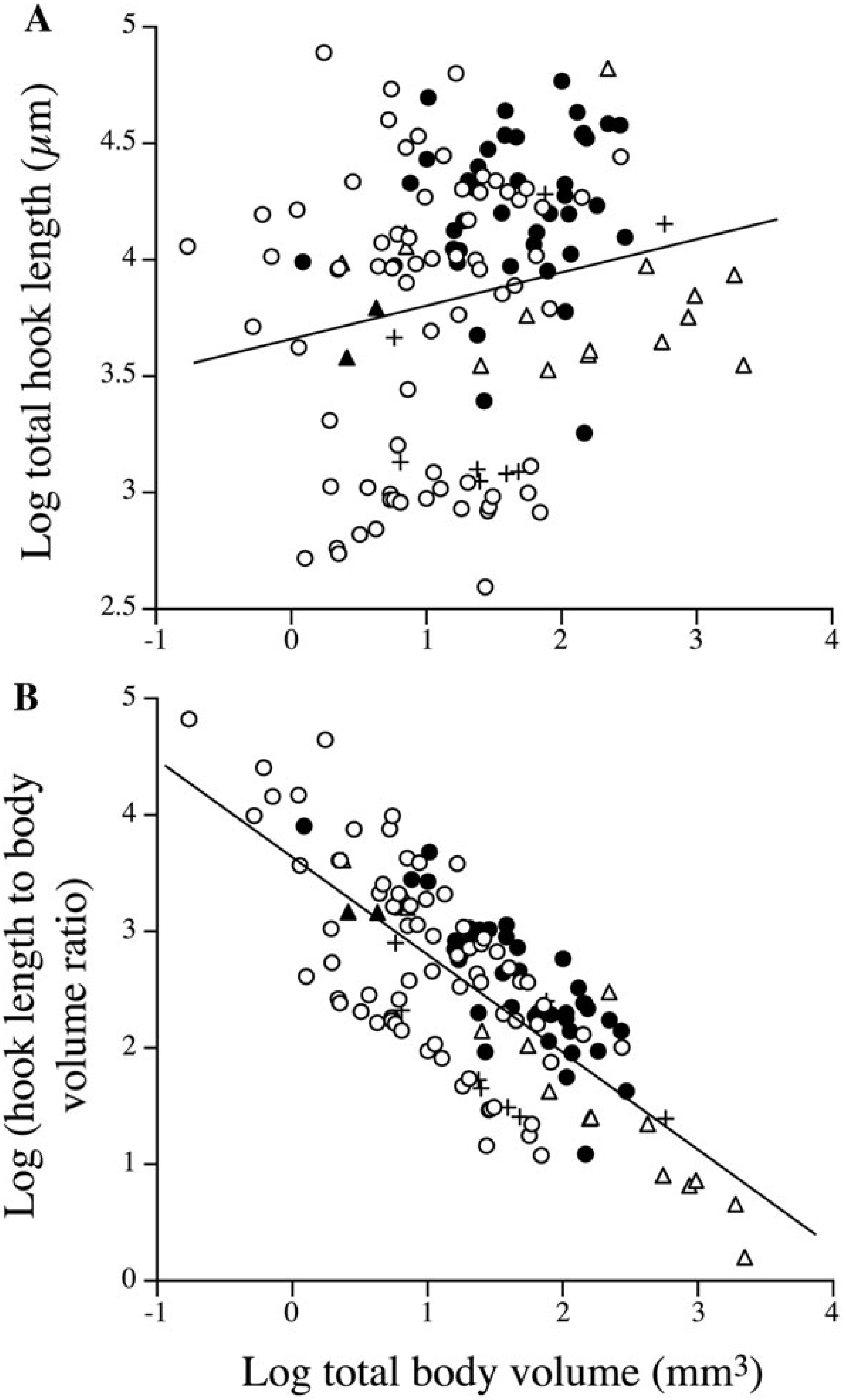

Figure 3. Relationship between total body volume and (A) the total length of all hooks borne on the parasite's proboscis, and (B) the ratio of total hook length to total body volume, across 138 acanthocephalan species using different taxa of definitive hosts (symbols are as indicated in Figure 1). The lines are the best-fit lines from simple linear regressions.

