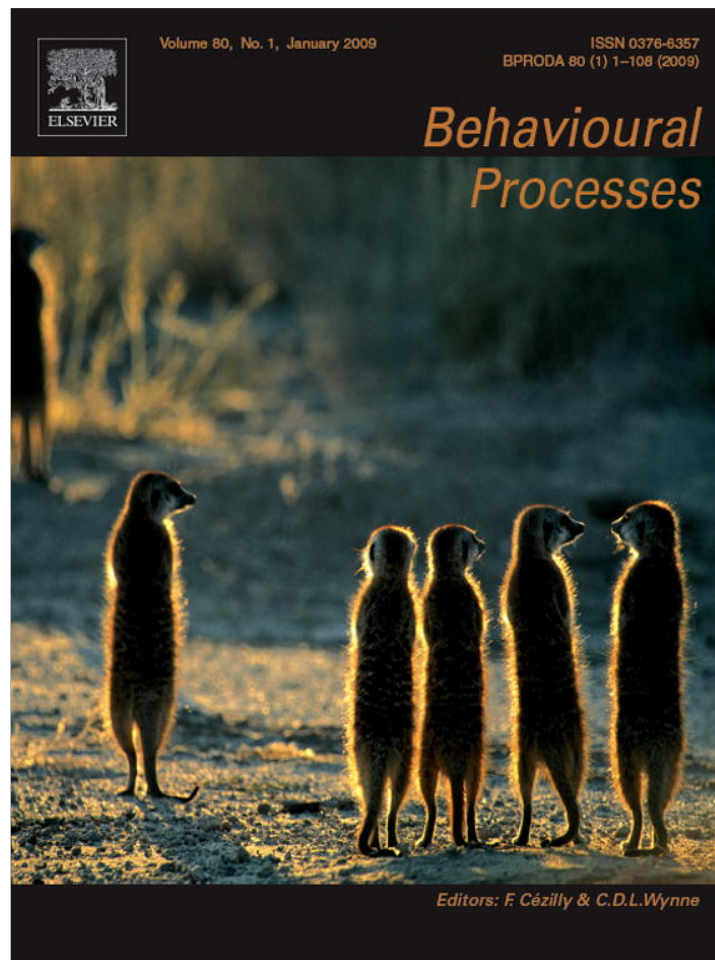


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Effects of a parasitic nematode on male mate choice in a livebearing fish with a coercive mating system (western mosquitofish, *Gambusia affinis*)

Raelynn Deaton*

Department of Zoology, The University of Oklahoma, 730 Van Vleet Oval Room 314, Norman, OK 73019, USA

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ABSTRACT

I examined the effects of the parasitic larval nematode, *Eustrongylides ignotus*, on male mate choice in the western mosquitofish, *Gambusia affinis*. I hypothesized that parasite presence influences male mate choice either directly (via reduction in male mating behavior due to presence of parasite in females) or indirectly (via reduction in male mating behavior due to reduced condition of infected females). Specifically, I tested the predictions that (1) males would mate preferentially with uninfected over infected females (scoring both mating attempts and association time with females); (2) parasitized females would be in poorer condition than non-parasitized females (measured as soluble fat stores); and (3) parasitized females would have reduced fecundity (measured as number of developing embryos). Males preferred to mate with non-parasitized over parasitized females, but showed no differences in association time between females. The nematode did not decrease female body condition, but did decrease female mass, and appeared to decrease female fecundity via reduction in broods (# embryos). Results support that parasites affect male mate choice in mosquitofish; however, the mechanisms used by males to differentiate between parasitized and non-parasitized females remain untested. This study provides the first empirical evidence of parasite effects on male mate choice in livebearing fishes, and suggest a potentially important role for parasite-mediated sexual selection in organisms that use coercive mating as the primary mechanism of obtaining mates.

