



Mate choice copying in two species of darters (Percidae: Etheostoma)

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Abstract

Mate choice copying is a form of social learning that is defined as the increased likelihood of an individual choosing a particular mate after observing another individual choosing that mate. Mate choice copying has been demonstrated in a range of taxonomic groups, but not usually for both sexes. Mate choice copying experiments were performed here using two congeneric sympatric darters, *Etheostoma flabellare* and *E. zonale*. In *E. flabellare*, males guard a nest site under a rock and care for developing eggs. In *E. zonale*, eggs are attached to filamentous green algae and neither sex provides parental care. Our results provide the first evidence that mate choice copying occurs in darters. Previously it was hypothesised that copying might be more common in species and sexes that provide parental care, the reasoning being that the costs of choosing poorly may be higher. However, mate choice copying was found in both sexes of *E. zonale* (no parental care) and in male but not female *E. flabellare* (male only parental care). Thus, the only group that did not mate choice copy was the one whose mate would be providing care, and even *E. flabellare* females copy the mate choice of other females by some definitions. The relationship, if any, between which sex provides parental care and whether copying occurs remains unclear, and the number of species for which such data are available is limited.

Keywords

darters, *Etheostoma flabellare*, *Etheostoma zonale*, mate choice copying, non-independent mate choice, sexual selection, social learning.

1. Introduction

A fundamental question in the study of sexual selection is how an individual chooses a mate. Among the variety of mate choice tactics, an individual's behaviour may fall anywhere along a continuum from choosing a mate at random to closely evaluating potential mates against a set of criteria (Lande,

1981; Alho et al., 2012; Watson et al., 2012). Potential benefits of choosing a high quality mate are more and higher quality offspring via increased parental care and 'good genes' (Fisher, 1930; Trivers, 1972; Jones & Ratnerman, 2009). However, choosing may also be costly. Searching for a mate can consume valuable energy and time for animals with large ranges or territories or short mating seasons. Searching may also increase vulnerability to predators, e.g., if done while in conspicuous nuptial colouring (Pomiankowski, 1987; Frommen et al., 2009; Fowler-Finn & Hebets, 2011). Social information, which includes social learning, public information use, and social eavesdropping (reviewed by Bonnie & Earley, 2007), can be used to reduce the costs associated with choosing a mate. Social learning includes any observation of or interaction with another individual that produces a change in behaviour. Public information provides an individual with information about quality of a resource, including potential mates, by observing other individuals' behaviour. Social eavesdropping also provides individuals with information about quality of a resource. However, rather than obtaining information by observing another individual's behaviour, as in public information use, social eavesdropping provides an individual with information about another individual's quality by observing a signal exchange between two or more individuals. Mate choice copying is a behavioural strategy that includes an integration of all three major types of social information use.

Mate choice copying can be defined as an increased probability of an individual choosing a prospective mate due to an observed sexual encounter between that prospective mate and another individual of the opposite sex. The idea of females being influenced by other females' mate choice first appeared in the 1970s (Wiley, 1973; Lill, 1974), and a large amount of research has focused on mate choice copying over the past few decades (e.g., Dugatkin, 1992; Pruett-Jones, 1992; Westneat et al., 2000; Witte & Massman, 2003; Widemo, 2006; Galef, 2008; Frommen et al., 2009). Support for mate choice copying has been found in a variety of taxa, including birds, rats, deer, fish, insects, and humans (reviewed by Vakirtzis, 2011). However, fish have become one of the most commonly used taxa in experiments studying mate choice copying (Table 1 in Vakirtzis, 2011). Fish are a good choice because they are easy to observe in aquaria, adaptable to captive conditions, and their sexual behaviour appears unaffected by the artificial environment (Amundsen, 2003). Furthermore, recent experimental evidence has shown

that social learning greatly influences many aspects of their behaviour (Laland et al., 2011). Although fish are a very diverse group, a limited number of species have been used in studies of sexual selection generally and mate choice copying more specifically.

Frommen et al. (2009) suggested that copying might be more common in species and sexes that have higher reproductive investment; and that females have high reproductive investment in eggs, and males have high reproductive investment in species where they provide care. High reproductive investment is expected to select for increased choosiness (Kokko & Johnstone, 2002), and copying should reduce the cost of choosiness (Dugatkin, 2005). Parental care is clearly not the only variable influencing whether selection would favor mate choice copying in a species. Species in which mate choice copying has been found in both sexes are species that lack parental care (sail-fin mollies (*Poecilia latipinna*) and Mexican mollies (*Poecilia mexicana*)), have paternal care (three-spined sticklebacks (*Gasterosteus aculeatus*)), and have primarily maternal care (Japanese quails (*Coturnix japonica*)) (Table 1 in Vakirtzis, 2011; Bierbach et al., 2011). However, most of these species are not closely related and inhabit very different environments, so parental care is only one of multiple differences among the species. Mate choice copying has been investigated in multiple *Poecilia* species (Table 1 in Vakirtzis, 2011), but all species in this genus have similar mating and reproductive systems; females' eggs are fertilised internally, fry are born live from the mother, and neither parent provides any other parental care (Plath et al., 2007). That environmental variation is important is suggested by within species variation in whether mate choice copying has been found, with some populations of guppies exhibiting mate choice copying while others do not (Table 1 in Vakirtzis, 2011). Why mate choice copying occurs in some species and some habitats but not others remains unclear (Witte, 2006).