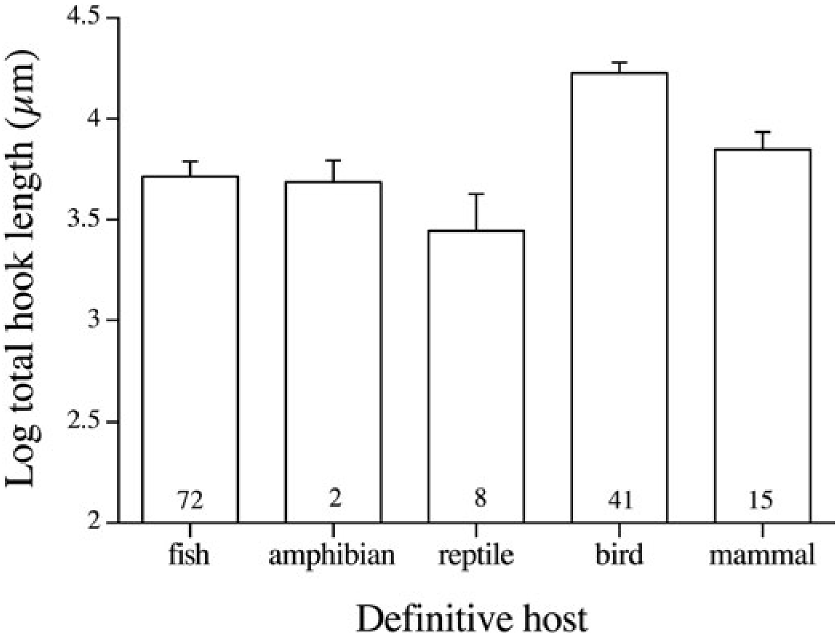

Figure 4. Mean ± standard error total hook length for acanthocephalan species using different vertebrate taxa as definitive hosts. Numbers on the bars indicate the numbers of species in each group.

production of hooks are also unavailable for other functions. For a given number of hooks, it would not be advantageous for a worm to produce hooks longer than the size necessary to ensure attachment. Apart from acanthocephalans parasitic in reptiles which all tend to produce relatively few but long hooks (Fig. 2), there are no indications that the host taxon used selects for one particular strategy over another. Interestingly, in many acanthocephalan species, hooks are already more-or-less fully developed at the cystacanth stage inside the arthropod intermediate host (Miller & Dunagan, 1985; Taraschewski, 2000). Thus, investments in future attachment are made prior to establishment in the definitive host.

Larger worms tended to have a larger proboscis, but there were exceptions to this pattern. For example, some species in the genus *Moniliformis*, with very large bodies (length typically > 8 cm), are characterized by a relatively tiny proboscis. The proboscis is a fluid-filled structure inserted into the gut wall of the host. In some acanthocephalans, such as *Pomphorhynchus* spp., a swelling of considerable size just below the proboscis becomes completely embedded in the intestinal wall, resulting in permanent attachment of the worm (Bush *et al.*, 2001). In most cases, however, it is not the proboscis itself as much as the number and length of the hooks it bears that anchor the worm in one location. Although larger worms tend to have a larger proboscis, and the larger the proboscis, the greater the total hook length it supports, the relationship between total worm size and total hook length is not a strong one (Fig. 3A). Indeed, by contrast to the prediction outlined in the Introduction, relative investments in attachment, measured as hook length per unit body volume, decrease as worm size increases (Fig. 3B). This suggests that, as we move from small-bodied to large-bodied acanthocephalan species, total hook length becomes increasingly less important for attachment. There are several possible explanations for this pattern. First, it may be that other strategies for remaining in place are available to large worms and not to small ones. For example, perhaps large worms can use their bodies to brace themselves against the host intestinal wall, without relying solely on their hooks for attachment. Second, in some species, a host tissue response around the insertion point of the proboscis may more-or-less permanently trap the proboscis (C. Kennedy, pers. comm.), and secure the attachment of the parasite independently of its total hook length. Third, another factor that could obscure the relationship between total worm size and total hook length is the precise site of attachment in the gut, which varies among acanthocephalan species. In some parts of the gut, gut content is liquid, whereas it includes solids elsewhere; the probability of dislodgement may depend on the nature of the food passing along the gut at the site of attachment. Because accurate information on site of attachment was rarely available, this variable could not be examined in the present study. Fourth, total hook length appears to remain more-or-less constant through the life of the worm, whereas total body volume increases with age.