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1. Introduction

Since Hamilton and Zuk's (1982) influential paper on parasite-mediated sexual selection, a wealth of research has been dedicated to understanding the effects of parasites on mate choice (see Moller, 1990; Barber, 2002; Moore, 2002). However, most studies have focused on female choice for males with obvious or exaggerated secondary sexual characteristics, such as bright color patterns of many birds (Zuk et al., 1990; Johnson, 1991; Sundberg, 1995; Wiehn et al., 1997) and fishes (Mikinski and Bakker, 1990; Lopez, 1999), presumably because those traits signal parasite resistance passed on to offspring (Hamilton and Zuk, 1982; Moller, 1990; Bronseth and Folstad, 1997). Few studies have considered male choice for females infected by parasites (Thomas et al., 1996, 1999), and most of these studies have focused on invertebrate species or sex-role reversed species (e.g. pipefish; Mazzi, 2004). Although in general, effects of parasites on mating behaviors is well studied, results often

are contradictory and vary among parasite species, host species, mating system and parasite virulence (see Moller, 1990; Moore, 2002).

For example, Kennedy et al. (1987) showed a negative correlation between number of parasites and the number of male sexual displays in the guppy, suggesting that parasite infection indirectly decreased male fitness by reducing frequency of courtship behaviors. Barber (2002) showed a negative correlation between the size of the dorsal fin and the number of ectoparasites in the sand goby (*Pomatoschistus minutus*), and suggested that parasite infections may affect important phenotypes used by females in mate choice. Parasites also may reduce male competitive ability by reducing condition, thus, causing males to put more energy into foraging than into mating (Forbes, 1991). In the two-spotted goby (*Gobiusculus flavescens*), parasitism had no effect on male condition, but was correlated with a decrease in male courtship intensity (Pelabon et al., 2005). Asexual mollies (*Poecilia formosa*) avoided mating with computer images of males infected with black spot disease, but the sexual relatives of amazon mollies, *P. latipinna* and *P. mexicana* females did not (Tobler et al., 2006). Tobler and Schlupp (2008) also showed that black spot disease affects shoaling behavior in the western mosquitofish (*Gambusia affinis*) where healthy females avoided associating with computer images of infected individuals.

* Present address: Department of Biology, Sam Houston State University, PO Box 2116, Huntsville, TX 77341, USA. Tel.: +1 936 294 1550/405 325 1319; fax: +1 936 294 3940/405 325 7699.

E-mail address: rdeaton@shsu.edu.

Despite the wealth of knowledge on parasite effects on sexual selection, research is lacking in two areas: (1) the effects of parasites on male mate choice; and (2) the effects of parasites in coercive mating systems, where mechanisms other than mate choice (i.e. forced copulations) also are important in sexual selection. Coercive mating systems, where males of all sizes use forced copulations as their primary means of obtaining mates, are known in a wide variety of taxa, including monarch butterflies (Solensky, 2004), water striders (Arnqvist and Rowe, 1995), garter snakes (Shine and Mason, 2005), bush crickets (Vahed, 2002), and some species of the livebearing fish family Poeciliidae (specifically the mosquitofishes; *Gambusia* spp. Bisazza et al., 2001). In these systems, female mate choice also may be present, but male coercion is considered the primary mechanism of sexual selection.

Mosquitofish provide an excellent opportunity for studying potential roles for parasites in mate choice because several mechanisms of sexual selection may be operating, including male choice (Deaton, 2008a), some level of female mate choice (Gould et al., 1999; Langerhans et al., 2005), variation in male mating behavior, and male–male competition (Hughes, 1985; Deaton, 2008b). Here, I examined the effects of the parasitic larval nematode, *Eustrongylides ignotus*, on male mate choice in the western mosquitofish, *G. affinis*. I hypothesized that parasites may influence male mate choice directly (via reduction in male mating behavior due to presence of parasite in females) or indirectly (via reduction in male mating behavior due to reduced female body condition and/or fecundity). Specifically, I tested the predictions that (1) males would mate and/or associate preferentially with uninfected over infected females (2) parasitized females would be in poorer condition (based on soluble fat stores) than non-parasitized females; and (3) parasitized females would suffer reduced fecundity (number of developing embryos).

