



# Turbidity affects association behavior in the endangered fountain darter (*Actinopterygii*, Perciformes)

Andrea S. Aspbury · Sophia L. DeColo · Cory B. Goff · Caitlin R. Gabor

Received: 26 October 2018/Revised: 30 April 2019/Accepted: 13 May 2019/Published online: 21 May 2019  
© Springer Nature Switzerland AG 2019

**Abstract** Turbidity levels in rivers increase from changes in water flow or high recreational use, which reduces visibility and affects the use of visual cues by aquatic organisms. Decreased visibility affects time spent associating with conspecifics and strength of preference (SOP) in fish that use visual cues. Here, we test the hypothesis that fountain darter (*Etheostoma fonticola*; a federally endangered species) body size preferences are affected by reduced visibility. We tested offspring of wild-caught fish using a dichotomous choice design with clear and reduced visibility treatments. Males and females spent more time associating with fish of the opposite sex in the clear treatment than in the reduced visibility treatment. Smaller females spent more time associating with other females in the clear treatment, whereas larger females spent more time associating with other females in reduced visibility. Smaller females had a higher SOP for larger males in the clear treatment, whereas larger females had a higher SOP for larger males in the reduced visibility treatment. Increased levels of turbidity that leads to reduced visibility affect the use of visual cues in *E. fonticola*, resulting in a reduction in

time spent in social interaction and affecting association preferences of this endangered species.

**Keywords** *Etheostoma fonticola* · Turbidity · Fountain darter · Visual cues

## Introduction

Many aquatic organisms use visual cues in social interactions. Turbidity, the amount of suspended particles in the water column, negatively impacts visual acuity and the efficacy of visual communication within aquatic systems by obscuring the information that is transmitted and received by visual signals (Endler, 1993; Candolin et al., 2016). Changes to the transmission and reception of visual signals as a result of turbidity can have consequences on organismal survival (Ferrari et al., 2010; Swanbrow Becker & Gabor, 2012; Candolin et al., 2016) and reproductive success (Sundin et al., 2010; Candolin et al., 2016). For example, higher levels of turbidity affect predator recognition in fish (Ferrari et al., 2010; Swanbrow Becker & Gabor, 2012), foraging behavior (Swanbrow Becker et al., 2016), and mate choice (Candolin et al., 2007; Heuschele et al., 2009; Sundin et al., 2010). Turbidity can also alter the amount of time individuals associate with and evaluate conspecifics, including potential mates (Sundin et al., 2010). In threespine

---

Handling editor: Grethe Robertsen

---

A. S. Aspbury (✉) · S. L. DeColo ·  
C. B. Goff · C. R. Gabor  
Department of Biology, Texas State University, 601  
University Dr., San Marcos, TX 78666, USA  
e-mail: aspbury@txstate.edu

stickleback (*Gasterosteus aculeatus*), turbidity reduces the strength of sexual selection by decreasing the efficacy of male visual courtship displays that consist of signals of male quality (Wong et al., 2007).

Preference for associating with larger conspecifics is found in many taxa (Ryan & Keddy-Hector, 1992) and can be exhibited by both males and females (Andersson, 1994; Gabor, 1999). In live-bearing fish, males often exhibit association or mating preferences for larger females, that may in part (but not always) be explained by direct fitness benefits to males via the higher fecundity of larger females (reviewed in Schlupp, 2018). Preferences for larger individuals may not arise solely as a function of mate choice. In fish, preference for larger individuals could arise as a response to predation pressures (Gabor, 1999). Individuals may prefer to forage (or engage in other behaviors) in the same vicinity of larger conspecific individuals, because predators generally prefer to consume larger prey items (Gill, 2003).

We examined effects of simulated turbidity on association preferences for both male and female Fountain darters, *Etheostoma fonticola*. In some darter species in the genus *Etheostoma*, females prefer to mate with larger males (*Etheostoma olmstedi*; Stiver & Alonzo, 2010), while females in other species in the genus do not prefer to mate with larger males (*Etheostoma spectabile*; Pyron, 1995) or exhibit limited mate choice (*Etheostoma caeruleum*: Fuller & Montgomery, 2003; Zhou et al., 2015). A number of studies have also examined male mate preferences in different species of *Etheostoma* (Pyron, 1996; Cicotto et al., 2013; King et al., 2013), but there are no generalizable patterns in male mate choice for female body size in this genus.