The fact that worm age varies among the many specimens used for measurements can only add noise to the relationship between total worm size and total hook length.

Acanthocephalans living in endothermic definitive hosts are significantly larger than acanthocephalans living in ectothermic hosts (Poulin *et al*., 2003). For a given body size, acanthocephalans in endothermic hosts display a significantly greater total hook length than those in ectothermic hosts. This supports the prediction that worms living in endothermic hosts invest more in attachment, to minimize their risk of being dislodged in hosts characterized by more passing food and greater peristalsis, and in which competition from other worms is likely to be intense. However, the difference in investment between species parasitic in mammal hosts and those parasitic in ectothermic hosts is rather small. It is in species parasitic in birds that total hook length is clearly substantially higher than in species from other hosts (note log-scale in Fig. 4). There may thus be differences between mammal and bird hosts in terms of 'living conditions' for acanthocephalans.

On a smaller taxonomic scale, variation in total hook length is not always easy to explain. For example, closely related acanthocephalan species with similar body sizes and using the same type of hosts, can have markedly different (i.e. often two- to three-fold differences) investments in hook production. This is where information on the digestive physiology of the host or the precise site of attachment of the worm might provide useful clues to the forces shaping the evolution of attachment structures.

In addition to interspecific variation in investment in attachment, intraspecific variation suggests that individual worms can adjust their investment to their current situation. Many acanthocephalan species, such as those parasitic in freshwater fishes (Poulin, 1992), are not strictly host-specific, and can develop and reproduce in a range of definitive host species. Both the relative dimensions of the proboscis and the relative number and size of hooks may vary as a function of the definitive host species in which a worm finds itself (Amin, 1975). This suggests that the optimal investment in attachment is not fixed within a species, but instead displays some degree of phenotypic plasticity.

In summary, the production of hooks in acanthocephalans appears to be costly, as indicated by the interspecific trade-off between the number of hooks and mean hook length. Relative investments in hook production tend to be lower in larger species, but they tend to be higher in species exploiting endothermic hosts, especially birds, than in those living in ectothermic hosts. These results support the general prediction that investments in attachment are, to some extent, shaped by the probability of being dislodged. This finding parallels the observation that in intertidal organisms, such as mussels with their byssus threads (Bell & Gosline, 1996, 1997), investments in attachment are a function of wave exposure, and thus a function of the risk of detachment from the substrate. The present study is the first quantitative analysis of interspecific patterns of investment in attachment structures in a taxonomic group of parasites. Other groups of parasitic helminths live in the gastrointestinal tract of vertebrates, using attachment structures (scolex in cestodes, suckers in trematodes) that are different from those of acanthocephalans but that can also be measured. It will be interesting to see whether similar trends exist in these groups, perhaps providing evidence for convergence in the evolution of attachment strategies among phylogenetically distinct lineages.

ACKNOWLEDGEMENTS

I am very grateful to Clive Kennedy and Tommy Leung for useful comments on an earlier version of the manuscript.

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