

Male-male interactions and their influence on the mating behavior and success in the fountain darter, *Etheostoma fonticola*

Sophia L. DeColo¹ · Andrea S. Aspbury¹ · Kenneth G. Ostrand² · Caitlin R. Gabor¹

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Abstract Behavioral interactions between individuals of the same sex can affect the outcome of intersexual selection. For this reason, intrasexual selection is oftentimes examined independently from intersexual selection in studies aimed at understanding mating behaviors. However, a more complete understanding of sexual selection effects within a population can only come from exploring both intrasexual and intersexual selection and the potential interactions between the levels of selection. Association preferences in male and female *Etheostoma fonticola* do not reveal a size preference for same sex or opposite-sex individuals. However, male-male interactions may influence female choice in *E. fonticola*. We examined whether male *E. fonticola* that differ in body size exhibit differences in agonistic behaviors and mating success. Larger males do exhibit higher rates of aggressive behaviors and smaller males, in turn, exhibit more defensive behaviors. However, differences between larger and smaller males in male-male interactions did not translate into differences in spawning success. These results suggest that male size influences dominance relationships in *E. fonticola* but not mating success. There were also no differences between large and small males in mating attempts, which could be an outcome of the year-round breeding season found in this species, females laying eggs singly, or males fertilizing eggs individually.

Keywords *Etheostoma fonticola* · Female preference · Fountain darter · Intersexual selection · Intrasexual selection

Introduction

Female mating preferences and subsequent mate choice often influence male mating success (review in Andersson 1994). Mating preferences are often assessed using dichotomous choice experimental designs, using association time as a proxy for mate preference. In some species of freshwater fish, association preferences exhibited in dichotomous choice trials are a reliable estimate of mate preference (Brooks and Endler 2001; Aspbury and Basolo 2002; Cummings and Mollaghan 2006; Lehtonen and Lindstrom 2008; Jeswiet et al. 2011). However, association preferences may not necessarily reflect mating preferences, as they may arise through other social behaviors or in response to predation risk (Gabor 1999). Additionally, dichotomous choice designs deliberately exclude the potential for interactions between individuals. Removing the influence of male-male interactions is useful for investigating female mate choice as well as determining which specific male traits are subject to intersexual selection (Hunt et al. 2009). However, both intrasexual and intersexual selection affects the evolution of sexually selected traits, and one selection process may counteract the outcomes of the other (Hunt et al. 2009). For example, female association preferences may accurately reflect female mate preferences, but competition between males (prior to, during, and after mating: Andersson 1994), alternative male mating strategies (Henson and Warner 1997), and post-copulatory mate choice (Eberhard 1996) could counteract female mating preference.

Female preference for larger body size is common in many species and may arise due to larger males possessing superior competitive abilities, genetics, or reproductive success (Ryan

✉ Sophia L. DeColo
Sophia.d.Snell@gmail.com

¹ Department of Biology, Texas State University, 601 University Drive, San Marcos, TX 78666, USA

² U.S. Fish and Wildlife Service San Marcos Aquatic Resource Center, 500 East McCarty Lane, San Marcos, TX 78666, USA

and Keddy-Hector 1992). Female mating preferences for larger individuals also may arise due to the increase in visual stimulation affected by increased body size (Rowland 1989). Male-male competition can also influence the evolution of larger body size (review in Andersson 1994). In direct contests between males, larger males are generally better able to dominate male competitors, and males that employ alternative mating strategies or tactics are typically smaller males (Basolo 2004). Larger body size may confer or be an outcome of superior competitive abilities but may also function as a signal to potential competitors, allowing males to evaluate each other and in some cases avoid the energetic costs and potential injuries that may result from direct conflicts (Maynard Smith and Parker 1976; Maynard Smith and Brown 1986).

Darters in the genus *Etheostoma* typically exhibit secondary sexual characteristics, particularly nuptial color patterns in males (Mendelson et al. 2007), which are important for conspecific recognition, female preferences, and male-male competition (Mendelson et al. 2007; Gumm 2011; Martin and Mendelson 2013). However, some *Etheostoma* species exhibit comparably muted coloration, suggesting that alternative visual stimuli, such as larger body size, may play a role in female preferences as well as aggressive interactions among males. Research has produced contrasting results on female preference for male size in *Etheostoma*, with some species exhibiting preferences for size (Fuller 2003; Stiver and Alonzo 2010), while others do not (Pyron 1995). In species that do not exhibit elaborate secondary sexual characteristics, such as ornate coloration, direct competitive interactions between males may be the primary determinant of mating success and larger body size may contribute to increased success in competitive interactions (Farr 1989). In some species of *Etheostoma*, female preference is not associated with male spawning success, but it is the ability of the male to guard the female from competing males that predicts spawning success (Pyron 1995; Fuller 2003). Therefore, association preferences may be a reliable indicator of female mate choice, but there may be other interactions that additionally influence male mating success.