1.1. Study system

Some Oklahoma and Texas populations of the western mosquitofish (*G. affinis*) are heavily infected with the larval gastrointestinal parasitic nematode *E. ignotus* [see Coyner (1998) for detailed description of parasite], which is known to have negative effects on reproduction in the western mosquitofish by decreasing brood size and increasing inter-brood intervals (Brooks, 2005; Deaton, unpublished data). The life cycle of *E. ignotus* is complex, because it relies on several hosts throughout its development. Its primary, or initial host, is a sediment-dwelling oligochaete, which is consumed by an intermediate host (e.g. mosquitofish or other vertebrate species). The nematode matures and reproduces in the definitive host, a piscivorous bird (Coyner, 1998; Coyner et al., 2001). This parasite is transferred horizontally in the intermediate hosts only through consumption of infected individuals. Other common internal parasites also are present in mosquitofish, including cestode larva and tapeworms, but these parasites have much lower prevalence than *E. ignotus* (<0.1%) in Oklahoma (Deaton, unpublished data). Further, *E. ignotus* larva can reach up to about half the body mass of female mosquitofish, suggesting that this nematode has potential to have significant negative effects on female reproductive success by reducing fecundity.

2. Methods

In 15–30 September 2003, I collected several fish (both parasitized and non-parasitized) from a small pond in Norman, Oklahoma and returned them to a greenhouse laboratory at the University of Oklahoma Aquatic Research Facility. I acclimated fish in two large 340-l community tanks for several weeks prior to

behavioral trials because I was unable to experimentally infect individuals with *E. ignotus* larva in the laboratory (see Coyner, 1998) and needed to allow for enough parasite growth to visually detect infected individuals. Fish were held at ambient temperatures and photoperiod to mimic natural conditions, and fed commercial flake food once daily.

2.1. Behavioral experiment

I conducted behavioral observations from 20 October to 10 November 2003. I used an open water experimental design (Houde, 1997; Deaton, 2008a), which allows fish to swim freely through the tank, and permits physical and chemical cues to males (Hughes, 1985; Park and Propper, 2002) that may be important for parasite detection. The more traditional dichotomous mate choice design (Houde, 1997; Wagner, 1998; Bisazza and Pilastro, 2000) eliminates the male's ability to inspect females closely. Because I felt it important for males to have direct contact with the females, and to measure actual copulation attempts (rather than time spent on either side of the tank), I employed the open water, rather than the dichotomous design, in this study.

Prior to each behavioral trial, I chose one parasitized and one non-parasitized female from community tanks (parasitized individuals were selected based on the asymmetrical appearance of presumed parasitized females; Deaton, unpublished data) and placed them in a 30-l aquarium with one randomly selected male ($N = 20$ males; $N = 40$ females). Other than presence/absence of parasites, I attempted to match females for size and phenotype [e.g. size of gravid spot, or dark pigmentation that appears in the abdominal region when female obtain ripe eggs (Snelson, 1989), and body pigmentation (yellow coloring that appears on the female abdominal region)]. This also allowed for some control over female reproductive state (Hughes, 1985; Park and Propper, 2002) and for determining whether parasites influence female fecundity and/or body condition.

I recorded association time of the male with each female (Houde, 1997; Bisazza et al., 2001), all male mating behaviors toward each female, and all female behaviors toward the male during a 10-min observation period. Association time was measured as males being in close vicinity to the females (within 2 cm; Houde, 1997). Male mating behaviors measured included orient (turn toward in close vicinity), chase (follow in close vicinity), circle, swim under, lateral display (lowering the gonopodium in close vicinity), nipping, and copulation attempt (or gonopodial thrust, which is when the male thrusts his gonopodium toward the female's gonopore in order to transfer sperm; Krotzer, 1990; Houde, 1997). Female behaviors measured included orient (see above), chase/follow and ignore (turn away when approached; Houde, 1997). Orient and chase/follow by females are typically considered to be receptive behaviors, while ignore (among others) is considered a sign of disinterest (Deaton, 2008a).