Darters provide a system for clarifying whether mate choice copying may be affected by differences in investment in reproduction in the form of parental care, given the diversity of reproductive behaviour and overlap in habitat range in darters in the genus *Etheostoma* (Page & Swofford, 1984). There are an estimated 201 species of darters in North America, with *Etheostoma* being the most diverse genus of North American fishes (Page & Burr, 2011). Darters are popular research subjects in studies of sexual selection (Fuller, 2003; Mendelson, 2003; O'Rourke & Mendelson, 2010; Stiver & Alonzo, 2010, 2011; Williams & Mendelson, 2010, 2011;

Gumm & Mendelson, 2011; Gumm et al., 2011). Female darters have cryptic coloration, whereas males of most species exhibit elaborate bright nuptial coloration, suggesting sexual selection is present (O'Rourke & Mendelson, 2010; Williams & Mendelson, 2010, 2011). Darters are stream benthivores that lack swim bladders and are small, with adults ranging from 37 mm to 168 mm in standard length (Page & Swofford, 1984). Since most species of darters have similar general habitat preferences (i.e., clear shallow streams), it is common to find several species coexisting in a stream system (Page & Swofford, 1984).

The present study examines mate choice copying in two congeneric species of darters collected from sympatric locations, but differing in parental care. This allowed us to address whether differences in parental care can affect copying while controlling to some extent for phylogenetic and ecological differences. Mate choice copying has not been examined in darters previously. The banded darter (*Etheostoma zonale*) and the fantail darter (*E. flabellare*) exhibit two of the four different spawning behaviours observed in darters. In *E. zonale* females approach males and attach eggs to nearby algae, and no parental care is provided. In *E. flabellare* a male defends a nest, and multiple females approach and lay eggs in the nest. The male then continues to guard the nest and provides parental care (Page & Swofford, 1984). Fertilisation occurs externally in both species (Page & Swofford, 1984).

2. Materials and methods

2.1. General methods

Etheostoma zonale and *E. flabellare* were collected during the breeding season between March and April 2012 from Big Rock Creek (Kane County, IL, USA) and Indian Creek (DeKalb County, IL, USA) using seines. Both species are common in these stream systems (Rung & Pescitelli, 2004; personal observation). The fish were separated by sex and maintained in mixed species holding tanks in the lab (O'Rourke & Mendelson, 2010), kept on a 16 h light/8 h dark cycle (Zoller, 1999) at 17–18°C. Incandescent lighting was used in the fishes' holding room. During trials, full spectrum (24 W 8000K bulb) and incandescent lighting was cast over the test tank. Holding tanks were filled with 2 cm of gravel substrate and had several rocks (5–10 cm) to provide cover and to reduce stress for the fish. The fish were fed daily ad libitum with frozen chironomid larvae and occasionally with live

blackworms. After all experiments were complete, fish were maintained in their holding tanks for use in further studies.

2.2. Mate choice copying experiments

Mate choice copying was tested in both sexes of both species using dichotomous mate choice trials following Frommen et al. (2009). The female choice experiment is described here but methods match those in the male mate choice experiment (but with males as the focal and stimulus fish and females as the mate choices). The female choice experiment asked whether females change which male they associate with after seeing the alternative male with another female.

These methods tested for copying based on visual cues only. Darters have been shown to rely strongly on visual signals to gain information about their surroundings (Swanbrow Becker & Gabor, 2012), especially when choosing a mate (Williams & Mendelson, 2010). For copying trials, a 75.7 litre aquarium ($61.0 \times 33.0 \times 43.2$ cm) was divided into five compartments: one main compartment in the centre of the tank (27×33 cm) and two stimulus compartments on each of the opposite short ends of the tank (17×16.5 cm) (Figure 1). Association zones were marked next to each stimulus compartment (9×16.5 cm). Clear plexiglass partitions sealed by caulk prevented fish from receiving any chemical cues from other fish. Removable opaque partitions were also used to selectively block individual fish visually as described below. The back and side of the test aquarium were covered with opaque paper. All experiments were conducted within the breeding season. All females were gravid and all males were in breeding condition (i.e., male *E. zonale* displayed nuptial coloration and male *E. flabellare* had egg spots on their dorsal fins) (Page & Swofford, 1984; O'Rourke & Mendelson, 2010). A sample size of 15 was used for each sex for each species' choice trials (Dugatkin, 1996; Witte & Massman, 2003; Frommen et al., 2009).

