

Sexual differences in larval life history traits of acanthocephalan cystacanths

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Abstract

Sexual differences in life history traits, such as size dimorphism, presumably arise via sexual selection and are most readily observed in adults. For complex life-cycle parasites, however, sexual selection may also have consequences for larval traits, e.g., growth in intermediate hosts. Two acanthocephalan species (*Acanthocephalus lucii* and *Echinorhynchus borealis*) were studied to determine, whether larval life histories differ between males and females. The size of female *A. lucii* cystacanths had a much stronger relationship with intermediate host size than males, suggesting females invest more in growth and are consequently more limited by resources. No relationship between host size and cystacanth size was observed for *E. borealis*. For both species, female cystacanths survived longer in a culture medium composed entirely of salts, which could suggest that females have greater energy reserves than males. A comparative analysis across acanthocephalan species indicated that sexual size dimorphism at the adult stage correlates with cystacanth dimorphism. However, the relationship was not isometric; cystacanths do not reach the same level of sexual dimorphism as adults, possibly due to resource constraints. Our results suggest that larval life histories diverge between males and females in some acanthocephalans, and this is seemingly a consequence of sexual selection acting on adults.

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1. Introduction

In dioecious parasites, like free-living taxa, the different reproductive role of males and females has likely resulted in divergent selective pressures on each sex (Andersson, 1994). Large females are generally favored by selection because of the near universal positive correlation between size and fecundity, but male reproductive success, on the other hand, does not necessarily increase as a function of size (Stearns, 1992). This asymmetry commonly leads to sexual dimorphism, which, precluding ecological divergence between the sexes (Shine, 1989), implicates the action of sexual selection. In the case of parasitic helminths, observations on sexual dimorphism (Crompton, 1985; Despres and Maurice, 1995; Poulin, 1997; Morand and Hugot, 1998),

male–male competition (Pica-Mattoccia et al., 2000; Poulin and Morand, 2000; Sasal et al., 2000; Sinisalo et al., 2004), mate choice (Lawlor et al., 1990), and patterns of testis size (Morand and Müller-Graf, 2000; Poulin and Morand, 2000) in diverse taxa suggest that sexual selection has strongly shaped the evolution of parasite life histories. Generally, however, studies investigating sexual selection have focused on the adult stages of parasites even though many dioecious parasites have complex life cycles. Thus, the ramifications of sexual selection on parasite life history may be manifested at more than one ontogenetic stage. For example, male and female schistosomes differentially exploit their mollusc intermediate host, presumably as a consequence of contrasting transmission strategies (Boissier et al., 1999). Sex-specific larval life history strategies may exist in other helminths (e.g., Amin et al., 1980; Steinauer and Nickol, 2003), but this phenomenon has not received much attention.

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The dioecious acanthocephalans have a complex life-cycle, involving two hosts and occasionally a paratenic host (Schmidt, 1985). There are several lines of evidence, suggesting that sexual selection operates in acanthocephalans. First, there is pronounced sexual dimorphism in many species (Crompton, 1985; Poulin and Morand, 2000). Second, there is indirect evidence of intrasexual competition amongst males for access to females (Parshad and Crompton, 1981; Lawlor et al., 1990; Sinisalo et al., 2004). Third, male testis size appears to vary as a function of sperm competition (Poulin and Morand, 2000; Sasal et al., 2000; Sinisalo et al., 2004). Finally, the spatial distribution of some species within the host intestine seems to be related to mating opportunity (Lawlor et al., 1990; Richardson et al., 1997; Sinisalo et al., 2004). Given these observations, acanthocephalans are a suitable group to investigate whether sexual selection affects intermediate host use.