Copulation attempt is the most informative response variable for male mate choice; however, several males ($N = 7$, or 35%) did not actually thrust their gonopodia toward females during the focal observations. Therefore, I performed a Pearson's correlation analysis on all measured male behaviors. Swim under (or positioning) and copulation attempt are sequential events in mating, and were highly correlated ($R = 0.44$, d.f. = 19, $p < 0.01$); therefore, I used the sum of these two behaviors as my response variable for male mating behavior (see methods, Husak and Fox, 2003).

2.2. Female characteristics

Following behavioral trials, I tested for effects of the parasitic nematode on female body condition and female fecundity. I euth-

anized females in MS-222, and preserved them in 10% formalin. I measured [to the nearest 0.5 mm standard length; SL (tip of the snout to the base of the caudal peduncle)], dissected, weighed, and calculated soluble fat stores (for condition analysis) in all 40 female subjects in the behavioral experiments, plus 11 additional females that were not included in behavioral analyses (for a total of $N=51$ females).

To assay body condition, I weighed carcasses and livers to the nearest 0.001 g, rinsed them six times overnight (or longer) in petroleum ether to extract soluble nonstructural fats (Huelett et al., 1995; Trexler, 1997), dried them overnight at 40 °C, and reweighed. I quantified body condition as the standardized residual from least squares linear regression of mass of somatic fat (calculated as pre-extraction mass minus post-extraction mass) on pre-extraction mass (see Marsh-Matthews et al., 2005; Marsh-Matthews and Deaton, 2006). Because female dry mass is a function of female size (SL), and female size and condition are often correlated, I used ANCOVA to test the effects of parasites on female mass and condition, using female SL as a covariate.

I removed the ovary from each female, counted and staged eggs and embryos (based on Meffe's six-stage scale, 1985), dried ovaries, eggs, and embryos at 40 °C for 10 days, and weighed each (to the nearest 0.001 g). I also removed parasitic nematodes from females, and dried and weighed each nematode (to the nearest 0.001 g) to calculate a parasite index [percent parasite body mass to female body mass (with ovary and eggs/embryos removed)] to test for correlations between parasite index, body condition and male mating behavior. All statistical analyses were conducted in SPSS 13.0 for Windows.

3. Results

3.1. Behavioral experiment

For behavioral trials, I assigned the majority of females correctly to treatments (parasitized versus non-parasitized), with the exception of two females that I assigned incorrectly as parasitized. Therefore, I excluded those two trials from behavioral analyses. Of the remaining 20 trials, males mated more often with non-parasitized over parasitized females (paired t -test, $t=-2.57$, d.f. = 19, $p<0.01$), but did not preferentially associate with non-parasitized females (paired t -test, $t=-1.36$, d.f. = 19, $p>0.05$).

To control for female reproductive state, I excluded the six females in the experiment carrying developing broods from the analysis. For the remaining 14 behavioral trials ($N=28$ females and $N=14$ males), males attempted more matings with non-parasitized than parasitized females (paired t -test, d.f. = 26, $t=2.1$, $p<0.05$; Fig. 1a) but did not differ in association time between non-parasitized and parasitized females (paired t -test, d.f. = 26, $t=-1.63$, $p>0.05$; Fig. 1b).

Non-parasitized and parasitized females did not differ in ignoring (paired t -test, d.f. = 26, $t=-0.30$, $p>0.05$) or orienting (paired t -test, d.f. = 26, $t=1.07$, $p>0.05$) behaviors toward males. However, non-parasitized females chased males more often than parasitized females (paired t -test, d.f. = 26, $t=2.25$, $p<0.05$; Fig. 2).