A focal female was placed in the central compartment of the test aquarium. A stimulus female of the same species was placed in each of the front two side compartments and a male of the same species was placed in each of the back two side compartments. Each focal female experienced a trial that consisted of a pre-treatment test (Figure 1a) followed by an exposure treatment (Figure 1b) and then a post-treatment test that matched the pre-treatment test in terms of which fish could see which other fish (Figure 1a).

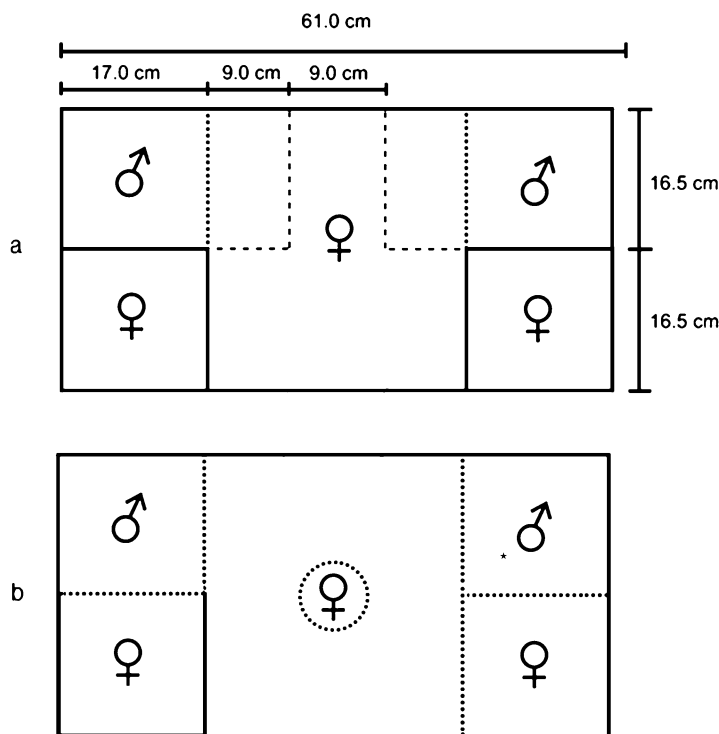


Figure 1. Experimental aquaria (shown for female experiment). (a) During test for both pre- and post-treatment. (b) During exposure treatment. Solid lines indicate opaque partition and dotted lines represent transparent plexiglass partitions. Light dashed lines represent association zones. Each compartment was sealed off from the other compartments, limiting fish to receiving only visual signals from other fish. *Originally non-preferred male.

Total length of each of the two males in a trial had been size-matched to the nearest 2 mm because mate choice copying is more likely when prospective mates are closely matched (Dugatkin, 1996; Witte & Ryan, 1998). Only fish with healthy, intact fins (i.e., no visible signs of fin damage or fin rot) were used, and total length was measured to the nearest 1 mm. To reduce stress, measurements were taken while fish remained in water. Accurate measurement was facilitated by use of a small container to reduce their movement (clear glass, 1.5 litre, $12.7 \times 12.7 \times 10.2$ cm), these species ‘freezing’ right after being startled or placed in a new environment (R. Moran, unpublished data), and their lack of a swim bladder (Page & Swofford, 1984). Prior to measurement, an effort was made to choose fish from the main holding tank that appeared to be close in size based on visual assessment. If a

pair of prospective mates was not within 2 mm of one another, more fish were removed from the main holding tank and measured until there was an appropriate size match.

After use in a trial, focal fish were moved to a separate holding tank in order to avoid reuse as focal fish. All stimulus fish and fish serving as prospective mates were returned to separate holding tanks, as well. Stimulus and prospective mate fish were reused in experiments as either stimulus or prospective mate fish, but not more than once in a 24-h period.

Throughout the pre-treatment, the stimuli females were present but separated visually from the other fish by opaque partitions (Figure 1a). In contrast, the focal female and the males were visually isolated from each other only for a 15-min acclimation period (O'Rourke & Mendelson, 2010). After the acclimation period, the opaque partitions between the males and the focal female were lifted. Following Frommen et al. (2009), after the focal female visited each male's association zone once and then returned to the neutral center area, the subsequent amount of time that the test female spent in each male's association zone was measured for a total of 15 min. Mate choice studies on other species of fish have demonstrated that time spent in the association zone of a prospective mate is a good indication of motivation to mate with that individual (Goncalves & Oliveira, 2003). Which male the focal female preferred was defined as the male whose association zone the focal female was in for more than 50% of the total time spent in both association zones; the other male is referred to as the non-preferred male (Dugatkin, 1996; Frommen et al., 2009).