*Etheostoma fonticola* is a federally endangered species, and is endemic to the clear, spring-fed headwaters of the Comal and San Marcos Rivers in central Texas, USA (Schenck & Whiteside, 1976). The headwater clarity generally ranges from 0.26 to 5.75 nephelometric turbidity units (NTUs) in the San Marcos River (Saunders et al., 2001) and from 0.81 to 4.48 NTUs in the Comal River (Hubbs, 2001). However, lower water levels due to increased drought, higher water consumption by humans, flooding events, and anthropogenic disturbance from recreational activities, all increase water turbidity (Recon Environmental Inc. et al., 2012), which can be as high as 102 NTU (Crawford-Reynolds et al., 2016). A

turbidity level of  $\geq 8.7$  NTU negatively impacts foraging behavior in *E. fonticola* (Swanbrow Becker et al., 2016). Because darters use visual stimuli for mate choice (Fuller & Montgomery, 2003; Gumm et al., 2011) and *E. fonticola* does not compensate for impaired vision by using chemical cues (Swanbrow Becker & Gabor, 2012), turbidity may also negatively affect association preferences in this species.

We tested the hypothesis that both male and female *E. fonticola* exhibit association preferences based on body size when paired with small and large individuals of both the opposite and the same sex, and that these size preferences are affected by simulated turbidity. Larger body size in female *E. fonticola* is correlated with increased number of eggs (Schenck & Whiteside, 1977), so males may exhibit mate preference for larger females. Female fish may prefer larger body size in males if larger males possess better competitive abilities, or offer other direct or indirect benefits (Ryan & Keddy-Hector, 1992). If size preference arises as a function of mate choice, rather than as a generalized preference for larger stimuli, then there would be no size preference for individuals of the same sex. Furthermore, there may be effects on expression of size preferences of the size of the choosing individuals, as mate preferences vary as a function of the state of the individual that is choosing (Amundsen & Forsgren, 2003; Ah-King & Gowaty, 2016). Simulated turbidity may result in a reduction of both male and female strength of preference (SOP), as compared to the SOP exhibited in clear water. We also examined how simulated turbidity affected the total time spent associating with conspecific individuals. Fish in simulated turbidity may show less total time in association with large and small conspecifics than those in clear water, due to an inability to distinguish between individuals. Alternatively, simulated turbidity may increase time spent associating with other individuals because of reduced visual information and/or because they perceive turbidity as cover (Zabierek & Gabor, 2016) which increases predation risk from weakened anti-predator responses (Swanbrow Becker & Gabor, 2012).

## Materials and methods

We used hatchery-reared, first-generation adult *E. fonticola* that were housed and maintained at the San

Marcos Aquatic Resource Center, in San Marcos, Texas. Breeding designs used at the fish hatchery were designed to maintain genetic diversity and population viability. At least 50–75 breeding pairs were used to produce the F<sub>1</sub> fish used in our experiments (K. Ostrand, personal communication; USFWS, 1996). The fish were maintained in two large fiberglass flow-through tanks with recirculating well water ( $22 \pm 2^\circ\text{C}$ ) and with a natural photoperiod. Each tank held approximately 60 individuals with an equal number of males and females. The tanks contained four 16-cm-long sections of 5-cm PVC pipe cut in half, which provide shelter, and native vegetation to provide fish with cover. All fish were fed a diet of live black worms (*Lumbriculus variegatus*), amphipods, and zooplankton ad libitum daily.

We conducted four body size association preference experiments with  $N = 20$  subject fish in each experiment: (1) female preference for female size, (2) female preference for male size, (3) male preference for female size, and (4) male preference for male size. Each experiment was composed of two treatments presented to each subject in a random order: (1) clear and (2) reduced visibility (simulated turbidity). Male subject fish were tested in June 2013, whereas female subject fish were tested in February 2014. *Etheostoma fonticola* spawns year-round with two annual peaks that include the summer months and the late winter/early spring months (Schenck & Whiteside, 1977). In captivity, *E. fonticola* live on average for 2 years, and were approximately 1 year old at the time of testing (K. Ostrand, personal communication).

#### Ethics statement

This study complied with the guidelines specified by ASAB/ABS (2004), and the study was approved by the Institutional Animal Care and Use Committee (IACUC) at Texas State University (protocol #1115\_1206\_35).

#### Experimental tank set-up

Testing was completed in 57-l aquaria (two) containing a fine gravel substrate and 10 cm of water (changed after each behavioral trial). Testing tanks were covered on three sides with opaque black plastic and the front facing side with one-way tinting to minimize disturbance and allow for observation. We

divided the tanks into three compartments using plexiglass dividers, which were placed 10 cm from either edge of the tank. Dividers were held in place using silicone guide rails, allowing them to be removed and replaced with the alternate visibility level (see below) between trials. We delineated the center compartment of the tank into three zones by marking lines on the outside of the tank designating a no preference, neutral zone flanked by two 5-cm association zones for each stimulus fish that was housed in the end compartments.

