Sexual competition in an acanthocephalan parasite of fish

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SUMMARY

Acanthocephalans are polygamous parasites of vertebrates and some species are known to aggregate in sexual congress to mate. Such a reproductive behaviour could lead to male–male competition for access to females and could have consequences for sexual selection. We dissected 87 gobiid fish, *Gobius bucchichii*, harbouring 891 acanthocephalans, *Acanthocephaloides propinquus*. The parasites were sexed and their body sizes were measured. Testicular volume was also evaluated in 82 males in order to establish their phenotypic sexual investment in relation to the estimated sex ratio. We found that parasite intensity (i.e. the number of individuals/fish) was not correlated with fish size, but that parasite size was significantly related to host size. Our results showed that there was a significant relationship between the mean female body size and their number within one host. We found that when the percentage of male parasites in a host increased, presumably increasing male–male competition for access to females, males had a larger testicular volume. We discuss these results in terms of energy allocation, sexual and sperm competition. We conclude that competition for space should be less important for males than competition for access to females. Moreover, increasing testis size should confer advantages to males especially for their reproductive success when sperm competition occurs.

Key words: Acanthocephalan, sexual competition, sex ratio, energy allocation.

INTRODUCTION

In many invertebrate taxa, females are larger than males and it has been hypothesized that the fecundity advantage (larger females usually produce more offspring) may have driven the evolution of sexual size dimorphism (Lewin, 1988; Charnov, 1993). The evolution of male body size is usually thought to be driven by sexual selection, which should favour larger male size where male–male competition is intense as large size usually correlates with greater access to females. Sexual selection theory predicts that the role of each sex will be determined by the operational sex ratio, or the sex ratio among individuals searching for mates at a given time (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996). Any variation in sex ratios may alter the level of male–male competition and thus affect body sizes. Numerous studies have investigated the evolution of sexual size dimorphism at both interspecific and intraspecific levels in free-living species (Shine, 1989; Møller, 1991), but there are few studies concerning parasite species (Poulin, 1998). Studies on parasite species have generally focused their aims to interspecific comparisons using recent comparative methods (Poulin & Hamilton, 1995; Morand *et al*. 1996; Poulin, 1997*a*,*b*; Poulin & Morand, 1997; Sorci, Morand & Hugot, 1997; Morand & Hugot, 1998) and intraspecific studies still remain very rare.

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The existence of a trade-off, in terms of resource allocation, between growth and reproduction is one major principle in life-history theory (Kozlowski, 1992; Roff, 1992). Resource allocation processes influence also the evolution of reproductive strategies (Maynard Smith, 1978; Reznick, 1985). We may expect to detect more easily these processes when resources are scarce or when competition increases, as the difficulty of choosing between survival and reproduction should be much greater.

In this paper we investigate the relationship between the observed sex ratio (assumed to be equivalent to the operational sex ratio) and the relative investments in male gonad development in an acanthocephalan parasite (*Acanthocephaloides propinquus* Dujardin, 1845) of the gobiid fish (*Gobius bucchichii* Steindachner, 1870). Generally, adult acanthocephalans parasitize the intestine of various vertebrate hosts as the definitive host. Acanthocephalans have life-cycles with arthropods as intermediate hosts. They are gonochoric parasites with a pronounced sexual size dimorphism, the females being larger than males, and often have a female-biased sex ratio (Crompton, 1985). Acanthocephalans appear to be polygamous and some species are known to aggregate in sexual congress to mate (Richardson, Martens & Nickol, 1997). This mating system suggests that each individual male can mate with several females and it has been shown experimentally that a male is able to inseminate as many as 17 females during a sexual congress (Crompton, 1974).

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Acanthocephalan males seal the female gonopore just after insemination, which prevents other insemination at least temporarily (Whitfield, 1970). This behaviour reduces multiple inseminations and sperm competition within a female, but increases male–male competition for access to females. Moreover, atypical sexual behaviour, such as homosexual forced copulation has been reported (Abele & Gilchrist, 1977; Crompton, 1985). This behaviour may prevent glued males from copulating. We can, thus, assume that male–male competition in acanthocephalans is intense with a high variance in male reproductive success.

Male body size seems to be particularly important during mating as larger males have been shown to enjoy an advantage in access to females in this group of parasites (Parshad & Crompton, 1981; Lawlor *et al*. 1990). Therefore, we estimated the effect of sexual competition by measuring both the body size of males and their testicular volume. We also hypothesized that any changes in the operational sex ratio should have a profound effect on the level of male–male competition and consequently on the level of investment in testes size. We tested for correlations between total volume of testis and the proportion of male parasites in a fish in order to evaluate the consequences of male–male competition on testes investment.