3.2. Female characteristics

For all females in the study ($N=51$), uninfected females ($N=25$) averaged 28.5 ± 5.3 mm SL and 103.9 ± 60.6 g dry mass, and infected females ($N=26$) averaged 26.5 ± 1.2 mm SL and 71.8 ± 51.9 g dry mass. There was no significant difference in average standard

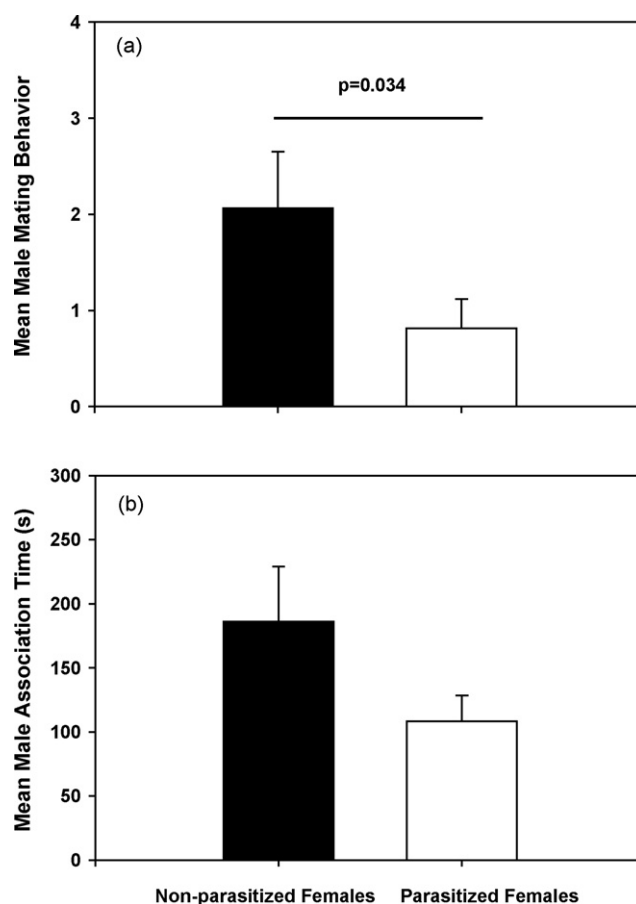


Fig. 1. Mean male mating behavior (a) and mean association time (b) with non-parasitized and parasitized females with six females carrying developing broods omitted. Bars represent one standard error.

length between infected and uninfected females (two-sample t -test, d.f. = 50, $t=1.096$, $p>0.05$), but mass (g) of infected females was significantly less than uninfected females (two-sample t -test, d.f. = 50, $t=2.05$, $p<0.05$).

For all females ($N=51$), nematode dry mass of parasitized females ranged from 1.064 g to 19.2 g, and averaged 9.93 ± 5.34 g. Parasite index ranged from 3.51% to 31.72%, and averaged

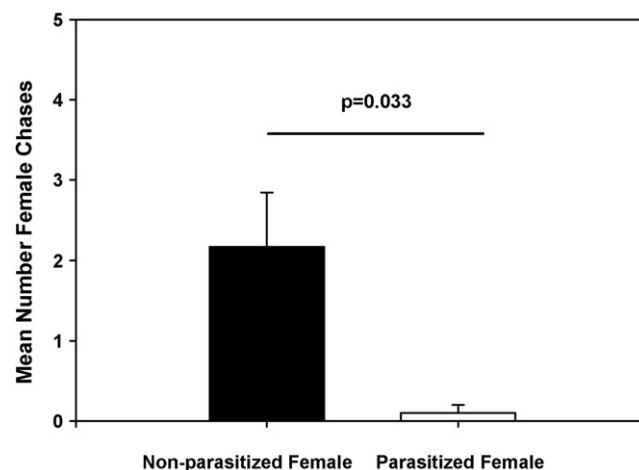


Fig. 2. Mean number of female chases toward males by non-parasitized and parasitized females. Bars represent one standard error.