#### Dichotomous choice body size preference tests

We used semi-transparent window tinting to simulate the reduced visibility caused by low levels of turbidity following established methods in Sundin et al. (2010) and Swanbrow Becker & Gabor (2012). The tinting allowed for 50% visible light transmission (VLT) and was affixed to clear plastic dividers. The turbidity range of the semi-transparent tinting was approximated to NTU by comparing the light absorbency to that of known NTU standards across the visible light spectrum (400–790 nm) using a spectrometer. The 50% VLT tinting corresponded with a turbidity range of 25–55 NTU. The clear dividers with no affixed tinting allowed for approximately 100% VLT, equivalent to zero NTU.

The clear treatment consisted of two clear dividers with holes to allow water and chemical cues to flow through. The reduced visibility treatment consisted of two clear dividers with 50% VLT window tinting affixed to one side and holes through both the plexiglass and the tinting to allow water and chemical cues to flow through.

For each of the turbidity-level treatments, a small and a large “stimulus” individual of the same sex was randomly chosen from stock tanks. These were the individual fish that the “subject” individuals would choose between (choice measured as association time). We measured their standard length [SL (mm); distance from snout to beginning of caudal fin], and placed each of the stimulus fish into one of the side compartments at either end of the test tank. Prior to each trial, the side in which the small and large stimulus individuals were placed was randomized. Stimulus individuals had a minimum of 5 mm difference in SL ( $\pm 1$  SD from the laboratory population mean of 35.5 mm SL). The subject fish was placed in

the neutral zone in an acclimation chamber, a clear 2-l plastic bottle with the bottom removed and holes in the sides, to allow the subject fish exposure to both visual and chemical cues from both stimulus individuals prior to each trial. The subject fish acclimated for a minimum of 40 min before we removed the acclimation chamber and began the trial. We observed the subject fish for 15 min, during which time we recorded the amount of time spent within each association zone using separate stopwatches. After 15 min, we again placed the subject fish inside of the acclimation chamber, removed the stimulus individuals, and placed them into the opposite side compartments, replaced the dividers with the dividers for the remaining visibility treatment, and repeated the 40-min acclimation period and 15-min behavioral observation. We measured and recorded the SL of the subject fish after the final trial. The values for SL measurements are found in Table 1. The order of the visibility treatment was randomized prior to each trial.

#### Statistical analyses

For each of the four experiments that combined the subject/stimulus fish sexes, we used individual linear mixed effects models to examine if the total time that focal fish spent associating with stimulus fish depended on our visibility treatment, the size of the stimulus fish (SL), and whether there was an interaction between SL and treatment. Our models also included the random effect of the focal fish individuals

(that were tested twice, under each of the visibility treatments).

We examined (for all four experiments involving the subject/stimulus fish sexes) the fixed effect of visibility treatment, the SL of the subject fish, and the SL by treatment interaction on strength of preference (SOP = time the subject fish spent associating with the larger stimulus fish/total time associating with both stimulus fish) for the larger fish. We again included the random effect of focal fish individual. We examined residual plots and confirmed assumptions of each model. We performed all statistical analyses using the statistical software JMP Pro version 14.

## Results

### Total association time

There was a significant interaction between the subject female body size (SL) and the treatment (simulated clear vs. reduced visibility conditions) on total association time with the stimulus females. Larger female *E. fonticola* spent more time associating with female stimulus fish in simulated clear conditions, whereas smaller female *E. fonticola* spent more time associating with female stimulus fish under reduced visibility conditions (Table 2a, Fig. 1). When tested with male stimuli fish, female *E. fonticola* spent more total time associating with stimulus fish in the clear treatment

**Table 1** Mean ( $\pm$ ) SE standard length (SL; mm) and range of SL of subject Fountain darters (*Etheostoma fonticola*) that were paired with large and small stimulus conspecifics in

Subject/stimulus sex	Mean $\pm$ SE SL (mm) and range subject fish	Mean $\pm$ SE SL (mm) and range large fish	Mean $\pm$ SE SL (mm) and range small fish
Female/female	30.45 $\pm$ 0.181	32.71 $\pm$ 0.346	26.65 $\pm$ 0.366
	27.59–32.05	30.23–39.83	24.39–34.22
Female/male	29.87 $\pm$ 0.357	33.49 $\pm$ 0.398	27.88 $\pm$ 0.562
	25.63–35.80	30.32–40.81	24.96–38.5
Male/female	33.35 $\pm$ 0.478	36.68 $\pm$ 0.500	29.64 $\pm$ 0.422
	28.74–40.13	31.62–41.13	26.01–34.04
Male/male	33.33 $\pm$ 0.320	36.91 $\pm$ 0.381	30.31 $\pm$ 0.335
	29.85–37.06	32.71–40.33	25.86–34.72

dichotomous choice design association time trials in clear and simulated turbidity conditions