MATERIALS AND METHODS

A total of 87 fish (*Gobius bucchichii*, Steindachner, 1870) harbouring 891 parasites *Acanthocephaloïdes propinquus* (Dujardin, 1845), were collected in and around the National Park of Port-Cros (Mediterranean Sea, France). The parasite species lives preferentially in the cloaca of this fish but may move into the intestine when the cloaca is crowded and saturated (de Buron-Brun, 1986). For each host, we counted the parasite intensity (number of parasites/host) and the sex ratio (number of mature females to the number of mature males). Parasite intensity was ln-transformed in order to normalize the data. For each parasite, total body length was measured from the bottom of the proboscis to the end of the body. Testes are ovoid and we measured the length (L) and the width (l) of both testes for 82 parasites removed from 30 fishes. Total testicular volume was then calculated by assuming that the testis is a regular ovoid $V = (\pi \times L \times l^2)/6$ and summing the volumes of both testes.

We suppose that the cloacal volume was correlated to the fish size. Thereafter, in order to avoid a confounding effect, we adjusted each variable for the standard length of host and used residuals of regressions. Testis volume was correlated with parasite body size. Values of testis volumes were controlled for both host and parasite body size.

RESULTS

Epidemiological data

All fishes used in this study were parasitized. Parasite intensity varied from 1 to 47 with a mean of $10{\cdot}2 \pm 0{\cdot}9$ parasites/fish. In total 511 female parasites (mean intensity $5{\cdot}9 \pm 0{\cdot}6$; range 0–29) and 380 males (mean intensity $4{\cdot}4 \pm 0{\cdot}4$; range 0–23) were recovered. A χ^2 test showed a significant biased sex ratio in favour of females ($P < 0{\cdot}01$). We found a significant positive relationship between the number of parasitic males and the number of parasitic females within each fish ($n = 87$; $R^2 = 0{\cdot}60$; slope $= 0{\cdot}99$; $P < 0{\cdot}001$) (Fig. 1).

Importance of host size

We found no relationship between host body size and parasite intensity (simple regression, $n = 87$; $P = 0{\cdot}43$). A lack of relationship with host body size was also found when parasitic males ($P = 0{\cdot}72$) and parasitic females ($P = 0{\cdot}37$) were analysed separately. There was no relationship between host body size and parasite sex ratio (simple regression, $n = 76$; $P = 0{\cdot}20$).

There was a significant relationship between host body size and mean size for parasitic males (simple regression, $n = 74$; $R^2 = 0{\cdot}12$; slope $= 0{\cdot}2$; $P = 0{\cdot}002$) and parasitic females (simple regression, $n = 75$; $R^2 = 0{\cdot}16$; slope $= 0{\cdot}3$; $P < 0{\cdot}001$). Therefore, we controlled parasite body size for host body size.

Importance of parasite body size

We found no relationships between sex ratio and mean body size of parasitic females ($n = 69$; $P = 0{\cdot}17$) and between sex ratio and mean body size of parasitic males ($n = 70$; $P = 0{\cdot}77$).

The correlation between the residuals of female body length and male body length (controlled for host body size) revealed a significant hypoallometric relationship (simple regression, $n = 69$; $R^2 = 0{\cdot}30$; slope $= 0{\cdot}63 \pm 0{\cdot}12$; $P < 0{\cdot}001$) (Fig. 2). Student's t-test of slope comparison revealed a significant deviation from the 1:1 relationship ($P < 0{\cdot}01$).

There was no significant relationship between parasite intensity (the number of both males and females) and mean parasite body size, either for females ($n = 75$; $P = 0{\cdot}09$) or for males ($n = 74$; $P = 0{\cdot}29$). Parasite male body size was neither significantly correlated to the number of males ($n = 74$; $P = 0{\cdot}64$) nor to the number of females within a host ($n = 74$; $P = 0{\cdot}19$). Parasite female body size was not significantly correlated to the number of males ($n = 75$; $P = 0{\cdot}45$). However, we found a significant negative relationship between the mean number of females and their mean body size (simple regression, $n = 75$; $R^2 = 0{\cdot}07$; slope $= -0{\cdot}07$; $P = 0{\cdot}02$).