The fountain darter, *Etheostoma fonticola*, is a small, endangered fish (IUCN Red list 2013) that is endemic to the spring-fed upper San Marcos and Comal Rivers in Hays County, TX, USA (Schenck and Whiteside 1976; Hubbs et al. 2008). This species lacks the typically striking secondary sexual dimorphism that is found in the genus *Etheostoma* (e.g., bands of color on the male dorsal fin and sometimes body). Male and female *E. fonticola* do not show association preferences for size in the same sex or the opposite sex when tested in a dichotomous choice design that measured time spent in association zones and prevented direct female-male interactions and all male-male interactions (DeColo et al. in review). Here, we use a free-mating design (that allows all

individuals to interact) to test the hypothesis that female *E. fonticola* exhibit mating preferences based on male size and that male mating success is influenced by male-male interactions. We predict that female *E. fonticola* will prefer to mate with larger over smaller males. We also predict that differences in aggressive behaviors between larger and smaller males will translate into variation in mating success between different sized males.

Materials and methods

We conducted trials in the laboratory using hatchery-reared, first-generation adult *E. fonticola* ($N=60$). We housed and maintained test fish at the San Marcos Aquatic Resource Center (SMARC) in San Marcos, Texas, in holding tanks with recirculating well water at a constant 22 ± 2 °C and a natural photoperiod. Each tank held approximately 60 individuals with an equal number of males and females. We separated males and females 2 weeks prior to testing into separate holding tanks.

The wild Spring Lake and SMARC male and female standard length (SL) are not significantly different (Spring Lake t test=0.08, $n=43$, $p=0.94$; SMARC $t=0.87$, $n=40$, $p=0.39$). The SL of the SMARC population ($n=211$, mean \pm SD=33.8 \pm 3.64-mm SL; range=24–39-mm SL; males=33.59 \pm 3.74-mm SL; females=33.97 \pm 3.61) closely matched the SL of the wild Spring Lake population from the San Marcos river ($n=43$, mean \pm SD=32.65 \pm 3.63; range=22.7–37.1-mm SL; males=32.7 \pm 4.5-mm SL, females=32.61 \pm 2.74-mm SL), but in the wild Spring Lake population, male size shows more variance (Levene's test=0.03). This suggests that size can play into mate choice because males have more variation in size and can be larger than females. Holding tanks contained four 16-cm-long sections of 5-cm PVC pipe cut in half, which provide shelter as well as a surface on which eggs may be attached. We fed test fish a diet of black worms (*Lumbriculus variegatus*), once daily. We conducted trials in March 2014.

Darters in the genus *Etheostoma* do not exhibit complex courtship behavior (Winn 1958). Typically, a mating event is characterized by a male following a female into an area suitable for egg laying, the male will assume a mounted position on top of the female, and both the male and female will vibrate their bodies rapidly, fertilizing and attaching a single egg to the surface of an aquatic plant (Winn 1958). *E. fonticola* spawn year round with two annual spawning peaks, one in late summer and one in late winter to early spring (Schenck and Whiteside 1977). *E. fonticola* will spawn readily in laboratory conditions without manipulation or acclimation and have been observed to spawn within hours of being placed in novel testing environments (Phillips et al. 2011).