In all but one trial for each subject/stimulus sex the subject was intermediate in size between the small and large and stimulus fish. In each of those exceptions the subject fish was within 5 mm of the small subject fish

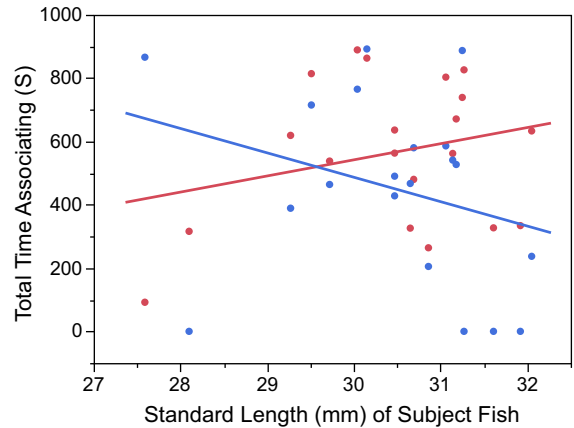
**Table 2** Parameter estimates from linear mixed effects models (“reduced visibility” treatment as intercept) explaining variation in total time associating (s) of subject Fountain darters (*Etheostoma fonticola*) with large and small stimulus conspecifics for (a) females with other females; (b) females with males; (c) males with females; and (d) males with other males

(a)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Subject ID	31,645.73	17,784.42	0.072	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	906.35	1342.48	0.68	0.508
Treatment [clear]	56.4	30.352	1.86	0.080
SL	– 13.071	44.058	– 0.30	0.770
Treatment × SL	64.019	26.726	2.40	<i>0.028</i>
(b)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Subject ID	31,720.66	23,634.38	0.180	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	506.992	755.07	0.67	0.511
Treatment [clear]	127.75	39.813	3.21	<i>0.005</i>
SL	– 1.135	25.205	– 0.05	0.965
Treatment × SL	– 34.14	17.820	– 1.92	0.071
(c)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Subject ID	9416.64	21,976.55	0.668	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	1242.34	567.06	2.19	0.042
Treatment [clear]	124.750	45.647	2.73	<i>0.014</i>
SL	– 24.175	16.937	– 1.43	0.171
Treatment × SL	– 1.746	15.297	– 0.11	0.910
(d)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Subject ID	– 17,434.64	24,896.86	0.484	

**Table 2** continued

Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	206.237	778.05	0.27	0.794
Treatment [clear]	71.2	55.139	1.29	0.213
SL	8.490	0.030	0.81	0.429
Treatment × SL	0.047	0.040	1.18	0.255

Estimate values are given as treatment contrasts; *p* values < 0.05 highlighted in italics



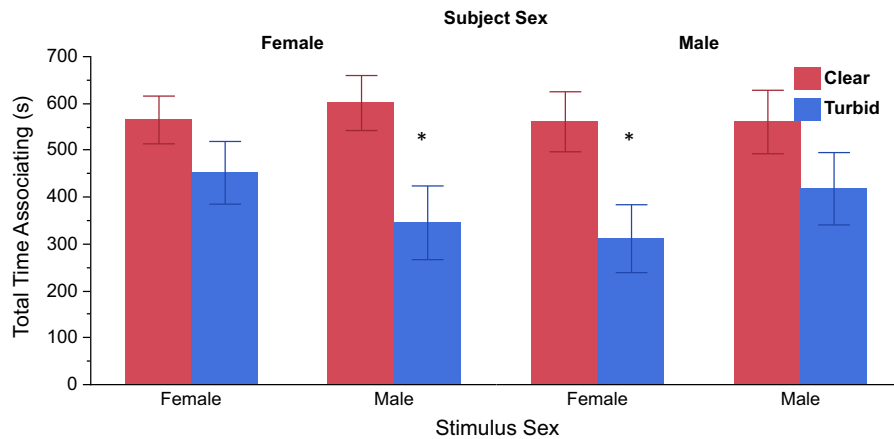
**Fig. 1** Relationship between subject female *Etheostoma fonticola* standard length (mm) and the total time she spent in association (s) with both large and small stimulus female *E. fonticola* in a dichotomous choice association time behavioral test under simulated clear water (red dots and fitted line) and turbid conditions (blue dots and line)

than in the reduced visibility treatment (Table 2b, Fig. 2).

