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PARASITE-RELATED PAIRING SUCCESS IN AN INTERMEDIATE HOST, *CAECIDOTEA INTERMEDIUS* (ISOPODA): EFFECTS OF MALE BEHAVIOR AND REPRODUCTIVE PHYSIOLOGY

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ABSTRACT: The acanthocephalan parasite *Acanthocephalus dirus* develops from the egg to the cystacanth stage inside the freshwater isopod *Caecidotea intermedius*. We have shown previously that cystacanth-infected male *C. intermedius* are less likely to initiate mating attempts with females than uninfected males in competitive situations. Here, we used a field-based experiment to examine whether cystacanth-infected males were also less likely to initiate mating attempts with females in noncompetitive situations. We found that infected males were less responsive to females than uninfected males, and we propose that the cystacanth-related change in male mating behavior is mediated by a change in the mating response of males to females rather than male–male competition. We then examined whether cystacanth-related changes in reproductive function, i.e., sperm content and fertilization ability, could explain this variation in male mating behavior. We found that cystacanth-infected males contained both developing and mature sperm and fertilized as many eggs as uninfected males. Thus, we propose that changes in reproductive function are unlikely to explain cystacanth-related variation in male mating behavior in *C. intermedius*.

Parasites often influence the mating dynamics of their hosts (e.g., Zuk, 1992; Dunn, 2005). In many cases, parasite presence correlates with a decrease in mating success because infection results in pathological effects on reproduction. However, when trophically transmitted parasites infect intermediate hosts, changes in mating behavior may be due to several mechanisms, e.g., pathology, parasitic manipulation, host counteradaptation (Poulin et al., 1994; Moore, 2002; Thomas et al., 2005). Thus, mechanistic studies that examine the relationship between parasite infection, and host behavior and physiology, provide valuable insight into parasite-related variation in mating behavior of intermediate hosts. We examined the relationship between parasite infection, male mating behavior, and reproductive physiology in an intermediate host to determine the relative importance of these mechanisms to parasite-related variation in male mating success in nature.

Acanthocephalans are trophically transmitted parasites that commonly use isopods, amphipods, and insects as intermediate hosts, and vertebrates as definitive hosts (Crompton and Nickol, 1985). Inside the intermediate hosts, acanthocephalans develop through the acanthor and acanthella stages before reaching the cystacanth stage, which is infective to definitive hosts. Cystacanth infection often correlates with changes in both antipredator behavior and color pattern, which increase conspicuousness to definitive hosts (Moore, 2002). In addition, acanthocephalan presence can correlate with a decrease in male mating success in nature, i.e., amphipods (Ward, 1986; Zohar and Holmes, 1998; Bollache et al., 2001) and isopods (Sparkes et al., 2006).

We examined the relationship between parasite infection and male mating success in the intermediate host *Caecidotea intermedius* (Isopoda) infected by the acanthocephalan parasite *Acanthocephalus dirus* (Van Cleave). Mating behavior in *C. intermedius* follows a predictable sequence that includes the following stages: male mate search, male–female encounter, male–female mating contest, mate guard, female molt, and copulation (Sparkes et al., 2006). Mating contests are initiated by males after encounters with females, and they provide both males and females with the opportunity to engage in mate choice (Jormalainen, 1998; Sparkes et al., 2000, 2002). Male isopods have been shown to exhibit preferences for females based on body size and molt status, whereas females exhibit preferences for males based on physical condition (Jormalainen, 1998; Sparkes et al., 2000, 2002). Our previous research on *A. dirus* and *C. intermedius* has shown that the presence of cystacanths correlates with a decrease in male pairing success that is absent in both acanthella-infected and uninfected males (Sparkes et al., 2006). We also have shown that this decrease is due to a change in male behavior rather than female behavior (Sparkes et al., 2006). Specifically, cystacanth-infected males do not initiate mating contests with females after an encounter. However, these trials contained rival males; hence, it is unclear whether cystacanth-infected males are less responsive to females because they are unable to compete with rival males or because they are not attracted to females. Here, we examined whether cystacanth-infected males were unresponsive to females in the absence of rival males to distinguish between these alternative mechanisms. We then quantified the relationship between cystacanth infection and both reproductive performance (fertilization success) and sperm content to determine whether changes in male mating behavior could be explained by detrimental effects of cystacanth presence on reproductive function.