We examined the mating preferences of adult female *E. fonticola* ($N=20$) for small males ($N=20$) and large males ($N=20$) in a free-spawning setup. Our experimental setup consisted of two 75-l aquaria ($61.60 \times 31.75 \times 42.55$ cm) containing fine gravel substrate and filled with 15 cm of water (changed after each trial). We covered each tank on three sides with black plastic to minimize disturbance with the front-facing side clear to allow for video recording. We divided each testing tank into three equal sections during acclimation periods using two clear Plexiglas dividers with holes drilled in them to allow all test fish access to visual and olfactory cues. We placed one plastic aquatic plant in the center of the back side of each testing aquaria. *E. fonticola* will deposit eggs on artificial plants that resemble natural vegetation types (Phillips et al. 2011). For each trial, we haphazardly chose one large and one small male stimulus individual from the male holding tank, measured their SL, and placed them into the sections on opposite ends of the testing tank. We randomized the side in which the small and large males were placed prior to each trial. Stimulus males differed in SL by at least 5 mm. Subsequently, we haphazardly chose one focal female from the female holding tank, measured her SL, and placed her into the center section of the testing tank. We allowed all test fish to acclimate to the testing aquaria for a minimum of 15 h. We recorded all trials between 0600 and 1500 hours via digital cameras (Canon HD Vixia HFR series). We set up digital cameras in the center of the front-facing side of the testing tank at a slight downward angle that comprised a full view of the front-facing side as well as the top of the water, allowing depth perception for the observer. We began video recording immediately prior to removing the dividers and continued recording for 5 h. We placed all individuals in a holding tank for tested fish after video recording was completed. No individuals were used in more than one trial.

We analyzed each 5-h video and recorded 10 behaviors (defined in Table 1). We broadly categorized the behaviors as mating (unsuccessful solicitation, successful solicitation, and total mating attempts), aggression (move toward, approach, follow, chase, and attack), or defensive (move away and hide). We chose these behaviors based on descriptions of mating behaviors typical of the genus *Etheostoma* of Winn (1958). Additionally, some behaviors had been measured previously in mating behavior studies of other *Etheostoma* species (Pyron 1995). One observer (SD) conducted all video analyses to ensure consistency in behavioral measurements. We recorded the number of times that each behavior was exhibited by each male toward the other male, each male toward the female, and the female toward each male. We analyzed the differences between large and small males for each combination of behavior and recipient using Wilcoxon signed rank tests, as our data did not conform to assumptions required for parametric tests. We carried out all analyses using JMP 11 software (SAS Institute, Inc., SAS Campus Drive, Building S, Cary, NC, 27513, USA).

Table 1 Description of behaviors of *Etheostoma fonticola* recorded for large male, small male, and female test fish

Behavior	Description
Move toward	Actor fish moves toward receiver fish within no more than one half of the length of the tank.
Move away	Actor fish moves away from receiver fish within no more than one half of the length of the tank.
Approach	Actor fish moves within one body length of receiver fish.
Follow	Actor fish moves toward the receiver fish several times along the same path at a normal pace.
Chase	Actor fish moves toward the receiver fish several times along the same path at a rapid pace.
Attack	Actor fish darts rapidly toward receiver fish with dorsal fin raised, deliberately making contact with body of receiver fish.
Hide	Actor fish buries all or part of body into gravel substrate and remains motionless for several seconds.
Unsuccessful solicitation	Actor fish mounts all or the majority of body on top of receiver fish and initiates body oscillations.
Successful solicitation	Actor fish mounts all or the majority of body on top of receiver fish and initiates body oscillations, female reciprocates body oscillations, and pair moves horizontally upward together.
Total mating attempts	The combination of unsuccessful and successful solicitations.

Results

There was no significant difference between larger and smaller males in the number of times that they move toward or approach other males (Table 2). However, larger males were significantly more likely than smaller males to perform aggressive behaviors toward other males such as attempt solicitations, follow, chase, and attack (Table 2; Fig. 1). Conversely, smaller males were significantly more likely than larger males to perform defensive behaviors toward other males such as move away (Table 2; Fig. 2a) and hide (Table 2; Fig. 2b).

There was no significant difference between the behaviors of larger and smaller males toward females (Table 3). There was no significant difference in the number of times that females move toward or follow larger and smaller males (Table 4). Females approach larger males significantly more often than they approach smaller males (Table 4; Fig. 3a). However, females also move away from larger males significantly more often than from smaller males (Table 4; Fig. 3b). In total, there were very few successful mating attempts. Only eight males had successful mating attempts out of the 32

Table 2 Mean (\pm SE) numbers of each behaviors and results from Wilcoxon signed rank tests for differences between the behavior of large and small males toward males

Behavior	df	Mean \pm SE large	Mean \pm SE small	<i>P</i>
Move toward	19	58.85 \pm 8.22	50.85 \pm 9.08	0.285
Move away	19	55.65 \pm 13.15	152.90 \pm 30.33	0.003
Approach	19	102.05 \pm 18.18	64.90 \pm 12.43	0.144
Follow	19	10.10 \pm 3.36	3.85 \pm 1.98	0.014
Chase	19	26.70 \pm 8.89	1.40 \pm 1.30	<0.0001
Attack	19	21.2 \pm 5.52	5.80 \pm 1.92	0.0003
Hide	19	0.75 \pm 0.19	2.10 \pm 0.38	0.007
Unsuccessful solicitation	19	7.70 \pm 3.15	3.45 \pm 2.68	0.006

Bold values indicate a significant difference ($P < 0.05$)

males that attempted to mate. Of the eight, five were the large males in the trial, while three were small males, although the difference in successful mating attempts between large and small males was not statistically significant (Table 3).

