Competitor size, male mating success and mate choice in eastern mosquitofish, *Gambusia holbrooki*

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Males usually compete for mates but, by choosing a favourable social environment (e.g. avoiding stronger competitors), males might increase their reproductive success. We first tested whether the mate choice of male eastern mosquitofish depended on the size of potential competitors. In two-choice trials, focal males preferred to associate with a group of large males over a group of small males. However, when both stimulus groups also contained females, focal males associated equally often with the group with large males and the group with small males. We then quantified the effect of competitor size on the relative mating success (proportion of all mating attempts) of males competing for access to a female. In mating trials, the relative mating success of focal males increased with focal male size. In addition, focal males had higher mating success when competing in a group of small males than a group of large males. We suggest that the benefits of associating with small male competitors in a mating context (greater mating success) are balanced by other benefits that have led to a general preference for associating with larger males.

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Males usually compete for mates, either in direct contests or indirectly through female choice (Andersson 1994). In general, males only compete with a subset of the population (e.g. males in the same social group or those likely to be sampled by the same female). A male's competitive ability relative to his immediate competitors therefore partly determines his reproductive success. Competitive ability is often context dependent, so a male's relative success depends on the local physical and/or social environment (Zajitschek & Brooks 2008). For example, a field study of fiddler crabs, *Uca mjoebergi*, showed that a male's relative attractiveness depended on the size of his neighbours (Callander et al. 2011). Previous work has focused on how males alter their behaviour to increase their mating success in the current social context (e.g. Farr 1976; Hill 1998; Jirotkul 1999; Martinez-Rivera & Gerhardt 2008). Males might also be selected to seek out environments that increase their relative competitive ability, effectively choosing the context in which they compete to improve their reproductive success. This has recently been shown in house finches, *Carpodacus mexicanus*: males that moved frequently between social groups increased their relative attractiveness and had greater pairing success than more sedentary males (Oh & Badyaev 2010).

Choosing the social context of mating competition is a form of mate choice. In males, as in females, mate choice can result from any factor that increases the profitability of certain mates above the cost of lowering the mating rate by rejecting some potential mates (Jennions & Kokko, in press). Males choose (or adjust their courting effort towards) mates on the basis of female traits, such as ornaments or body size, that reflect fecundity/condition (Jones et al. 2001; Pack et al. 2009) or correlate with compatibility (Ryan & Altman 2001), relatedness (Lihoreau & Colette 2010), receptivity (Guevara-Fiore et al. 2010) or mating status (Arnaud & Haubruge 1999; Ruiz et al. 2008). However, the value of a female decreases as the number of competitor males she attracts increases, lowering the average fertilization success of competing males (Servedio & Lande 2006). Male choice can incorporate information both on the number of competitors, so that males are distributed between females according to female value (Herdman et al. 2004), and on male relative competitive ability, leading to size- or quality-based assortative mating ('prudent choice': Fawcett & Johnstone 2003; Härdling & Kokko 2005; Bel-Venner et al. 2008). Thus even if females do not vary in 'quality', the value of a female to a male varies with his competitive ability relative to the males already competing to mate with her.

Animals that associate in groups choose between different social environments when deciding which group to join. While factors such as predator avoidance and foraging competition are known to affect group-joining decisions (e.g. in fish: Hoare et al. 2000, 2004)

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reproductive considerations are also likely to contribute. There is some evidence that numbers and/or densities of potential mates and competitors influence male group-joining decisions (Lindström & Ranta 1993; Agrillo et al. 2008). Groups can also vary in the quality of competitors, and males should choose to associate with less attractive or less competitive males in order to increase their relative competitive ability and resultant reproductive success (Dugatkin & Sargent 1994; Greene et al. 2000; Bateson & Healy 2005), although males might also preferentially associate with more attractive males in order to increase their chance of encountering females (e.g. in lekking species: Beehler & Foster 1988; Jiguet & Bretagnolle 2006). A male's absolute competitive ability can affect the benefits he gains from choosing his social environment (Oh & Badyaev 2010): if the best males do well in all contexts, choosing between contexts may bring little additional benefit. Choice of social context could thus be a conditional strategy employed by some males to reduce a competitive disadvantage. The intensity of competition could also affect the importance of choosing between competitors. For example, if male–male competition decreases when females are relatively abundant, the competitive ability of rivals might matter less under these conditions than when females are scarce and competition is stronger.