Likewise, adult male *E. fonticola* also spent more time associating with female stimulus fish in the clear treatment than in the reduced visibility treatment (Table 2c, Fig. 3), but the reduced visibility treatment did not affect the total time that males spent associating with stimulus male fish (Table 2d, Fig. 2).

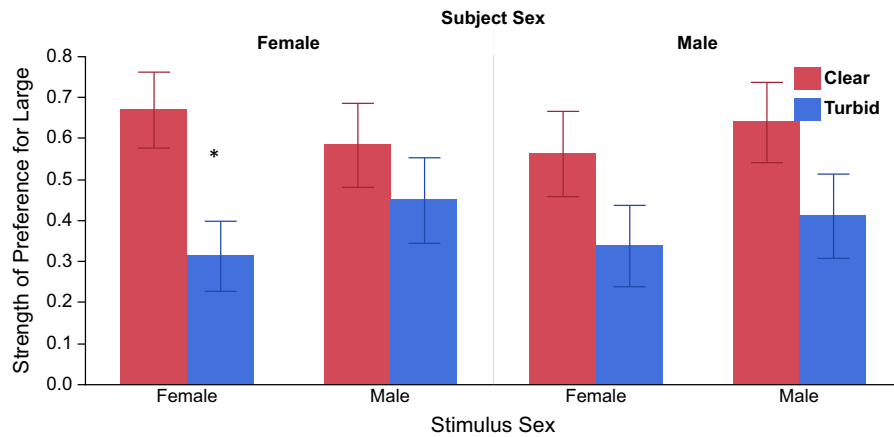
**Strength of preference**

Female *E. fonticola* had a higher SOP for larger female stimulus in the clear treatment than in the reduced visibility treatment (Table 3a, Fig. 3). Female size affected their SOP for large males differently in the two treatments: smaller females had a higher SOP than did larger females in the clear treatment, but larger females had a higher SOP in the



**Fig. 2** Mean ( $\pm$  SE) total association time (s) by male and female *Etheostoma fonticola* with same and opposite sex fish in clear and reduced visibility treatments. Indicates a significant

difference in total association time (s) between the clear (red) and turbid (blue) treatments. \* Denotes significant difference in time associating between the treatments



**Fig. 3** Mean ( $\pm$  SE) strength of preference (SOP) for large stimulus fish by male and female *Etheostoma fonticola* with same and opposite sex fish in clear and reduced visibility

treatments. Indicates a significant difference in total association time (s) between the clear (red) and turbid (blue) treatments. \* Denotes significant difference in SOP between the treatments

reduced visibility treatment (Table 3b, Fig. 4). Thirteen of the twenty females had a change in SOP between the clear and reduced visibility treatments. Of those, nine showed a preference for smaller males in the reduced visibility treatment and a preference for larger males in the clear treatment. The remaining four females had a higher SOP in the reduced visibility than in the clear treatment. Male SOP did not vary in any of the treatment/stimulus fish sex combinations (Table 3c and d, Fig. 3).

## Discussion

Both male and female *E. fonticola* spent more total time associating with opposite-sex stimulus fish in the clear treatment than in the reduced visibility treatment, demonstrating that simulated turbidity decreases the amount of time these fish spend evaluating potential conspecific mates. In addition to effects on total time spent evaluating conspecifics, reduced visibility also altered female strength of preference for large conspecifics. Turbidity or simulated turbidity also affects association preferences and mate choice in other fish species (sailfin mollies: Heubel & Schlupp, 2006; pipefish: Sundin et al., 2010; stickleback: Candolin

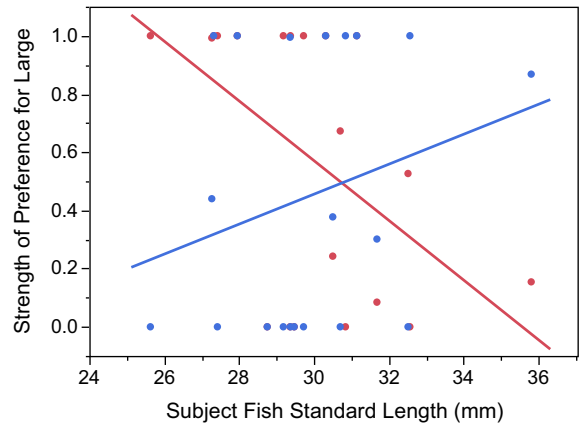
**Table 3** Parameter estimates from linear mixed effects models (“reduced visibility” treatment as intercept) explaining variation in “strength of preference” (SOP: time associating with large conspecific/total time associating with both small and large conspecifics) of subject Fountain darters (*Etheostoma fonticola*) with large and small stimulus conspecifics for (a) females with other females; (b) females with males; (c) males with females; and (d) males with other males