Side bias appears not to have been an issue. Previous studies of mate choice in fish, including darters, have defined side bias as a focal individual having spent more than 80% of the total observation time on one side of the experimental aquaria (i.e., in one particular preference zone) (Schlupp & Ryan, 1997; Dosen & Montgomerie, 2004; Hoysak & Godin, 2007; Williams & Mendelson, 2010, 2011). According to this criterion, none of the focal fish in the present study exhibited a side bias. In addition, the prospective mate originally preferred by a focal fish was also not more likely have been on one side of the experimental aquaria versus the other (two-tailed binomial test: female *E. zonale*: $p = 1.00$; male *E. zonale*: $p = 0.61$; female *E. flabellare*: $p = 1.00$; male *E. flabellare*: $p = 1.00$). Earlier mate choice experiments on *E. zonale* and *E. barrenense* also have shown no significant evidence of side-bias (Williams & Mendelson, 2010). Following earlier studies of darters,

a control for shoaling was not performed (Williams & Mendelson, 2010, 2011) because darters do not participate in shoaling, but rather are solitary benthic fish (Webb, 1980; Page & Swofford, 1984; R. Moran, personal observation). Thus, if an individual approaches a member of the opposite sex during the breeding season, it is most likely for mating purposes.

For the treatment, initially the opaque partitions were used again to visually isolate all fish from each other's view while the focal female was placed in a transparent glass chimney in the center of the test aquarium (Figure 1b). Then enough opaque partitions were removed so that each male was able to see the stimulus female adjacent to himself and the focal female, but the focal female was only able to see both males and the stimulus female that was adjacent to the originally non-preferred male. Following Dugatkin (1998), the focal female was allowed to see this for 10 min. Then the stimulus female next to the originally non-preferred male was replaced with a new female for an additional 10 min. The reason for using two consecutive females rather than one was to increase public information provided to the focal female, which can increase the likelihood that mate choice copying will occur (Dugatkin, 1998).

Post treatment mate preference was determined next and in the same manner as in the pre-treatment (Figure 1a). Specifically, all fish were visually isolated again by dropping the opaque partitions between all compartments; after which the focal female was released from the glass chimney. The opaque partitions between the focal female and the males were then removed, and the focal female's preference was measured a second time.

2.3. Statistical analysis

Mate choice copying was said to occur if the relative time that a focal fish spent with the originally non-preferred prospective mate significantly increased after the exposure treatment, i.e., in the post-treatment relative to the pre-treatment. The relative time spent in the association zone next to the originally non-preferred prospective mate was calculated ($\text{relative time} = \text{time}_{\text{non-preferred}} / (\text{time}_{\text{non-preferred}} + \text{time}_{\text{preferred}})$). Relative time was used as a measure of preference because of the considerable variation among fish in time spent in association. Relative time was compared between pre-treatment and post-treatment for each sex of each species as a generalised linear mixed model (GLMM). GLMM was appropriate because the dependent variable,

relative time, was a proportion (Bolker et al., 2009). Fish was considered a random factor, with each focal fish having a pre-treatment and a post-treatment measure. The fixed factor was treatment (pre and post), for which we assumed an underlying binomial distribution. The complementary log-log was used as the link function for the fixed factor because some fish had values of relative time at the extremes (0, 1), leading to an increased variance, i.e., overdispersion. Overdispersion is not uncommon in biological data in which repeated observations are made on the same individuals or cluster (McCullagh & Nelder, 1989; Myers et al., 2010). The random factor, fish, was assumed to have an underlying normal distribution with an identity link function. Analyses were done in GenStat 15.1 using the hierarchical GLMM routine (Lee et al., 2006).

We also analysed total time spent choosing among mates, which was measured by total time spent in both association zones combined. Whether total time differed between the pre- and post-treatment levels was analysed as a GLMM, with pre vs. post-treatment as the fixed factor, and fish as the random factor. The fixed factor was analysed as having a gamma distribution with a logarithm link function based on fit statistics. The random factor was analysed as having a normal distribution with an identity link function. The analyses for each species and each sex were performed in GenStat 15.1 using the GLMM routine.

3. Results

3.1. Female *E. zonale*

Female *E. zonale* significantly increased the relative time spent in the association zone next to the male that had been visibly courted by stimulus females (Wald statistic = 10.04, $p \approx 0.002$, Figure 2). The majority of focal females (10 out of 15, 66.7%) switched which male they associated more with, i.e., increased the time spent in the association zone of the originally non-preferred male after he was shown associating with the stimulus females (Figure 2). Total time spent in both males' association zones combined did not differ significantly pre and post-treatment (mean $\pm$ SE: before 393.53 $\pm$ 58.25 s, after 418.67 $\pm$ 76.02 s, Wald statistic = 0.06, $p = 0.812$).