In the present study, the larval life histories of two acanthocephalan species, *Acanthocephalus lucii* and *Echinorhynchus borealis*, were investigated. The definitive host of *A. lucii* is the European perch (*Perca fluviatilis*), a widespread freshwater fish. The similarly widespread isopod species *Asellus aquaticus* serves as intermediate host. Burbot (*Lota lota*), a benthic carnivorous fish, is the definitive host for *E. borealis*, and the benthic amphipod *Pallasea quadrispinosa* is the intermediate host. Both parasites achieve an advanced state of sexual maturity, i.e., well-developed testes and ovarian tissue fragmentation, in their intermediate hosts. However, the two species differ in the level of sexual dimorphism at the adult stage (*A. lucii* > *E. borealis*) and the size of their intermediate hosts (*A. lucii* < *E. borealis*). Thus, by comparing these species some of the factors influencing divergence in larval life history traits between the sexes may be hypothesized.

The goal of this study was to evaluate whether male and female acanthocephalans differ in their life history strategies at the level of the intermediate host. Particularly, the exploitation strategies of *A. lucii* and *E. borealis* in their intermediate host were assessed by examining the determinants of cystacanth size for each sex. Additionally, the in vitro longevity of cystacanths was used to assess the energetic reserves of males versus females. Finally, data on sexual size dimorphism at the cystacanth and adult stages was compiled for several acanthocephalan species to evaluate whether adult life history traits are pertinent to larval growth strategies.

2. Materials and methods

2.1. Determinants of cystacanth size

Isopods infected with *A. lucii* cystacanths were collected from Lake Jyväsjärvi, Central Finland (62°14 N 25°44 E) in September and October, 2005. The isopods were used in various other studies but at the end of all other experiments isopods were dissected and cystacanths were counted

and sexed. All cystacanths were placed into refrigerated tap water overnight to relax and extend them before being measured. Cystacanth length and width was measured to the nearest 0.01 mm using an ocular micrometer on a light microscope. Worms were considered cylindrical in shape, so cystacanth volume (mm³) was calculated using the equation $(\pi l w^2)/4$, where l is worm length and w is worm width. Isopod length was measured to the nearest 0.5 mm. To determine if host size affects cystacanth volume, an ANCOVA was used. Specifically, cystacanth sex was used as a categorical factor and host size was a covariate. The interaction between these two factors was also assessed. A blocking factor representing the experimental source of infected isopods did not significantly contribute to the ANCOVA model, so data on cystacanth volume from all infected isopods were pooled for the analysis. All cystacanths used in the analysis (male $n = 63$; female $n = 70$) came from single infections. Cystacanth volume was square root transformed to homogenize variance.

Amphipods infected with *E. borealis* were collected from Lake Pääjärvi, Southeastern Finland (61°5 N 25°1 E) in November, 2005. The length of amphipods from the tip of the head to the end of the eleventh segment was measured to the nearest 0.5 mm. Cystacanths from infected amphipods were maintained in vitro (described below) and, after death, their length and width were measured. Cystacanth measurements were taken and volume was calculated in a manner identical to that described for *A. lucii* cystacanths. The determinants of *E. borealis* size were investigated with an ANCOVA employing cystacanth sex (male $n = 28$; female $n = 26$) and infection status (either single $n = 25$ or multiple $n = 29$ infections) as independent factors and host size as a covariate. Non-significant interactions between factors were removed from the model.

2.2. In vitro survival of cystacanths

Live cystacanths of *A. lucii* ($n = 34$) and *E. borealis* ($n = 54$) were dissected from their intermediate hosts and placed in saline. The saline solution was based on the specifications of Van Harrevald (1936) and included NaCl (12 g/L), KCl (0.4 g/L), CaCl₂ (1.5 g/L), NaHCO₃ (0.17 g/L) and MgCl₂·6H₂O (0.5 g/L). Cystacanths were maintained in 3.5 cm diameter culture dishes at 4 °C and they were checked daily to determine survival. As individuals neared death, they lost the ability to osmo-regulate, gradually swelled and became turgid. After worms died, they were placed in tap water overnight and then measured as described above.

For *A. lucii*, all worms came from single infections, so only cystacanth sex and volume (range 0.25–0.78 mm³ for males and 0.72–1.54 mm³ for females) were considered as factors influencing in vitro longevity. These two terms were included in a Cox regression, a procedure commonly used for survival analyses. In the case of *E. borealis*, multiple

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