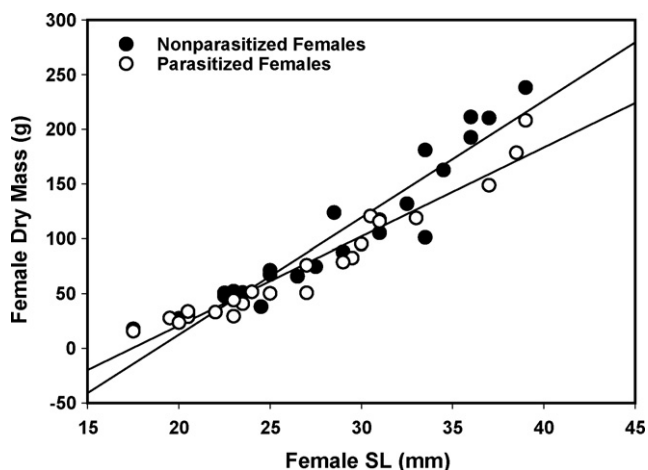


Fig. 3. Results of ANCOVA showing female dry mass (g) as a function of standard length (SL) for non-parasitized (closed circles) and parasitized (open circles) females.

$16.25 \pm 5.34\%$. Parasite rate (mean number of parasites per individual including non-parasitized individuals) was 0.08 (two females were infected with two nematodes; all other females were infected by only one nematode). In 18 infected females for which parasite index was available, regression analysis showed that female parasite index was not a good predictor of female condition ($R^2 = 0.018$, d.f. = 15, $p > 0.05$). However, female parasite index accounted for about 17% of the variation in male mating ($R^2 = 0.174$, d.f. = 15, $p > 0.05$), although this relationship was only approaching significance.

I used ANCOVA to test the effects of parasites (parasite presence/absence as the independent variable) on both female mass and condition (dependent variables), using female SL as a covariate for both analyses. The overall model was significant for female mass (ANCOVA, $F_{2,50} = 238.558$, $p < 0.001$; Fig. 3), but not for female condition (ANCOVA, $F_{2,50} = 1.131$, $p > 0.05$). However, for female mass, there was a significant female SL \times nematode interaction (ANCOVA, $F_{1,50} = 5.496$, $p < 0.05$) and female SL was a significant covariate (ANCOVA, $F_{1,50} = 439.568$, $p < 0.001$).

Mean number of developing embryos (Meffe's stage 2–6; blastodiscs to close to parturition, respectively) was significantly higher in non-parasitized females (two sample t -test, $df = 50$, $t = -2.55$, $p < 0.05$; Fig. 4a). Only seven females (from total analysis of $N = 51$) had developing embryos, all of which were non-parasitized. Twenty-eight percent of non-parasitized females, and zero percent of parasitized females were carrying developing broods (Fig. 4b). Of the 28% of females carrying developing broods, three were carrying stage 2 (blastodiscs), one stage 4 (eyes full-sized but little to no pigment), and three stage 6 (close to parturition).

4. Discussion

In this study, males discriminated between parasitized and non-parasitized females, showing mating preferences for uninfected individuals. This occurred even after I controlled for female gravid state by removing six trials from the analysis (those including the reproductive females). However, because I was unable to infect individuals experimentally, it is possible that females parasitized in nature were initially different from those that were not. Thus, males may have been responding to cues correlated with this initial difference. However, this is unlikely because I matched females for both size and phenotype. Regardless, males did mate preferentially with non-parasitized females, indicating that males cued in on some female characteristic (directly or indirectly) associated