3.2. Male *E. zonale*

Male *E. zonale* significantly increased the relative time spent in the association zone next to the female that had been visibly courted by stimulus

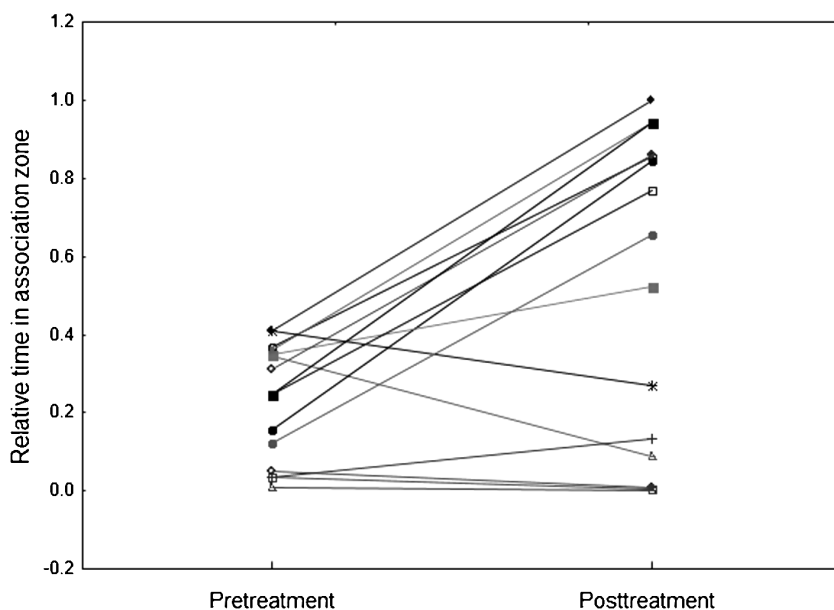


Figure 2. Female *E. zonale* preferences pre- and post-treatment. Compared to pre-treatment (before stimulus), in the post-treatment (after stimulus) focal females spent significantly more relative time next to the male that had been shown next to the stimulus females.

males (Figure 3, Wald statistic = 6.905, $p \approx 0.009$). The majority of individuals (10 out of 15, 66.7%) increased time spent in the association zone of the originally non-preferred female after they were shown associating with the stimulus males (Figure 3). Total time spent in both females' association zones combined did not differ significantly between the pre and post-treatments (mean $\pm$ SE: before 307.00 ± 33.25 s, after 307.93 ± 48.11 s, Wald statistic = 0.22, $p = 0.65$).

3.3. Female *E. flabellare*

Female *E. flabellare* did not significantly increase the relative time spent in the association zone next to the male that had been visibly courted by stimulus females (Wald statistic = 0.1845, $p \approx 0.174$, Figure 4). There were nearly an even number of fish that showed an increase (7 out of 15, 46.7%) or a decrease (8 out of 15, 53.3%) in the time they spent next to the originally non-preferred male after they were shown associating with the stimulus females (Figure 4). Total time spent in both males' association zones combined did not differ significantly between the pre and post-treatments (mean $\pm$

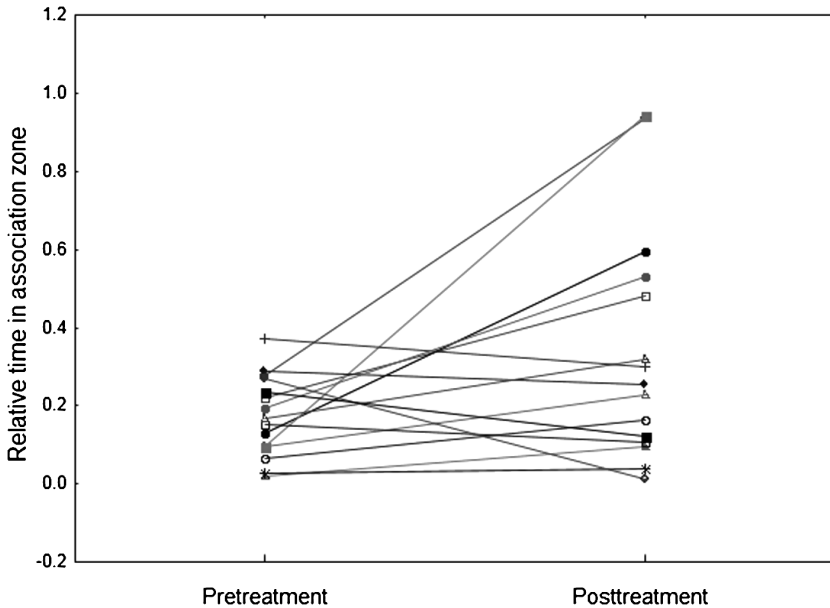


Figure 3. Male *E. zonale* preferences pre- and post-treatment. Compared to pre-treatment (before stimulus), in the post-treatment (after stimulus) focal males spent significantly more relative time next to the female that had been shown next to the stimulus males.