Here, we asked whether male association preferences reflect the effects of competitor size on male mating success. Eastern mosquitofish naturally form mixed-sex shoals of varying size and sex ratio (Agrillo et al. 2008). Males do not court females but coerce matings by positioning themselves below and slightly behind a female and thrusting forward their gonopodium, an intromittent organ modified from the anal fin, to transfer sperm to the female (Bisazza & Marin 1995). Some female mate choice occurs (Bisazza et al. 2001; Kahn et al. 2009), but direct male competition for mates is extremely important. Male size at maturity is highly variable and affects mating success (Bisazza & Marin 1995). Greater manoeuvrability allows small males to make more frequent mating attempts than large males in the absence of competitors (Pilastro et al. 1997). In groups with several males, however, the largest male makes the majority of mating attempts by preventing smaller males from gaining access to females (Bisazza & Marin 1995).

We presented focal males with a choice between two stimulus groups, one containing exclusively large males and the other exclusively small males. To determine association preferences in a nonmating context we presented male-only stimulus groups. To determine association preferences in a mating context we presented stimulus groups that also contained females, at male-biased, even and female-biased sex ratios. We expected males to associate preferentially with groups containing small males, assuming these are weaker competitors. We also expected preference strength to increase with the ratio of males to females because when the number of males in a group increases, male dominance interactions increase and the total number of mating attempts decreases (Smith 2007), which should increase the importance of male dominance under male-biased sex ratios. We also predicted that preference strength (and possibly direction) would change with focal male size because of effects of size on male competitive ability. Finally, we compared the mating success of focal males placed with small or large competitors, to test the adaptive significance of association preferences based on competitor size.

METHODS

In February 2011 we used hand nets to collect about 250 adult fish from wild populations in Canberra, Australia, where the eastern mosquitofish is an introduced pest in urban lakes (Australian Capital Territory collection permit no. LT2006204). Fish were transported to the laboratory in water from their collection location and brought to laboratory temperature before being transferred to 120-litre aquaria (ca. 30 fish/tank), which contained water dechlorinated with commercial aquarium chemicals. Fish were maintained on a 14:10 h photoperiod at 28 °C and fed ad libitum with _Artemia_ nauplii and commercial fish flakes. At the end of our study all fish were retained for stock breeding purposes, under the same laboratory conditions. This research was approved under Australian National University Ethics permit F.BTZ.26.08.

Choice Trials

Male association preferences were tested in two-choice trials. Focal males were classed as small (standard length, mean $\pm$ SD $= 19.7 \pm 0.3$ mm, $N = 20$), medium (22.9 ± 0.5 mm, $N = 20$) or large (25.9 ± 0.5 mm, $N = 20$). Each focal male was placed in a clear plastic cylinder in the central compartment (48×45 cm and 10 cm high) of a tank divided into three with clear Plexiglas barriers; each end compartment (6×45 cm and 10 cm high) held a group of five stimulus fish containing either large (>24.5 mm) or small (<21 mm) males. After a 10 min acclimation period, the focal male was released and his movements recorded for 10 min using a digital video camera. Association preference was measured as the time spent within 6 cm of each end compartment. Each focal male was tested under four sex ratio treatments: (1) stimulus groups contained only males (5M:0F); (2) groups were male-biased (4M:1F); (3) groups contained similar numbers of males and females (2M:3F); (4) groups were female-biased (1M:4F). Treatment order was randomized and large and small stimulus males were alternated between the two end compartments. Focal males were housed individually in 1-litre tanks, and tested only once per day.

Stimulus fish were drawn from a stock of 64 small males (19.6 ± 1.1 mm), 57 large males (25.0 ± 1.1 mm) and 60 females (35.8 ± 3.2 mm), housed in single-sex 120-litre tanks (ca. 30 fish/tank). Stimulus fish were used in multiple trials but each focal male encountered novel stimulus fish in each of the four treatments. Different focal males encountered different combinations of stimulus fish. Females in each trial were size-matched (± 1 mm).