MATERIALS AND METHODS

Study organisms

The study organisms were collected from Buffalo Creek situated approximately 60 km northwest of the DePaul University campus in Lake County, Illinois. In this stream, the macroinvertebrate community is dominated by *C. intermedius*, and prevalence of *A. dirus* is relatively high (prevalence = 54%, n = 934; Sparkes et al., 2004, 2006). Infection of *C. intermedius* occurs between June and August, and development into the cystacanth stage is typically complete by November (Sparkes et al., 2004). The breeding season in this population lasts from March to September; hence, it incorporates time periods dominated by both cystacanths (March–May) and acanthellae (June–September). The cystacanth-related decrease in male mating success described above was recorded during both March (2004) and April (2003). For these samples, mating was positively size assortative, but male body size did not correlate consistently with either mating success or infection status (Sparkes et al., 2006).

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Male mating response and pairing success

We used a field-based behavioral experiment to examine whether cystacanth-infected male *C. intermedius* were less responsive to females than uninfected males in the absence of rival males. To reach this objective, we exposed individual males to reproductive females and recorded whether males initiated mating contests with females after an encounter. We predicted that infected males would be less likely to initiate mating contests with females than uninfected males if mating activity is dependent on cystacanth-related variation in the responsiveness of males to females rather than inhibitory effects of rival males on male mating behavior. We also used a field survey to quantify the infection status of paired and unpaired males to determine whether the relationship between infection status and male pairing success identified in previous breeding seasons (2003, 2004) was also present in the current breeding season (2005).

Male mating response was examined using 60 behavioral trials (n = 30 uninfected, n = 30 cystacanth-infected) that were run between 0900 and 1600 hr (March 2005, n = 20; 3 April 2005, n = 40). Unpaired males were collected at random from the stream, and their infection status identified using a dissecting microscope. Females were obtained by collecting mate-guarding pairs and separating the females from the males. Five females were placed into an experimental arena (square plastic container, 11 × 11 × 3 cm, partially filled with stream water, located on the stream bank), along with an experimental male. Each trial had a potential duration of 20 min. If the male either initiated a mating attempt with a female, i.e., a male engaged in a physical struggle with a female after contact, or he had 10 encounters with females before this time, the trial was terminated. For each trial, we recorded both the number of encounters (1–10) and whether the male initiated a mating attempt with a female after an encounter. A male was scored as either ''responsive'' or ''unresponsive'' based on whether he initiated a mating attempt with a female. Trials were run in groups of 20, and male infection status was alternated between trials. The same 5 females were used for each group of 20 trials (26 March 2005, n = 5 females; 3 April 2005, n = 10 females).

Male mating response was compared between infected and uninfected males by using a McNemar's test for paired categorical data (Samuels and Witmer, 2003). For this analysis, males were paired based on the time of trial (e.g., trial 1 and 2 were paired, trial 3 and trial 4 were paired). This approach allowed us to account for the time of day in the analysis. We also used a *G*-test to determine whether male mating behavior differed among the different female groups used in the experiment (Sokal and Rohlf, 1995).