SE: before 349.60 ± 40.30 s, after 388.67 ± 52.65 s, Wald statistic = 0.32, $p = 0.579$).

3.4. Male *E. flabellare*

Male *E. flabellare* significantly increased the relative time spent in the association zone next to the female that had been visibly courted by stimulus males (Wald statistic = 6.590, $p \approx 0.010$, Figure 5). The majority (13 out of 15, 86.7%) of male *E. flabellare* showed an increase in the time they spent next to the originally non-preferred female after they were shown associating with the stimulus males, but the remaining two out of 15 *E. flabellare* males showed a decrease in the time spent in the association zone of the originally non-preferred female after they were shown associating with the stimulus males (Figure 5). Total time spent in both females' association zones combined did not differ significantly between pre and post-treatments (mean $\pm$ SE: before 322.67 ± 49.65 s, after 318.93 ± 45.53 s, Wald statistic = 0.03, $p = 0.87$).

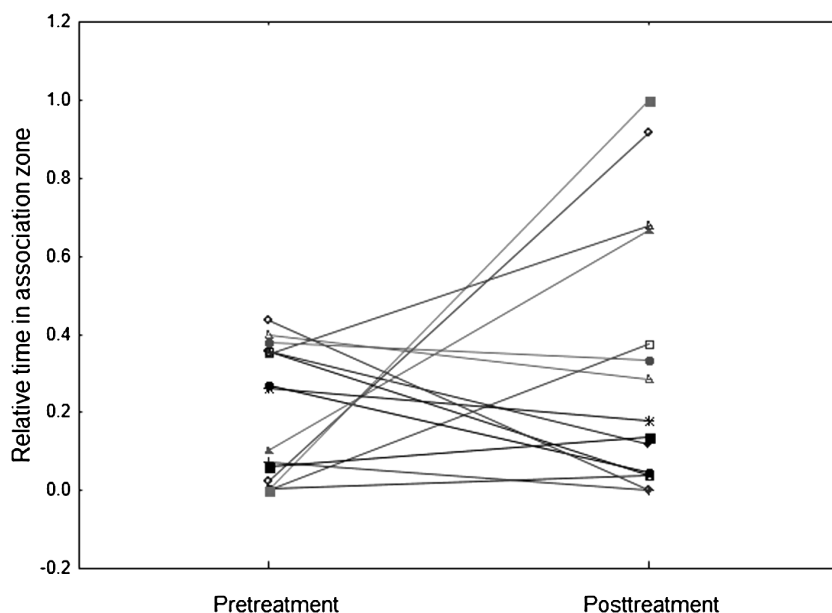


Figure 4. Female *E. flabellare* preferences pre- and post-treatment. Compared to pre-treatment (before stimulus), in the post-treatment (after stimulus) focal females did not significantly increase time spent next to the male that had been shown next to the stimulus females.

4. Discussion

4.1. Who copies in *E. zonale* and *E. flabellare*?

The current study is the first to examine mate choice copying in both sexes of two species that occur sympatrically and are within the same genus but that differ greatly in parental care strategy. This study also provides the first evidence of mate choice copying in darters. Both sexes of *E. zonale* and male *E. flabellare* showed significant evidence of mate choice copying (i.e., increasing the amount of time spent associating with an initially less preferred prospective mate after observing that prospective mate associating with stimulus fish of the opposite sex), but female *E. flabellare* did not.

These results contrast with Frommen et al.'s (2009) prediction that mate choice copying would be more likely to occur in both sexes when males invest in reproduction in the form of parental care. Instead, the sexes and species that exhibited mate choice copying in this study (both sexes of *E. zonale* and male *E. flabellare*) were those whose mates would not be provid-