Mating Trials

We then quantified male mating success for the same 60 focal males in groups with only small or only large competitors. Focal males were immobilized in cold water ($4 °C$) and marked with elastomer (Northwest Marine Technology, Shaw Island, WA, U.S.A.) injected subcutaneously behind the caudal fin. After marking, males were returned to their individual tanks where they regained normal activity within 30–60 s. Trials were not run sooner than 4 days after marking. Each focal male was placed in a tank (45×20 cm and 10 cm high) with four large or four small competitor males. After a short (3–5 min) acclimation period a female was introduced to the tank, and the behaviour of all males was recorded for 10 min using a digital video camera. Each focal male was tested with both small competitors and large competitors. Trial order was alternated, and each focal male was tested only once per day. The number of insemination attempts by focal and competitor males was used as a proxy for mating success. We defined every gonopodium thrust made by a male positioned below and slightly behind the female as an insemination attempt. While not every attempt is successful we assumed that the number of attempts correlates with mating success.

We used the stimulus males from the choice trials as competitor males. As before, we used competitor males in new combinations for each focal male. We used a new virgin female from existing laboratory stocks for each trial (32.3 ± 2.6 mm, $N = 120$).

We analysed the time focal males spent associating with the large-male group as a proportion of the total time spent associating with both groups in a generalized linear mixed model with binomial error using the cbind function in S-plus 8.2 (TIBCO Spotfire, Somerville, MA, U.S.A.). Focal male size, sex ratio, trial order and all two-way interactions were included as fixed factors in the initial model, with focal male identity as a random factor. We also re-ran the model after excluding 18 of 240 trials in which the focal male spent less than half the trial associating with either group ('reduced data set'). The average time spent associating with either group ranged across treatments from 75.5 to 89.2% of the 10 min trial.

To examine the mating success of focal males in small- and large-competitor trials, we used the proportion of all insemination attempts that were made by the focal male as the dependent variable in a generalized linear mixed model with binomial error. Focal male size, competitor male size, female size and all two-way interactions were included as fixed factors and focal male identity as a random factor. We also investigated the effects of these predictor variables on the total number of attempts made by all males in a group using a linear mixed-effects model. In all analyses we used model simplification and sequentially removed nonsignificant fixed effects to generate the final model (Crawley 2005).

RESULTS

Choice Trials

The proportion of time focal males spent with the large-male group was significantly affected by the sex ratio ($F_{3,177} = 7.58$, $P < 0.001$). In the male-only (5:0) treatment, focal males spent about 78% of their total association time with the group of large males, whereas in all other treatments focal males did not preferentially associate with the group containing large males (46−51% of time with the large-male group; Fig. 1). There was no effect of focal male size ($F_{2,57} = 1.36$, $P = 0.26$), trial order ($F_{3,174} = 0.67$, $P = 0.57$) or any interaction terms (all $P > 0.1$) on time spent with the large-male group. The results were qualitatively similar for the reduced data set: again, only sex ratio had a significant effect ($F_{3,159} = 6.93$, $P < 0.001$).
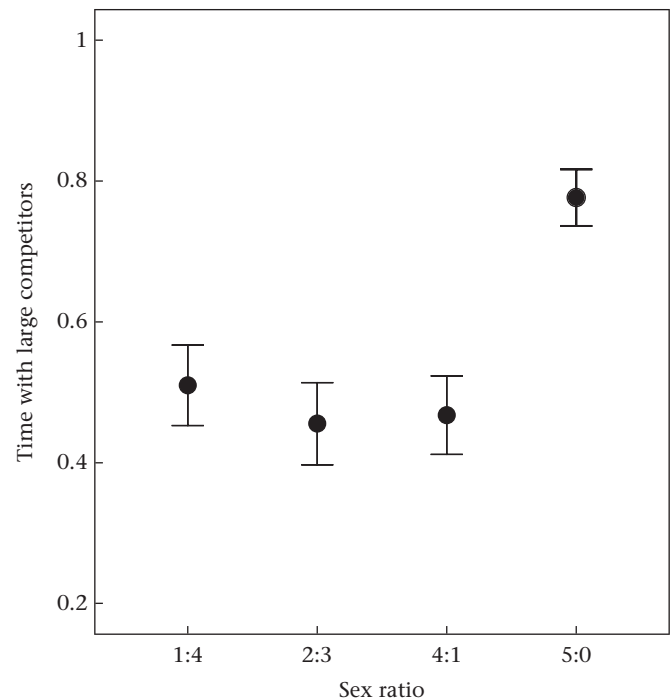
Mating Trials