(a)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Focal ID	0.074	0.043	0.084	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	0.366	2.073	0.18	0.862
Treatment [clear]	0.178	0.048	3.73	<i>0.002</i>
SL	0.004	0.068	0.06	0.952
Treatment × SL	0.042	0.042	1.00	0.330
(b)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Focal ID	− 0.001	0.045	0.973	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	1.280	0.919	1.39	0.180
Treatment [clear]	0.067	0.069	0.97	0.343
SL	− 0.026	0.031	− 0.83	0.415
Treatment × SL	− 0.077	0.031	− 2.49	0.023
(c)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Focal ID	− 0.053	0.053	0.314	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	0.166	0.718	0.23	0.820
Treatment [clear]	0.112	0.082	1.37	0.189
SL	0.009	0.021	0.40	0.695
Treatment × SL	0.006	0.028	0.21	0.838
(d)				
Random effects	Estimate	Standard error	Wald <i>P</i> -value	
Focal ID	− 0.054	0.049	0.270	
Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Intercept	− 0.291	1.010	− 0.29	0.776
Treatment [clear]	0.114	0.080	1.43	0.169
SL	0.025	0.030	0.81	0.429

**Table 3** continued

Fixed effects	Estimate	Standard error	<i>t</i> -ratio	<i>P</i>
Treatment × SL	<i>0.047</i>	0.040	1.18	0.255

Estimate values are given as treatment contrasts; *p* values < 0.05 highlighted in italics



**Fig. 4** Relationship between subject female *Etheostoma fonticola* standard length (mm) and the strength of preference for large male *E. fonticola* in a dichotomous choice association time behavioral test under simulated clear water (red dots and fitted line) and turbid conditions (blue dots and line)

et al., 2016). Reducing the amount of time spent associating with and evaluating mates may require an increase in the amount of time and energy expended on courtship to compensate and elicit comparable attention (Sundin et al., 2010).

In this study, body size of stimulus fish varied, such that the assessment presumably differed based on the visual cues associated with body size differences. Fuller & Montgomery (2003) found that *E. caeruleum* use visual cues when evaluating conspecifics but that their association preferences do not signify female mate choice. Associating more with larger conspecifics may be adaptive in contexts other than mate choice. The preference of female *E. fonticola* for larger females in the clear treatment in our study may be due to a generalized preference for larger size. A generalized preference for large size could be an elicited response of the visual system of the fish for a larger lateral projection area (LPA; MacLaren et al., 2004), or it could be adaptive in the context of minimizing predation risk (Gabor, 1999; Aspbury & Basolo, 2002). Prey fish may associate with larger

conspecifics due to predator choice for larger over smaller prey items (Gill, 2003). Even if association preference is due to other adaptive responses such as preference for larger individuals due to mitigation of predation effects, changes in preferences with changes in turbidity could have negative implications for the survival of this species.

Female size affected their SOP for large males differently in the two treatments: larger female size was associated with a stronger SOP for large males in the reduced visibility treatment, whereas larger females had a weaker SOP for large males than smaller males in the clear treatment. The change in female association preference based on female size and simulated turbidity suggests that females may be behaviorally affected by turbidity. Associating with larger males as a larger individual in turbid conditions may have some adaptive value that does not hold true in clear conditions. Further field studies would be necessary to evaluate possible hypotheses for this finding.

Although male total time associating with stimulus fish was affected by simulated reduced visibility, similar to females, male SOP was not variable across the treatments. There was no difference in male SOP for larger females or larger males between the clear or the reduced visibility treatments. Furthermore, male size also did not affect their SOP. We do not know if the failure to detect a difference in SOP in males when one was found in females is due to a biologically meaningful difference or due to some experimental constraint (e.g., males and females were tested in different times of the breeding season).

Fish that consistently occupy habitats with very low turbidity levels, as has been historically found at the headwaters of the San Marcos and Comal Rivers, may be less adapted to utilizing alternate signal modalities (Sundin et al., 2010) and at recognizing that turbidity does not necessarily function as cover (Zabierek & Gabor, 2016). Increased turbidity levels may affect aquatic species differently depending on their relative ability to compensate for impaired vision by relying on alternate signaling modalities. Here, we found that males and females of *E. fonticola* decrease association time in reduced visibility conditions. This species may not do well relying on alternate signal modalities. However, females vary in their preference based on their size and the stimulus fish size, suggesting that they do have some ability to respond behaviorally to

turbid water but we do not know whether this response is adaptive, and if so in what context.