To determine whether cystacanth infection correlated with male pairing success, we quantified parasite-related pairing success during March and April 2005 (14 March, n = 155; 3 April, n = 126). On both days, paired and unpaired males were captured from the stream (0900–1200 hr), transported to the laboratory, and body length recorded. Each individual was then dissected, and both the number of parasites and the developmental stage of each parasite were recorded. Pairing success was estimated using males that were of reproductive size, i.e., the length of the smallest paired male collected in that sample, following Ward (1988). We used a *G*-test (with Yates continuity correction; Sokal and Rohlf, 1995) to examine the relationship between infection status and male pairing success (Bonferroni adjusted critical values, following Rice, 1989). The relationship among male body size, infection status, and collection date was examined using analysis of variance (following tests for normality and homogeneity of variances). The pattern of size assortative mating was assessed using a Pearson correlation coefficient, and logistic regression analysis was used to determine the relationship between infection status, male body size, and male pairing success (saturated model: infection status, body size, infection status × body size). We used Systat 10 (SPSS, Inc., Chicago, Illinois) for analysis that required statistical software.

Fertilization success

To determine whether cystacanth-related effects on male mating behavior could be explained by variation in reproductive performance, we examined the relationship between cystacanth presence and male fertilization success. Research on another stream isopod has shown that unresponsive males will often become responsive if they are present during a female's reproductive molt (Sparkes et al., 2002). Thus, we provided cystacanth-infected and uninfected males with access to females during the females' reproductive molt. We then compared the fertilization success of uninfected and cystacanth-infected males. In *C. intermedius*, unfertilized eggs are deposited along with fertilized eggs in the brood pouch. Thus, fertilization success was estimated by recording the number of fertilized and unfertilized eggs present in the brood pouch. We predicted that if cystacanth presence negatively impacted reproductive performance, infected males would have lower fertilization success than uninfected males.

We collected 97 males (48 infected, 49 uninfected) on 8 April 2005 (0900–1100 hr), and we identified infection status by using a dissecting microscope. Females were collected from mate-guarding pairs (n = 97) on the same day, and they were transported to the laboratory in individual vials. Experimental trials consisted of 1 female and 1 male in an experimental arena (round plastic container 18 cm in diameter × 8 cm in depth, partially filled with streamwater, and a 0.8-cm-diameter leaf disc for food). Females were monitored every 6 hr until molt, and pairing status was recorded during each spot-check. If the female did not molt the posterior half of the exoskeleton (containing the genital pores), she was classified as ''field-mated'' and removed from this part of the analysis. These females were excluded because they have typically been inseminated by their original mates (Sparkes et al., 2002). Females that molted were provided with additional leaf material for 14 days to allow offspring development to occur. After this time, the females were preserved (70% ethanol) and dissected. We examined the relationship between infection status and reproductive performance by comparing both fertilization success (*G*-test; Sokal and Rohlf, 1995) and offspring production (analysis of covariance [ANCOVA], covariate = female size) between infected and uninfected males. To determine whether variation in the mating behavior of infected males correlated with either the number or size of parasites present, we used logistic regression analysis (saturated mode = intensity, total volume, intensity × volume). For this analysis, total parasite volume was calculated for each male by summing values obtained for individual parasites [volume = (π × length × width^2)/6, following Dezfuli et al., 2001]. We also used logistic regression analysis to determine whether either the size ratio of males to females or the amount of time each male was exposed to a premolt female correlated with male mating activity (saturated model = size ratio, time exposed, size ratio × time exposed). Finally, we examined whether transferring the organisms to the laboratory influenced reproduction by comparing both fertilization success (*G*-test) and offspring production (ANCOVA, covariate = female body size) between the field-mated and lab-mated females.

To determine whether females stored sperm between broods, we collected 12 females from mate guarding pairs on 30 April 2005 (0900–1100 hr). These females were housed in the laboratory (as described above) but without access to males during their reproductive molts. The number of fertilized and unfertilized eggs present in the brood pouch after 14 days of incubation was then recorded. We predicted that all of the eggs deposited in the brood pouch would be unfertilized if interbrood sperm storage did not occur.