Focal males obtained a greater proportion of mating attempts when placed with small competitors than with large competitors (50% versus 41%; $F_{1,55} = 5.65$, $P = 0.02$). Focal male size also had a significant effect, with large focal males obtaining the greatest proportion of mating attempts ($F_{2,54} = 3.61$, $P = 0.03$; Fig. 2). Neither female size ($F_{1,54} = 0.17$, $P = 0.68$) nor any interaction terms (all $P > 0.52$) had a significant effect on focal males' mating success.

Larger females attracted significantly more mating attempts ($F_{1,54} = 19.69$, $P < 0.001$), but there was no effect of focal male size ($F_{2,54} = 0.15$, $P = 0.86$), competitor male size ($F_{1,54} = 0.07$, $P < 0.79$) or any interactions (all $P > 0.11$) on the total number of mating attempts in a trial.

DISCUSSION

In the absence of females, male mosquitofish preferred to associate with groups of large males over groups of small males. There was no preference, however, when females were present. Superficially the latter result suggests that the size of competitor males did not affect focal males' association preferences despite the potential benefit of increasing their relative share of mating

Figure 1. Mean ± SE proportion of association time spent with the large-competitor group under different sex ratio treatments.

attempts: mating trials showed that males with small competitors had the greatest estimated mating success. We suggest, however, that males trade off the benefits of associating with large males against the costs of competing with them for mates. The net result is that no association preference is observed in a mating context.
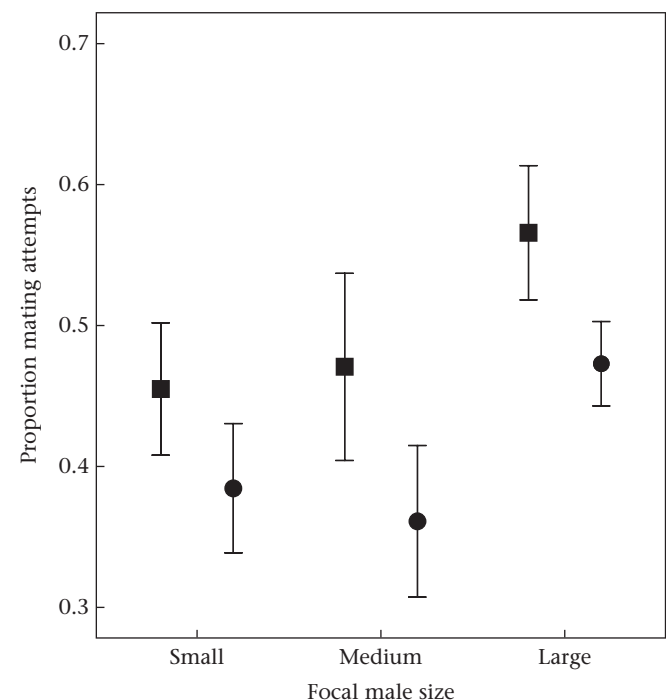
Figure 2. Mean ± SE proportion of mating attempts made by small, medium and large focal males placed with small competitors (squares) and large competitors (circles).