The results found here, combined with prior studies on *E. fonticola* (Swanbrow Becker & Gabor, 2012; Decolo et al., 2016; Swanbrow Becker et al., 2016) provide a multi-faceted argument for how visual impairment caused by turbidity has consequences on behaviors that are important for the survival and possibly mating of *E. fonticola*, a federally endangered species. Rising levels of turbidity may be especially detrimental to the behavior of species that are not adapted to environments that are typically characterized by high turbidity (Bonner & Wilde, 2002). Therefore, the implications of this study are not limited to *E. fonticola* or the San Marcos and Comal Rivers, but may be relevant to other historically clear freshwater systems and species that are adapted to low turbidity levels. For example, the Barton Springs salamander, *Eurycea sosorum*, which is also adapted to clear streams, shows the non-adaptive turbidity as cover response that *E. fonticola* may also exhibit (Zabierek & Gabor, 2016). Change in association preference in combination with turbidity as a cover response may be associated with future population declines. As environmental changes and anthropogenic stressors associated with elevated turbidity continue to threaten aquatic ecosystems, these findings should be informative for the conservation and management of threatened and endangered species in the San Marcos and Comal Rivers or other similar systems.

**Acknowledgements** We thank the USFWS's San Marcos Aquatic Resources Center staff, and especially K. Ostrand for use of facilities and support. We also thank the members of the GASP Lab, for their insight and suggestions. Additionally, we thank J. Gumm for helpful advice on experimental design. Finally, we thank the associate editor and two anonymous reviewers for helpful comments on previous drafts of the manuscript.

## References

- Ah-King, M. & P. A. Gowaty, 2016. A conceptual review of mate choice: stochastic demography, within-sex phenotypic plasticity, and individual flexibility. *Ecology and Evolution* 6: 4607–4642.
- Amundsen, T. & E. Forsgren, 2003. Male preference for colourful females affected by male size in a marine fish. *Behavioral Ecology and Sociobiology* 54: 55–64.