Sperm presence

To examine the relationship between cystacanth presence and sperm presence, we collected 40 males on 6 May 2005 (1100–1500). These males were placed in Formalin (10% sodium phosphate-buffered solution) for 24 hr and then stored in 70% ethanol. Males were dissected, and both parasite intensity and total parasite volume recorded as described above. For each male, we then isolated the reproductive system and identified whether developing sperm were present in the testes and mature sperm present in the vas deferens. In *C. intermedius*, sperm are relatively large, and they can be identified by visually inspecting the unstained testes and vas deferens by using a dissecting microscope (×40).

RESULTS

Male mating response and pairing success

The relationship between cystacanth infection and male pairing success for the current breeding season was consistent with the pattern identified in the 2 previous seasons. Specifically,

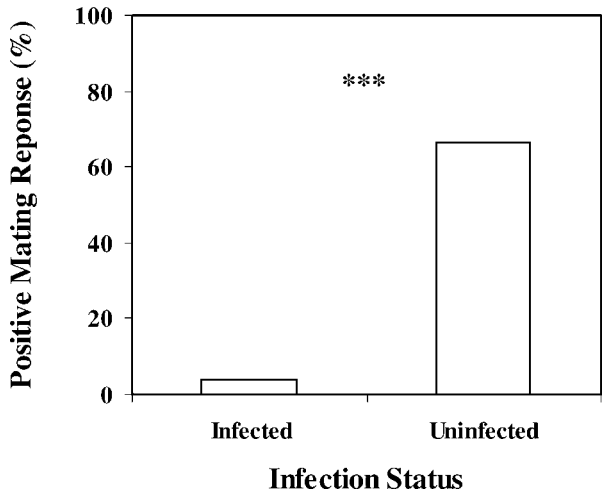

FIGURE 1. Relationship between *Acanthocephalus dirus* infection and the mating response of male *C. intermedius*. A positive mating response was assigned to a male if he initiated a mating attempt with a female during a trial. ***$P < 0.001$.

cystacanth-infected males were less likely to be found in pairs than uninfected males (combined sample: $G_7 = 31.9$, $P < 0.001$; March: $G_1 = 4.8$, $\alpha_{crit} = 0.05$, $P < 0.05$; April: $G_1 = 14.3$, $\alpha_{crit} = 0.025$, $P < 0.001$, n = 209), and this relationship did not correlate consistently with variation in male body size (combined sample: final model = infection status, body size, $G_1 = 44.4$, $P < 0.001$; March: final model = infection status, body size, $G_1 = 44.8$, $P < 0.001$; April: final model = infection status, $G_1 = 17.0$, $P < 0.001$). Overall, less than 1% (1/78) of paired males were infected (intensity = 1), 29% (38/131) of unpaired males were infected (mean intensity = 1.25, SE = 0.09), and less than 1% (1/78) of paired females were infected (intensity = 1).

To determine the relationship between cystacanth infection and male mating behavior, we ran 60 trials (30 uninfected males, 30 infected males). However, dissections revealed that 1 ''uninfected'' male was infected and 2 ''infected'' males were uninfected. These males were excluded from the analysis, along with the males they had been paired with for analysis. In addition, 3 males were considered nonreproductive because they were smaller than the smallest male collected from pairs (Ward, 1988). These males also were excluded from the analysis, along with the males they had been paired with for analysis. Thus, we ran statistical analysis on 24 of the original 30 paired trials. For these trials, male body size did not differ between experimental groups (infected: mean = 11.8 mm, SE = 0.5, n = 24; uninfected: mean = 11.4 mm, SE = 0.3, n = 24; paired *t*-test, $t_{23} = 1.0$, $P = 0.32$), and all of the *A. dirus* present were in the cystacanth stage (mean intensity = 1.4, SE = 0.12, n = 33). Analysis of the male mating behavior revealed that infected males were less likely to initiate mating attempts with females than uninfected males (McNemar's test for paired samples, $\chi^2_1 = 15.0$, $P < 0.001$). Specifically, only 4% (1/24) of infected males showed a positive mating response, whereas 67% (16/24) of uninfected males showed a positive mating response (Fig. 1). Male mating response did not vary significantly among the 3 female groups used in the experiment ($G_2 = 1.3$, $P > 0.5$).