Discussion

Consistent with our previous work examining association preferences in *E. fonticola* (DeColo et al. in review), we found no support for female mate choice based on male size. Female mate choice in *E. fonticola* had not been tested previous to this study and may be based on other visual stimuli or other cues not directly evaluated here such as UV reflectance, banding patterns on the body, or coloration on the dorsal fin.

In contrast to the lack of association preferences for larger males previously found in *E. fonticola* (DeColo et al. in review), we found that females approach larger males more than smaller males. Females may be evaluating some characteristic other than size that larger males possess, but this behavior

does not translate into a mating advantage for those males because either females are not choosing to mate with those males or male-male interactions may be interfering with the ability of females to exercise their preferences. Additionally, females move away from larger males more than smaller males. This may be due to the increased number of times that females approach larger males. Females were not preferentially mating with those males, which may result in the females also moving away from the larger males more frequently.

While there was no difference in the mating behaviors exhibited by large and small male *E. fonticola*, males differed significantly in their interactions with other males. We found that larger males exhibited more aggressive behaviors. Larger males follow, chase, and attack the other male more often than smaller males. Larger males are also more likely than smaller males to solicit mating attempts toward the other male. To our knowledge, this behavior has not been described as an aggressive behavior before in *Etheostoma*. Winn (1958) found that in several *Etheostoma* species, males will mount other males and were even observed to initiate body vibrations. However, Winn (1958) suggested that this behavior is due to the absence of sex recognition in males in these species. Even though *E. fonticola* lack the extreme sexual dimorphism in visible coloration that is characteristic of other *Etheostoma* species, there are many differences in the behaviors male *E. fonticola* direct toward males and females such as being more aggressive toward other males than females. These findings suggest that male *E. fonticola* are capable of sex

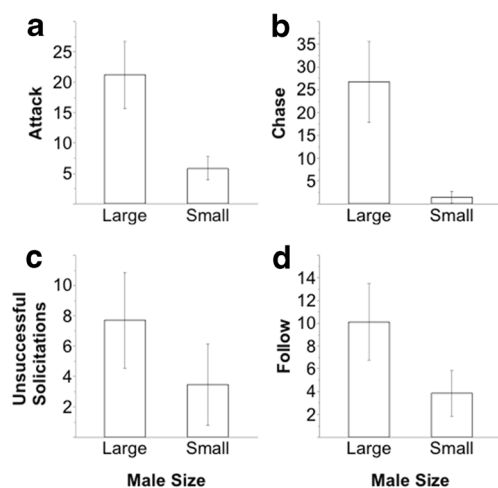


Fig. 1 Differences between large and small male *Etheostoma fonticola* in aggressive behaviors toward other males in mean \pm 1 SE **a** attack, **b** chase, **c** unsuccessful solicitations, and **d** follow

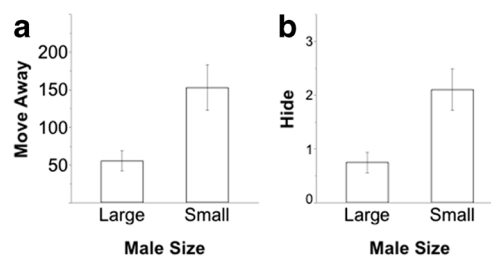


Fig. 2 Differences between large and small male *Etheostoma fonticola* in defensive behaviors towards other males in mean \pm 1 SE **a** move away and **b** hide

Table 3 Mean (\pm SE) numbers of each behaviors and results from Wilcoxon signed rank tests for differences between the behavior of large and small males toward females

Behavior	df	Mean \pm SE large	Mean \pm SE small	P
Move toward	19	78.70 \pm 10.57	66.05 \pm 11.09	0.273
Move away	19	46.95 \pm 6.10	38.75 \pm 5.82	0.291
Approach	19	151.40 \pm 25.00	88.15 \pm 13.78	0.076
Follow	19	24.60 \pm 5.19	12.65 \pm 3.79	0.078
Chase	19	6.80 \pm 3.34	1.25 \pm 0.62	0.481
Unsuccessful solicitation	19	15.90 \pm 3.94	9.55 \pm 3.55	0.142
Successful solicitation	19	5.65 \pm 3.69	2.95 \pm 2.64	0.473
Total mating attempts	19	21.55 \pm 7.00	12.50 \pm 5.50	0.153

recognition. We propose that a male mounting a competing male is an aggressive behavior for establishing dominance relationships.