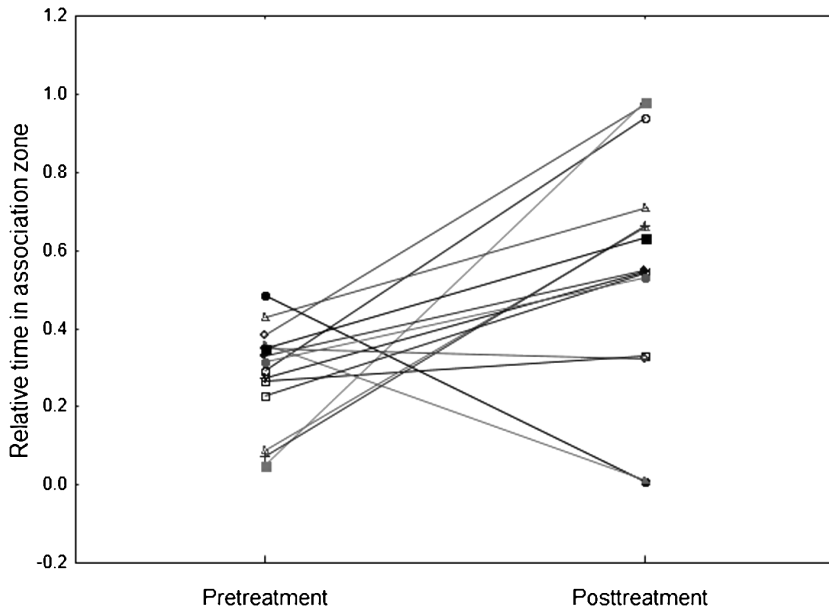


Figure 5. Male *E. flabellare* preferences pre- and post-treatment. Compared to pre-treatment (before stimulus), in the post-treatment (after stimulus) focal males spent significantly more time next to the female that had been shown next to the stimulus males.

ing care. In contrast, female *E. flabellare*, whose mates provide care, did not mate choice copy.

4.2. Why this pattern of copying?

As noted previously, mate choice copying is predicted to occur when the information other individuals have about mate quality is likely higher, or perceived as being higher, than what an individual already knows from previous experience (Pruett-Jones, 1992). Factors that may influence whether a conspecific is likely to have greater knowledge include relative: (1) sensory acuity, e.g., vision; (2) environmental conditions, e.g., lighting to assess mates; (3) knowledge of a prospective mate's mating history, and hence the number of gametes remaining; (4) in species with parental care, knowledge of a prospective mate's ability to provide parental care and (5) knowledge of any other features of the prospective mate that will influence the success of one's own gametes. We hypothesise that the latter two are particularly relevant to which groups copied in our study. Specifically, we hypothesise that presence of another female's eggs provides more valuable public informa-

tion than does the presence of another female per se when a mate is not just a mate but also a parent, as for female *E. flabellare*.

Females prefer large males in *E. olmstedii*, another *Etheostoma* that provides paternal care (Stiver & Alonzo, 2010). However, particularly in the absence of size differences, as in the present study, the most reliable predictor of future offspring success may be direct assessment of the nest rather than assessment of features of the male directly or by copying. In many species in which males provide paternal care, including *E. flabellare*, females prefer to mate with males that have eggs already present in their nests (Ridley & Rechten, 1981; Constantz, 1985; Jamieson & Colgan, 1989; Knapp & Sargent, 1989; Forsgren et al., 1996). The presence of eggs indicates that the eggs have not been eaten yet and that other females chose to lay eggs, which may be predictive of future offspring success by indicating superior male genes, parental ability, or nest quality. The presence of eggs may also protect eggs against predation via the dilution effect (Forsgren et al., 1996; Stiver & Alonzo, 2011). *E. flabellare* males guard a nest site and care for eggs in it (Winn, 1958; Moretz & Rogers, 2004). Females cruise among male territory sites, and males swim out from their territories to solicit females. The females then attach their eggs in the nests of multiple males. The importance of the presence of eggs to *E. flabellare* females is further supported by the males' egg mimicry (fleshy egg-looking knobs on the dorsal fins of males) and by female preference for the mimicry (Knapp & Sargent, 1989).

Choice of nests with eggs is extremely similar to mate choice copying as the term is often used in empirical studies (Knapp & Sargent, 1989) and fits some broader definitions of mate choice copying (e.g., Pruett-Jones, 1992). Because fertilisation is external, laying eggs and the final choice of a mate are simultaneous. What is different from traditional mate choice copying is that the information that *E. flabellare* females use is one step later, being the other females' eggs rather than the presence of other females per se. Thus, this type of copying may fall more appropriately under the term public information use, since females are not observing a direct signal between two individuals (as in social eavesdropping), or any direct interaction between individuals (as in social learning), but are receiving information about the quality of a resource (i.e., the nest and the male; Bonnie & Earley, 2007).

Whether female *E. flabellare* copy other females when nests are present along with the males, but eggs are not, remains to be tested. That eggs alone may be used in female choice is suggested by data on blennies (*Aidablennius*

sphinx) and sand gobies (*Pomatoschistus minutus*). When females of these species choose a nest in which to deposit eggs, they do not respond to male quality or behaviour but only to the presence of the eggs themselves (Kraak & Groothuis, 1994; Forsgren, 1996); both studies controlled for nest differences by assigning artificial nests to males. Like *E. flabellare* females, female sand gobies do not mate choice copy (Forsgren et al., 1996).