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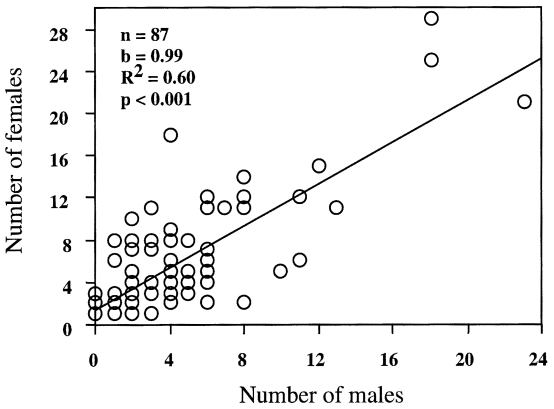


Fig. 1. Relationship between the numbers of females and males of *Acanthocephaloides propinquus* (Acanthocephala) within *Gobius bucchichii* (Teleostei).

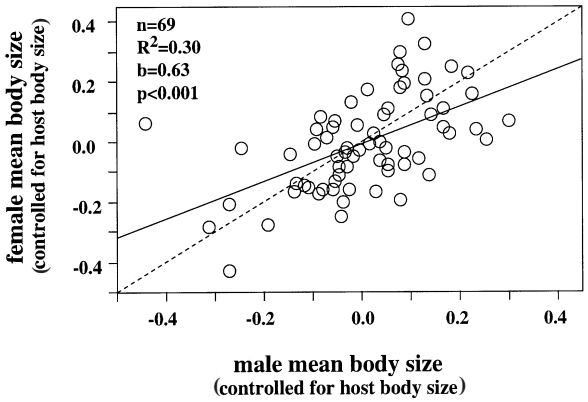


Fig. 2. Relationship between body size of females and males (in ln) for *Acanthocephaloides propinquus* (Acanthocephala) within *Gobius bucchichii* (Teleostei). Dashed line represents relationship with slope = 1. Note that if the outlier in the top left corner is excluded, the regression slope remains significantly different from 1 ($n = 69$; $R^2 = 0{\cdot}38$; slope = $0{\cdot}77 \pm 0{\cdot}12$; $P < 0{\cdot}05$).

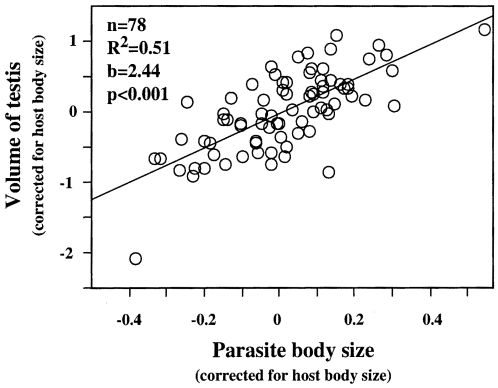


Fig. 3. Relationship between male body size and testis volume for *Acanthocephaloides propinquus*.

There was a significant relationship between testes volume and both male parasite body size (simple regression, $n = 78$; $R^2 = 0{\cdot}63$; slope = $2{\cdot}71$; $P < 0{\cdot}001$) and host body size (simple regression, $n = 78$; $R^2 = 0{\cdot}28$; slope = $1{\cdot}38$; $P < 0{\cdot}001$). Thereafter, we controlled data for host body size and we found a significant positive relationship between

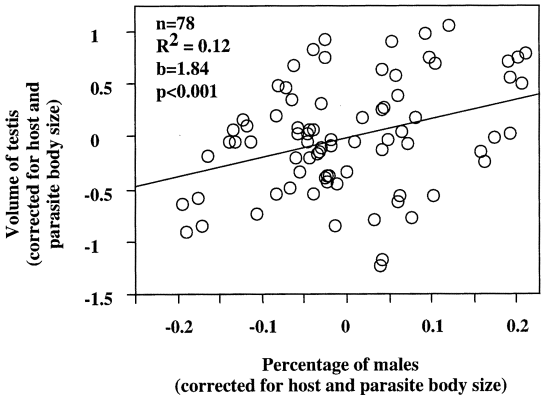


Fig. 4. Relationship between percentage of males within 1 host and the volume of their testes. Data are corrected for host and parasite body size.

parasite body size and testis volume (simple regression, $n = 78$; $R^2 = 0{\cdot}51$; slope = $2{\cdot}44$; $P < 0{\cdot}001$) (Fig. 3). We found a significant relationship between percentage of males within a host and their testis volume, this variable being controlled for both host and parasite body size (simple regression, $n = 78$; $R^2 = 0{\cdot}12$; slope = $1{\cdot}84$; $P < 0{\cdot}001$) (Fig. 4).