- Andersen, M. C., 1994. Sexual Selection. Princeton University Press, Princeton.
- ASAB/ABS, 2004. Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* 99: 1–9.
- Aspbury, A. S. & A. Basolo, 2002. Repeatable female preferences, mating order and mating success in the poeciliid fish, *Heterandria formosa*. *Behavioral Ecology and Sociobiology* 51: 238–244.
- Bonner, T. H. & G. R. Wilde, 2002. Effects of turbidity on prey consumption by prairie stream fishes. *Transactions of the American Fisheries Society* 131: 1203–1208.
- Candolin, U., T. Salesto & M. Evers, 2007. Changed environmental conditions weaken sexual selection in sticklebacks. *Journal of Evolutionary Biology* 20: 233–239.
- Candolin, U., I. Tukiainen & E. Bertell, 2016. Environmental change disrupts communication and sexual selection in a stickleback population. *Ecology* 97: 969–979.
- Ciccotto, P. J., J. M. Gumm & T. C. Mendelson, 2013. Male association preference for conspecifics in the Redband Darter, *Etheostoma luteovinctum* (Teleostei: Percidae) based on visual cues. *Copeia* 2013: 154–159.
- Crawford-Reynolds, M., O. Agare, K. Kollaus, P. Williamson, T. Hardy, W. Nowlin, 2016. Suspended Sediment Impacts on Texas Wild-Rice and Other Aquatic Plant Growth Characteristics and Aquatic Macroinvertebrates. Edwards Aquifer Authority Proposal No 133-14-HCP. [http://www.eahcp.org/files/uploads/EAHCP\\_TWR\\_Invert\\_Turbidity\\_on\\_TRACS\\_1\\_6\\_2017.pdf](http://www.eahcp.org/files/uploads/EAHCP_TWR_Invert_Turbidity_on_TRACS_1_6_2017.pdf)
- DeColo, S. L., A. S. Aspbury, K. G. Ostrand & C. R. Gabor, 2016. Male–male interactions and their influence on the mating behavior and success in the fountain darter, *Etheostoma fonticola*. *Acta Ethologica* 19: 15–20.
- Endler, J. A., 1993. Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 340: 215–225.
- Ferrari, M. C. O., K. R. Lysak & D. P. Chivers, 2010. Turbidity as an ecological constraint on learned predator recognition and generalization in a prey fish. *Animal Behaviour* 79: 515–519.
- Fuller, R. C. & W. L. Montgomery, 2003. Disentangling female mate choice and male competition in the Rainbow Darter, *Etheostoma caeruleum*. *Copeia* 2003: 138–148.
- Gabor, C., 1999. Association patterns of sailfin mollies (*Poecilia latipinna*): alternative hypotheses. *Behavioral Ecology and Sociobiology* 46: 333–340.
- Gill, A. B., 2003. The dynamics of prey choice in fish: the importance of prey size and satiation. *Journal of Fish Biology* 63: 105–116.
- Gumm, J. M., K. D. Feller & T. C. Mendelson, 2011. Spectral characteristics of male nuptial coloration in darters (*Etheostoma*). *Copeia* 2011: 319–326.
- Heubel, K. U. & I. Schlupp, 2006. Turbidity affects association behaviour in male *Poecilia latipinna*. *Journal of Fish Biology* 68: 555–568.
- Heuschele, J., M. Mannerla, P. Gienapp & U. Candolin, 2009. Environment-dependent use of mate choice cues in sticklebacks. *Behavioral Ecology* 20: 1223–1227.
- Hubbs, C., 2001. Environmental correlates to the abundance of spring-adapted versus stream-adapted fishes. *Texas Journal of Science* 53: 299–326.
- King, B., C. Von Ende & R. L. Moran, 2013. Mate choice copying in two species of darters (Percidae: Etheostoma). *Behaviour* 150: 1255–1274.
- MacLaren, R. D., W. J. Rowland & N. Morgan, 2004. Female preferences for sailfin and body size in the sailfin molly, *Poecilia latipinna*. *Ethology* 110: 363–379.
- Pyron, M., 1995. Mating patterns and a test for female mate choice in *Etheostoma spectabile* (Pisces, Percidae). *Behavioral Ecology and Sociobiology* 36: 407–412.
- Pyron, M., 1996. Male orangethroat darters, *Etheostoma spectabile*, do not prefer larger females. *Environmental Biology of Fishes* 47: 407–410.
- Recon Environmental Inc., H. C., Zara Environmental LLC, BIO-WEST, 2012. Edwards Aquifer Recovery Implementation Program: Habitat Conservation Plan. Edwards Aquifer Authority. <http://www.eahcp.org/files/uploads/Final%20HCP%20November%202012.pdf>.
- Ryan, M. J. & A. Keddy-Hector, 1992. Directional patterns of female mate choice and the role of sensory biases. *The American Naturalist* (suppl) 139: S4–S35.
- Saunders, K. S., K. B. Mayes, T. A. Jurgensen, J. F. Trungale, L. J. Kleinsasser, K. Aziz, J. R. Fields & R. E. Moss, 2001. An evaluation of spring flows to support the upper San Marcos River ecosystem, Hays County. Resource Protection Division, Texas Parks and Wildlife Department, Austin.
- Schenck, J. R. & B. G. Whiteside, 1976. Distribution, habitat preference and population-size estimate of *Etheostoma fonticola*. *Copeia* 1976:697-703
- Schenck, J. R. & B. G. Whiteside, 1977. Reproduction, fecundity, sexual dimorphism, and sex ratio of *Etheostoma fonticola* (Osteichthyes: Percidae). *American Midland Naturalist* 98: 365–375.
- Schlupp, I., 2018. Male mate choice, female competition, and female ornaments as components of sexual selection. *Current Zoology* 64: 321–322.
- Stiver, K. A. & S. H. Alonzo, 2010. Large males have a mating advantage in a species of darter with smaller, allopaternal males *Etheostoma olmstedi*. *Current Zoology* 56: 1–5.
- Sundin, J., A. Berglund & G. Rosenqvist, 2010. Turbidity hampers mate choice in a pipefish. *Ethology* 116: 713–721.
- Swanbrow Becker, L. J. & C. R. Gabor, 2012. Effects of turbidity and visual vs. chemical cues on anti-predator response in the endangered Fountain darter (*Etheostoma fonticola*). *Ethology* 118: 994–1000.
- Swanbrow Becker, L. J., E. M. Brooks, C. R. Gabor & K. G. Ostrand, 2016. Effects of turbidity on foraging behavior in the endangered fountain darter (*Etheostoma fonticola*). *The American Midland Naturalist* 175: 55–63.
- U.S. Fish and Wildlife Service, 1996. San Marcos/Comal/Edwards Aquifer rare, threatened, and endangered species contingency plan. Revised version dated May 1996: 59.
- Wong, B. B., U. Candolin & K. Lindstrom, 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *American Naturalist* 170: 184–189.
- Zabierek, K. C. & C. R. Gabor, 2016. Multimodal communication, mismatched messages and the effects of turbidity on the antipredator behavior of the Barton Springs

salamander, *Eurycea sosorum*. Behavioural Processes 130: 4–10.

Zhou, M., E. Loew & R. Fuller, 2015. Sexually asymmetric colour-based species discrimination in orangethroat darters. Animal Behaviour 106(171–179): 171–179.

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.