Focal males associated equally often with large-male and small-male groups whenever groups contained females. This might suggest that there is no cost to competing against larger males for mates, and that males choose between groups randomly with respect to competitor size. This interpretation does not, however, account for the fact that males no longer preferred groups containing large males, as they had in the male-only treatment. Assuming the decision to join a group is adaptive, it is difficult to envisage a benefit of associating with large males that disappears with the arrival of a female. A more likely alternative, given a general benefit of associating with large males, is that males trade off conflicting preferences in a mating context. That is, a baseline preference for associating with large males is counterbalanced by a cost of competing with them for mates. This could explain the apparent absence of choice observed in trials with females. If the magnitudes of benefit and cost are roughly equivalent there is no net benefit of an association preference for large males. The results of our mating trials provide some support for the latter scenario: focal males with small competitors had greater mating success than males with large competitors. This confirms our assumption that there is a mating advantage to associating with smaller rather than larger males (see also Bisazza & Marin 1995). Our result held regardless of the focal male's size. Large focal males did, however, make a greater proportion of mating attempts than small and medium-sized focal males, independently of the size of their competitors. Even so, small and medium-sized focal males still made a fairly large proportion of mating attempts when placed with large competitors (38 and 36%, respectively). Our results raise the possibility that a smaller male in a group mainly composed of large competitors can partly compensate for his dominance disadvantage. As large, dominant males are more aggressive towards similar-sized males (McPeek 1992), small males could obtain access to females left unattended during aggressive interactions between large males.

One conundrum is why focal males preferred large-male groups in the male-only treatment. In addition to reproductive opportunities, factors such as resource competition and predator avoidance can also influence the group-joining decisions of individuals (Elgar 1989). It is unclear, however, whether these factors can explain a preference for associating with large males in the eastern mosquitofish. In fish, competition and antipredator behaviour more often result in size-assortative shoaling (reviewed in Hoare et al. 2000) than a preference for larger individuals. Associating with similar individuals lowers predation risk through predator confusion (Krakauer 1995). Indeed, the 'oddity effect' (e.g. Landeau & Terborgh 1986) predicts that a small male in a group of large males is more conspicuous and faces greater predation risk. It is possible, however, that a small fish represents a less valuable resource to a predator than its larger associates (Peuhkuri 1997; Rodgers et al. 2011). Associating with 'more profitable' targets has been hypothesized to explain why female mosquitofish prefer to associate with larger females when harassed by male conspecifics (Agrillo et al. 2006). Associating with larger individuals could also be advantageous if they are more successful at actively deterring predators (Jordan et al. 2010). Finally, associating with larger males might increase the likelihood of encountering females, as female mosquitofish sometimes prefer to associate with larger males (Bisazza et al. 2001; Kahn et al. 2009).

It is important to remember that males can also improve their reproductive success through other means than choosing their social context. The best strategy might simply be to pursue the first female encountered and persist until some minimum threshold of success is reached. Choosiness itself carries costs, including time and energy spent, and predation risks associated with moving between groups. Another possibility is that males change their behaviour in a condition- or context-dependent manner (Bateson & Healy 2005). For example, in fiddler crabs, *Uca annulipes*, males increase their display rate as the number of competitors increases (Milner et al. 2012). If male mosquitofish adjust their mating behaviour (e.g. choose to 'sneak' or chase rivals) depending on their size relative to competitors, there might be little additional benefit to also choosing competitors. Studies of mosquitofish and other poeciliid fishes indicate that high variance in male body size at maturation persists because there is a mating advantage of small male size owing to an increased ability to sneak matings that seems to counter the advantage large males gain through social dominance (Bisazza & Pilastro 1997; Pilastro et al. 1997). Even so, our mating trial results suggest that small males do not fully compensate for their size disadvantage under direct male competition. The mating success of male mosquitofish is still affected by their size relative to that of competitors.

Finally, it is worth noting that if we had not included the male-only treatment we could easily have concluded that competitor size had no effect on male mate preferences. In contrast, because we documented the behaviour of males in the absence of females to establish a baseline nonmating preference, we detected a conflicting association preference that masked the response of males to potential mating competitors. Grouping decisions based on non-mating criteria are common in many taxa (e.g. Landeau & Terborgh 1986), so we suggest that all studies of male mate choice based on social context need first to document baseline preferences. In sum, if we take the preference for associating with larger males in the absence of females as a baseline, reduced mating success in the presence of large competitors can partly explain the tendency for males to spend less time in association with large males when females are present. The net result is that males did not show a mate preference based on the size of potential mating competitors.

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