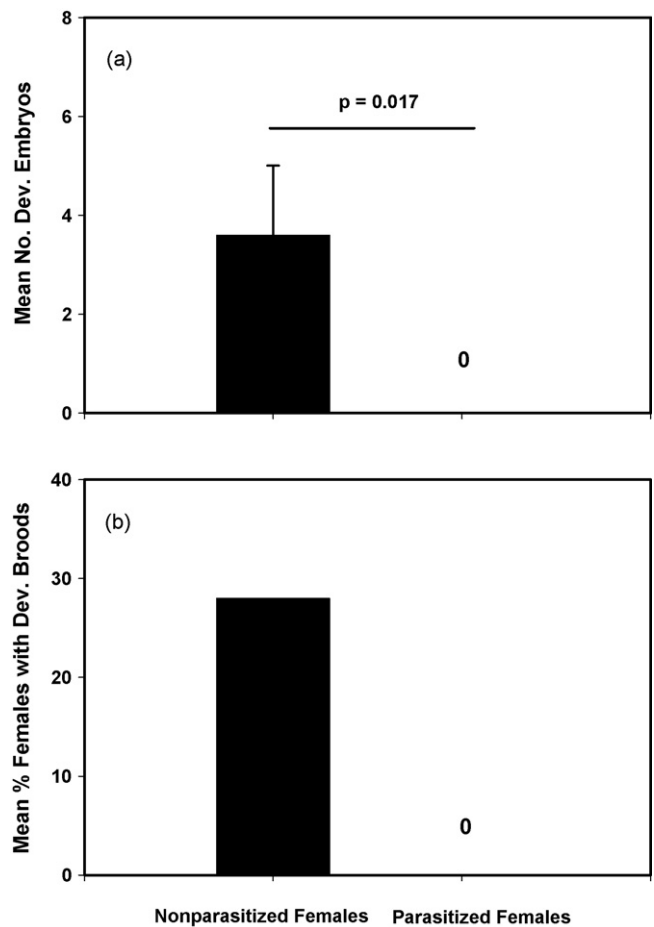


Fig. 4. Mean number of developing embryos for non-parasitized versus parasitized females (a) and mean percent females with developing broods for non-parasitized versus parasitized females (b). Bars represent one standard error.

with the parasite. These findings support the hypothesis that parasites influence male mate choice in the western mosquitofish. Thus, parasite-mediated sexual selection may be important in parasitized populations of mosquitofish, at least in terms of male mate choice.

Alternatively, infected females may have avoided males, rather than males avoiding parasitized females. Kennedy et al. (1987) showed reduced mating behaviors in parasitized male guppies. Here, parasitized females did not ignore or orient toward males differently than non-parasitized females, indicating that parasitized females were not avoiding males. But, parasitized females did chase males less than non-parasitized females, suggesting that infected females either suffered decreased energy and/or reduced swimming abilities due to parasite infection, which has been shown in the three-spined stickleback (Barber et al., 2004), or that infected females were less interested in males. Lopez (1999) found that parasitized female guppies (*P. reticulata*) did not prefer showy males, but non-parasitized females did, indicating a change in behavior of infected females. To my knowledge, this has not been tested in other livebearing fishes.

Contrary to mate choice results, males did not preferentially associate with non-parasitized females, suggesting three possibilities. First, association time may not be a strong measure of male mating preferences in mosquitofish (as shown in guppies, eastern mosquitofish, mollies, and swordtails; Kodric-Brown and Nicoletto, 1997; Baer et al., 1995; Rosenthal and Evans, 1998; Bisazza et al., 2001; Tobler et al., 2006). Second, males may have been associating with females as a means of inspecting the quality or phenotype

of a female, and not necessarily as an indicator of mating preferences. Finally, males may have been exhibiting shoaling behavior with females for reasons other than mate preference, including predation, shoaling, and size-associative preferences (Gabor, 1999).

Although parasite index (ratio of parasite mass to female mass) was not a significant predictor of male mating behavior, it accounted for about 17% of the variation in male mating attempts, suggesting that parasite mass relative to that of the female may be important for male mating decisions. Although these results were not significant ($p=0.09$), I believe they may be important because several males did not mate with parasitized females. Further, sample size was somewhat low for this analysis, including only 14 parasitized females, yet, female parasite index predicted nearly one-fifth of the variation in frequency of male mating behavior. In the beetle, *Timarcha maritima*, males assorted preferentially with non-parasitized females, avoiding those females heavily infected by protozoan gut parasites (Thomas et al., 1999). Females infected with large nematodes have asymmetrically shaped abdomens, usually having a larger bulge on one side of their body. This change in female phenotype may be a direct mating cue used by male *G. affinis* to assess female quality, and may have influenced male mating preferences. Further tests (i.e. separating vision and olfactory cues) are necessary to understand specific signals and/or phenotypes used by males when choosing to mate.