DISCUSSION

Sex ratio and parasite intensity

The observed sex ratio was globally biased in favour of females and a significant relationship between the number of males and the number of females was found, across all intensities of infection. We can assume that each fish acquired their parasites randomly in regard of their sex and that the observed sex ratio is directly related to the operational sex ratio. Because primary sex ratio in acanthocephalans is supposed to be equilibrated (Crompton, 1985), a biased sex ratio may be the result either of a differential aggregation between sexes in individual hosts (Anderson, 1982; Morand *et al.* 1993) or of a higher mortality of males compared with females (Crompton, 1970). The males' higher mortality rate may be the result of a male–male competition for access to females. This hypothesis is reinforced by the fact that this differential mortality occurs after the sexual maturity (Abele & Gilchrist, 1977).

Parasite competition and host body size

We found no relationship between host size and parasite intensity but a significant relationship between host size and parasite size. A positive relationship between host and parasite body size has been previously found in several comparative studies (Kirk, 1991; Skorping, Read & Keymer, 1991; Morand *et al.* 1996; Sorci, Morand & Hugot, 1997). Two kinds of explanations have been given. The first one refers to the fecundity advantage (Morand & Sorci, 1998), where large hosts are assumed to provide more resources and to allow the parasites to

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live longer. A second explanation, as postulated by Crompton (1973) and Sasal & Morand (1998) in the case of parasitic monogenean species, refers to physical constraints such as attachment sites within hosts. Acanthocephalans prefer to live in the fish's rectum. We assumed that rectum volume is related to fish size and thereafter the host parasite body size relationship should be a consequence of available space.

The lack of relationship between host size and parasite intensity may be indicative of an absence of niche saturation and/or weak competition between individuals for resources. However, acanthocephalan parasites are able to move into the intestine when there is no more available space in the preferred niche (Nagasawa, Egusa & Ishino, 1982; de Buron-Brun, 1986), which can apparently reduce the level of competition for space. Elsewhere, Hine & Kennedy (1974) have shown that individuals of the acanthocephalan, *Pomphorhynchus laevis*, localized outside the fish rectum are not able to release eggs. Concerning the females, the negative relationship observed between the number of females within one host and their average body size, may reflect both the effect of competition for resources and for space. Therefore, we may assume that growth of females is limited (even if a reproductive advantage for larger size females is generally accepted (Charnov, 1993)), thereby reducing the competition for space in the rectum. The absence of such a relationship for males suggests that males are less affected by space competition because of their smaller size and/or because of the supposed male–male competition. Finally, males are usually much more active (Parshad & Crompton, 1981) and smaller than females, therefore, we suggest that competition for space should be less important for males, than competition for access to females.

Sexual size dimorphism and parasite size

There is a strong correlation between female body size and male body size. The value of the regression slope ($b = 0{\cdot}63$) indicates a hypoallometry between female and male body size, meaning that the sexual size dimorphism declines as size increases. According to Fairbairn & Presiosi (1994) the hypoallometry (slope < 1) we found between female and male body sizes does not seem to support the hypothesis that sexual size dimorphism in these parasites is a consequence of sexual selection.

Testes size, sex-ratio and evidence for sexual competition

We found a significant positive correlation between male parasite body size and their testicular volume. Several studies concerning vertebrate (Harcourt *et al*. 1981; Møller, 1988*a*, *b*, 1989) or invertebrate (Gage, 1994) species have shown that there is a significant relationship between testis size and ejaculate efficiency for reproduction (i.e. higher sperm production rate, larger reserve and more sperm per ejaculate). Investment in testis size should be important for males as sperm competition is considerable for sexual selection (Birkhead & Hunter, 1990; Westneat, 1996). We also found a significant relationship between the percentage of males within an individual host and their mean testicular volume (all other things being controlled). This result strongly suggests that an increase in male–male competition leads to greater investment in testis size. As the copulatory caps are not permanent in acanthocephala, female worms are able to mate sequentially with more than 1 male (Crompton, 1974). We can therefore hypothesize that sperm competition may occur (Svärd & Wiklund, 1989). Increasing testis size should confer several advantages for males: inseminating a high number of females and/or increasing the proportion of available spermatozoids within a given inseminated female (Birkhead & Hunter, 1990; Cook & Wedell, 1996). Such a sperm competition, if it occurs, may select for enlarged testis size.

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