Fertilization success

Eighty-seven females underwent reproductive molts; hence, they were included in the analysis (Table I). Overall, we found that male mating activity increased in the laboratory relative to the field (infected = 73%, uninfected = 97%), but that uninfected males were still more likely to mate with females than infected males ($G_1 = 4.6$, $P < 0.05$). Of the males that mated, 62% (n = 47) engaged in precopulatory mate guarding (infected = 47%, n = 19; uninfected = 72%, n = 28), and 96% (45/47) fertilized all of the eggs deposited by females (1 infected male fertilized 8%, 1 uninfected male fertilized 60%). Overall, there was no difference between infected and uninfected males in either fertilization success ($G_1 = 0.08$, $P > 0.5$; Table I) or the total number of eggs fertilized (ANCOVA: $F_{1,42} = 0.6$, $P = 0.4$; outliers associated with the 2 partial fertilizations were removed). Comparison of fertilization success between field-mated and lab-mated females revealed that transporting the organisms to the laboratory did not result in any detectable effects on reproduction (fertilization success: $G_1 = 0.008$, $P > 0.9$; offspring number: $F_{1,60} = 0.6$, $P = 0.5$). In addition, females that molted in the absence of males deposited only unfertilized eggs (Table I), indicating that females did not store sperm between broods. Thus, the values obtained for fertilization success in the experimental trials represented the mating activity of the experimental males.

Analysis of the infection characteristics of the infected males that mated revealed that 89% contained only 1 parasite (mean intensity = 1.1, SE = 0.08, n = 19), with a total parasite volume of 0.42 mm^3 (SE = 0.07). In contrast for the infected males that did not mate, only 43% contained 1 parasite (mean inten-

TABLE I. Relationship between *A. dirus* infection and reproductive performance in *C. intermedius*. Experimental males are identified as lab—uninfected male and lab—infected male. Females that underwent reproductive molts before collection are identified as field—male present. Females that underwent reproductive molts in the absence of males are identified as lab—male absent. Mating success shows the percentage of females that contained fertilized eggs. Fertilization success shows the percentage of females that contained only fertilized eggs (for mated females).

Group	n*	Female length (SE)	Mating success, % (n)	Fertilization success, % (n)	Mean no. of fertilized eggs (SE, n)
Lab—uninfected male	29	7.87 (0.12)	97 (29)	96 (28)	95.8 (5.5, 28)
Lab—infected male	26	7.73 (0.11)	73 (26)	95 (19)	95.4 (7.4, 19)
Field—male present	20	7.93 (0.17)	90 (20)	100 (18)	96.8 (7.2, 18)
Lab—male absent	12	7.72 (0.31)	0 (12)	—	—

* Sample size.

sity = 1.4, SE = 0.2, n = 7), with a total parasite volume of 1.13 mm^3 (SE = 0.30). Logistic regression analysis revealed that parasite volume was the only predictor of male mating activity (final model: $G_1 = 8.2$, $P = 0.004$) and that volume correlated negatively with mating activity. Logistic regression analysis on the relationship between the size ratio of males and females and the amount of time each male was exposed to a premolt female revealed that neither variable correlated with male mating behavior (saturated model: $G_3 = 0.78$, $P = 0.8$).

Sperm presence

All of the males examined contained both developing and mature sperm (mean intensity = 1.25, SE = 0.08, mean parasite volume = 1.04 mm^3, SE = 0.11, n = 40). Thus, there was no obvious relationship between sperm presence and either parasite intensity or parasite volume.