I found a significant relationship between parasites and female mass, but not with female body condition as predicted. Analysis of covariance showed decreased dry mass of infected individuals, where female standard length was a significant covariate. These results suggest that parasites do influence female mass by decreasing the mass of parasitized individuals. It is known that male mosquitofish prefer larger females (Deaton, 2008a); therefore, if parasites decrease female body mass, then the parasite could negatively influence female reproductive success via reduction of male mating preferences for infected females. Parasites may reduce female mass by selectively infecting smaller individuals (which may occur if smaller individuals forage differently than larger individuals), retarding growth of infected individuals, as shown in stickleback (Blake et al., 2006) or by causing decreased fecundity of females, as shown in mosquitofish (Deaton, unpublished data). Further studies will help tease apart these potential mechanisms.

Parasites did not affect female condition, contrary to results from stickleback (Bagamian et al., 2004). This may be due to housing fish in the laboratory for several weeks prior to behavioral trials, while feeding them on a high-quality diet. Previous experiments showed that fish held in the lab on a commercial flake food diet were in better condition than field caught individuals (Marsh-Matthews, pers. commun.). Therefore, the high-quality diet may have ameliorated the effects of the parasite on female condition. However, in a separate study, Brooks (2005) showed that parasitized mosquitofish were actually in better condition than non-parasitized individuals, suggesting that infected females may be diverting fat stores from reproduction to long-term energy stores. But, this would only be true if the parasite significantly decreases female fecundity, which appears to be true. Alternatively, body condition (measured as soluble fat stores) may not be a good indicator of female fitness and other traits may be more important for males when making mating decisions (e.g. female age, reproductive state, etc.).

In this experiment, parasites appeared to cause reduced fecundity in females. Few females were carrying developing broods, all of which were non-parasitized. In stickleback, the cestode macroparasite, *Schistocephalus pungitii*, reduces fecundity by decreasing clutch size (Heins et al., 2004) and offspring size (Heins and Baker, 2003). Similar results have been reported for amphipods (Thomas et al., 1995) and beetles (Thomas et al., 1999). In this study, all six reproductive females were uninfected, which suggests that lar-

val nematodes negatively affect female reproductive success via reduced fecundity. In a separate study on the same population of mosquitofish (August, 2002), I showed that females infected with *E. ignotus* did, in fact, suffer reduced fecundity (measured as embryo number; Deaton, unpublished data). In addition, Brooks (2005) showed that *E. ignotus* significantly reduced offspring production in *G. affinis*, by increasing inter-brood interval (time between reproductive bouts).

The breeding season of *G. affinis* in Oklahoma usually extends from mid-late March to late October or early November. Several females in this study may not have had developing broods because females were beginning to “shut down” reproduction over winter. However, males readily mate with females late in the breeding season, even when they are no longer carrying developing broods (Deaton, unpublished data), presumably because females can store sperm for long periods of time (several months; Constantz, 1989). This may be important in parasitized populations of mosquitofish because males may use female girth as an indicator of parasite presence, especially later in the reproductive season when mean parasite intensity is greater, but fecundity is low.

In conclusion, most studies to date on fish and other organisms have investigated parasite effects on female mating preferences for males (see Moller, 1990; Barber, 2002,). Few studies have investigated the effects of parasites on male mate choice and have focused mainly on invertebrates (Thomas et al., 1996, 1999). To my knowledge, this is the first empirical evidence showing that parasites can influence male mating behavior in a species in which males of all sizes use coercive mating as their primary reproductive strategy. Based on results from this study, it is unclear whether males discriminate against parasitized females using direct cues (phenotype, olfaction) or if they discriminate indirectly by avoiding poorer quality females, assuming parasites somehow reduce female fitness. Parasites did not appear to affect male mate choice indirectly by decreasing female body condition (soluble fat stores), but may have via reduced fecundity (# embryos), although further tests are needed to draw definitive conclusions regarding fecundity. This study provides new evidence that parasites may influence sexual selection via intersexual mate choice in species where males typically do not show strong mating preferences for females. In order to determine whether this parasite actually plays a role in mediating sexual selection, future studies also must test whether male fitness increases by avoiding parasitized females, and/or if female fitness is affected by male preference for uninfected females.

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