In contrast to female *E. flabellare*, for *E. zonale* a female's best predictor of her future offspring's success may be the qualities of the male with which she mates, e.g., brightness of nuptial coloration as an indicator of resistance to parasites and the ability to produce sexy sons. In *E. zonale*, egg distribution is less clumped and eggs are distributed amongst algae, making the eggs harder to detect (R. Moran, personal observation). This may explain why mate choice copying was observed in the present study in female *E. zonale* but not in female *E. flabellare*.

4.3. Is the same pattern seen in other species?

Mate choice copying has most commonly been studied in females only. Among fish, some evidence of female mate choice copying has been found in 7 of 8 species without paternal brood care versus 3 of 7 with paternal brood care (Table 1). Species in which female mate choice copying has been seen despite paternal care are the three-spined stickleback (*Gasterosteus aculeatus*) (Frommen et al., 2009), the ocellated wrasse (*Symphodus ocellatus*) (Alonzo, 2008), and the whitebelly damselfish (*Amblyglyphidodon leucogaster*) (Goulet & Goulet, 2006). However, for *G. aculeatus*, although evidence for mate choice copying in both sexes was found in one study (Frommen et al., 2009), another study found no evidence for female mate choice copying (Patriquin-Meldrum & Godin, 1998) and one study was inconclusive (Goldschmidt et al., 1993). That *A. leucogaster* and *S. ocellatus* females copy is based on field studies (Goulet & Goulet, 2006; Alonzo, 2008). Clearly field studies are important, but a limitation is that males are not randomly assigned to females being present versus absent, making it difficult to be sure that choice is due to copying rather than to unmeasured aspects of males that covary with the presence of females. However, female choice in *S. ocellatus* was examined for each male both when other females were present and when they were absent, i.e., within males, eliminating aspects of males and their nests that do not change with time (Alonzo, 2008).

Although female copying has been found in some non-fish species, whether female mate choice copying occurs in any non-fish species with

Table 1.
Empirical studies of mate choice copying in fish.

Species	Maternal brood care	Paternal brood care	Female mate choice copying	Male mate choice copying
Japanese medaka, <i>Oryzias latipes</i>	No	No	1 Yes, 1 No	NA
Humpback limia, <i>Limia nigrofasciata</i>	No	No	1 Yes	NA
Perugia's limia, <i>Limia perugiae</i>	No	No	1 No	NA
Banded darter, <i>Etheostoma zonale</i>	No	No	1 Yes ²	1 Yes ²
Guppy, <i>Poecilia reticulata</i> ^d	No	No	13 Yes, 3 No	NA
Sailfin molly, <i>Poecilia latipinna</i> ^d	No	No	7 Yes ^a	2 Yes ^a
Amazon molly, <i>Poecilia formosa</i> ^d	No	No	1 Yes	NA ^b
Mexican molly, <i>Poecilia mexicana</i> ^d	No	No	1 Yes	1 Yes ¹
Pipefish, <i>Syngnathus typhle</i> ^e	No	Yes	1 No	1 Yes ^c
Ocellated wrasse, <i>Symphodus ocellatus</i>	No	Yes	1 Yes ^a	NA
Whitebelly damselfish, <i>Amblyglyphidodon leucogaster</i>	No	Yes	1 Yes ^a	NA
Three-spined stickleback, <i>Gasterosteus aculeatus</i>	No	Yes	1 Yes, 1 No, 1 Inconclusive	1 Yes
Sand goby, <i>Potamoschistus minutus</i>	No	Yes	1 No	NA
Common goby, <i>Potamoschistus microps</i>	No	Yes	1 No	NA
Fantail darter, <i>Etheostoma flabellare</i>	No	Yes	1 No ²	1 Yes ²

References in Vakirtzis (2011), except ¹Bierbach et al. (2011); ²present study. NA, data are not available.

^a Data include a field study.

^b *Poecilia formosa* is a unisexual fish consisting of only females and, therefore, cannot show male mate choice copying.

^c Because *Syngnathus typhle* exhibit sex role reversal, male mate choice copying in *S. typhle* is evolutionarily equivalent to female mate choice copying in species with traditional sex roles.

^d Livebearing fish with internal fertilisation.

^e Fertilisation and brood care occurs within the male's body.

paternal care has yet to be tested. Paternal brood care is less common in non-fish species, but does occur (reviewed by Eens & Pinxten, 2000). Further studies of mate choice copying in species with male only parental care are needed in order to further clarify any patterns relating parental care to the presence of mate choice copying.

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