DISCUSSION

We have shown previously that cystacanth-infected male *C. intermedius* were less responsive to females than both uninfected and acanthella-infected males when rival males were present (Sparkes et al., 2006). Here, we showed that only 4% (n = 24) of cystacanth-infected males initiated mating attempts with females, whereas 67% (n = 24) of uninfected males initiated mating attempts. These values are consistent with the values obtained in a previous study in which rival males were present (cystacanth-infected = 9%, n = 34; uninfected = 59%, n = 45; Sparkes et al., 2006). Thus, we propose that the cystacanth-related decrease in male pairing success observed in nature can be explained by a change in the responsiveness of males to females rather than a change in the ability of these males to compete with rival males for females. In addition, because this change occurs only after the parasite has developed into the cystacanth stage (Sparkes et al., 2006), we propose that it is unlikely to be explained by differences in the behavior of males that occurs independently of infection.

The results obtained here are consistent with other studies that have demonstrated parasite-related changes in the responsiveness of males to females in the laboratory. For example, male cockroaches (*Periplaneta americana*) infected with the acanthocephalan *Moniliformis moniliformis* (Carmicheal et al., 1993), and male mealworm beetles (*Tenebrio molitor*) infected with the metacestode *Hymeolepsis diminuta* (Hurd and Parry, 1991), are less responsive to females than uninfected males. Similarly, male amphipods (*Gammarus lacustris*) infected with the acanthocephalans *Polymorphus paradoxus* and *P. marilis* (Zohar and Holmes, 1998), and male amphipods (*Gammarus pulex*) infected with the acanthocephalan *Pomphorhynchus laevis* (Bollache et al., 2001), are less likely to pair with females than uninfected males in noncompetitive situations. However, the results presented here provide the first demonstration of a direct relationship between the male mating response and cystacanth-related changes in male pairing success in nature.

We also showed that cystacanth infection did not correlate with obvious changes in either sperm content or reproductive performance of males. Infected males contained both developing and mature sperm, and they were as successful at fertilizing eggs as uninfected males. Thus, we propose that cystacanth-related changes in male mating behavior do not seem to be associated with detrimental effects of infection on male reproduction function. Consistent with this interpretation, previous studies on acanthocephalan–host relationships have shown that infected males that are rarely found in pairs possess mature sperm, i.e., amphipods (Zohar and Holmes, 1998) and isopods (Oetinger, 1987). In addition, lab-based studies have shown that acanthocephalan-infected male amphipods (Spaeth, 1951) and isopods (Brattey, 1983) are capable of reproducing. However, in both of these cases, it is not known whether males that are reproductively active in the laboratory experience a parasite-related decrease in pairing success in nature. Thus, the results presented are the first to demonstrate that infected males that are unresponsive to females in nature are capable of reproducing.

At this time, it is unclear whether the cystacanth-related changes in male mating behavior are due to pathological effects of infection, parasitic manipulation, or possibly part of a host response to infection. Consistent with a pathological effect, we found that male mating activity correlated negatively with parasite volume in the lab-based experiment. However, we also found that 47% of the infected males used in the experiment engaged in precopulatory mate guarding before insemination. Since mating contests precede mate guarding, this indicates that almost half of the infected males underwent a reversal of mating behavior in the laboratory. This type of rapid reversal of mating response is not consistent with a pathological effect of infection. Thus, pathology alone is unlikely to explain the variation in mating behavior observed in males in nature.

Parasitic manipulation is expected if a decrease in male mating activity either increases energy availability for the parasite (e.g., Baudoin, 1975) or increases the amount of time infected males spend exposed to definitive hosts. Little is currently known about either mechanism. However, it is known that paired males are found almost exclusively in refuge, whereas unpaired males are often in the open (Holomuzki and Short, 1990; Sparkes et al., 1996). Thus, decreased mating activity could potentially increase the amount of time that infected males spend exposed to predatory definitive hosts. Alternatively, a decrease in male mating activity could be part of a host response to infection. For example, reduced mating activity may allow males to increase the amount of energy that they can redirect toward immune defense (Forbes, 1993), or occur as part of a ''malaise syndrome'' that accompanies activation of the immune system (Dunn et al., 1994). Future work will attempt to distinguish between these alternative mechanisms in this parasite–host relationship.

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