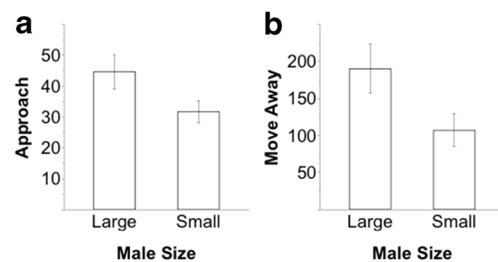
Although our data do not support the hypothesis that male body size influences female mating preferences in *E. fonticola*, larger and smaller males do differ in their behavior toward other males. It is important to note that we only tested pairs of males that differed in SL by 5 mm and did not test pairs of males that were size-matched or any other variation of size combinations. When the size difference between competing males is decreased, males may increase agonistic interactions in order to establish dominance relationships or they may be able to assess that their competitive abilities are more evenly matched and subsequently reduce direct contests. For example in the mosquitofish, *Gambusia holbrooki*, when there is less size differentiation between male competitors, the frequency and intensity of aggressive interactions decrease (McPeck 1992). Examining male-male interactions across a spectrum of size differentiation would provide insight into male dominance relationships in *E. fonticola*.

In other species of *Etheostoma*, male behaviors such as guarding females are correlated with male spawning success, while aggressive behaviors such as attacks and chases are not

Table 4 Mean (\pm SE) numbers of each behaviors and results from Wilcoxon signed rank tests for differences in behaviors of females toward large and small males

Behavior	df	Mean \pm SE large	Mean \pm SE small	P
Move toward	19	47.95 \pm 5.80	43.55 \pm 4.73	0.626
Move away	19	189.9 \pm 33.17	107.1 \pm 21.37	0.011
Approach	19	44.6 \pm 5.40	31.7 \pm 4.9	0.027
Follow	19	1.75 \pm 0.53	1.40 \pm 0.42	0.720

Bold values indicate a significant difference ($P < 0.05$)

**Fig. 3** Differences in female *Etheostoma fonticola* behaviors toward large and small males in mean \pm 1 SE **a** number of times approach and **b** number of times move away

correlated with spawning success (Pyron 1995; Fuller 2003). Neither male guarding behavior was directly tested in this study nor were males observed guarding females in any trials. The absence of guarding behavior in *E. fonticola* may explain why larger males do not experience increased mating success although they exhibit more dominant behaviors than smaller males. Alternatively, our experimental design may not have provided the appropriate conditions for males to exhibit guarding behavior such as a more strongly male-biased sex ratio. However, the 2:1 sex ratio used in this study is a strongly biased male-female sex ratio, suggesting that male guarding behavior may not be present in *E. fonticola*.

Consideration of several life history traits and environmental factors may offer some insight into the mating behavior of *E. fonticola* and may provide insight into the lack of female mating preferences for male size. For instance, there is no parental care exhibited in *E. fonticola*, eggs are attached to the surface of a plant and subsequently abandoned. Female preferences for a variety of male traits have been found in several species of *Etheostoma* in which there is parental care (Grant and Colgan 1983; Knapp and Sargent 1989; Strange 2001; Porter 2002; Stiver and Alonzo 2010; O'Rourke and Mendelson 2014). Additionally, the native habitat of *E. fonticola* is characterized by a temporally and spatially uniform distribution of native vegetation types that *E. fonticola* are primarily associated with (Schenck and Whiteside 1976; Linam et al. 1993) and that are preferentially used by *E. fonticola* for spawning (Phillips et al. 2011). The large supply and predictable availability of spawning sites would suggest that there is little need for male *E. fonticola* to defend resources or territories in order to gain access to mates. Considering the combination of these behavioral, biological, and environmental elements, it is not surprising that we found no evidence for female preferences for male size in *E. fonticola*.

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Ethical standards This experiment was approved by the Institutional Animal Care and Use Committee (IACUC) at Texas State University (No 1115_1206_35).

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