

Original Article

The effect of competitor presence and relative competitive ability on male mate choice

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Recent studies suggest that males might respond in an adaptive manner to an elevated likelihood of male–male competition for mates by facultatively altering their mating preferences. Little is known, however, about how male choice is influenced by a male's relative competitiveness or by the risk posed by increased physical competition for access to mates compared with greater risk of sperm competition. We investigated how the relative size and presence of a competitor influences male choice using 2-choice experiments in the mosquito fish, *Gambusia holbrooki*. We varied the size of the focal male, the size of a competitor, and whether the competitor remained alongside the preferred female (physical and sperm competition) or was removed (only greater sperm competition). Prior to viewing a competitor, males, regardless of size, significantly preferred larger females. After a male had viewed a competitor alongside his preferred female, however, he subsequently spent significantly less time associating with her. This change in male choice was not influenced by focal male size, competitor size, or whether or not the competitor was physically present during the choice trial. After viewing a competitor, however, larger males spent significantly more time than did smaller males near their preferred female. Our results suggest that male mating preferences are sensitive to the risk of increased physical or indirect sperm competition, but there was no evidence that males adjust their mate choice in response to the relative size (and therefore presumed competitiveness) of rivals. *Key words*: competition, direct costs, indirect costs, male mate choice, mosquito fish. [*Behav Ecol* 22:769–775 (2011)]

INTRODUCTION

Male mating preferences are relatively easy to explain when 2 or more females are simultaneously available. Males should choose the female that confers the greatest benefits (e.g., the larger, more fecund female) as rejection of the other female does not reduce the male's mating rate. This type of male mate choice occurs in many animal taxa (review: Bonduriansky 2001). When females are encountered sequentially, however, male choice is more difficult to explain because it requires that a male reject a currently available female, thereby lowering his mating rate (mini-review: Barry and Kokko 2010). Even when several females are simultaneously available, however, there is another factor that makes it difficult to predict male mate choice decisions: the presence of competitors. This is more important for male than female choice as male–male competition for reproductive opportunities is far more common than female–female competition (but see Bro-Jørgensen 2007; Kokko and Jennions 2008). Greater competition for a female reduces the mean share of paternity and can impose costs by increasing the risk of injury or death, using up energetic resources, and depleting sperm supplies (Wedell et al. 2002).

If all males have identical mating preferences then the greater competition for preferred females will reduce the share of paternity and impose costs that could exceed the original benefits of choosing them as mates (Servedio and Lande 2006; Servedio 2007). This suggests that male mating preferences will evolve that generate variation in male choice. First, males might evolve facultative or context dependent

mating preferences (for the effect of variation in mates on comparative evaluation of mate quality, see Bateson and Healy 2005) based on assessment of the number of competitors that will lead to an ideal free distribution of males across females so that the rate of return per female is identical (i.e., the ratio of the value of the female to the number of competitors she attracts; Herdman et al. 2004). This would require that there is no cost to moving between females and that males have complete information about the arrival rate of females and potential competitors. Alternatively, males might use rules of thumb that lead to an approximately ideal free distribution. Second, males might evolve innate mating preferences that reflect the average level of competition each type of female will generate given the mating preferences of other males. The situation is more complicated, however, if there is variation among males in their competitiveness. Male competitiveness could vary due to differences in success in events that occur before and/or after copulation (e.g., mating access to females and the ability to convert copulations into fertilization). Such variation can lead to "prudent male choice" where the benefits conferred by courting with a given female are weighed against the likelihood of mating with her, the resultant share of paternity, and the relative cost per mating (e.g., costs of greater competition). Consequently, the mean level of competition might reliably vary among females because males that differ in competitive ability vary in the extent to which they reject higher or lower quality females that, in the absence of competition, confer greater or smaller benefits (Fawcett and Johnstone 2003; Härdling and Kokko 2005). It is often stated that prudent choice will lead to more competitive males preferring more valuable females (e.g., more fecund females) and less competitive males either preferring less valuable females or mating indiscriminately, but the available models show that there are also situations where all males or even only more competitive males mate indiscriminately (e.g.,

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Fawcett and Johnstone 2003; Härdling and Kokko 2005; Härdling et al. 2008).

If males facultatively adjust their mate choice, they might use currently available cues about the level of mating competition, such as the presence/absence of rivals, the number of rivals, and their relative competitiveness to decide which female is the most profitable to court, guard, or pursue. For example, in 2-choice experiments, male mosquito fish (*Gambusia holbrooki*) spent less time with an originally preferred female after they had viewed a competitor near her (Wong and McCarthy 2009). On the other hand, experiments with mollies (*Poecilia mexicana*) on audience/social effects suggest that males might deceive competitors by swimming near less preferred females but return to their originally preferred females once the competitor departs (Plath et al. 2008, 2010). In general, larger males are better at gaining access to females during direct physical contests (Blanckenhorn 2005; Kelly 2008), although some males might pursue alternative mating tactics (e.g., sneak copulations) that favor smaller body size. The effect of male size on postmating reproductive success is less clear as fertilization success depends on ejaculate size (Parker 1998), ejaculate quality (Snook 2005), and cryptic female choice.

Although a few studies have shown that competitor presence influences mate choice (e.g., Plath et al. 2008, 2010; Wong and McCarthy 2009), to date, no study has explored how relative male competitiveness and the risks due to direct physical and indirect sperm competition affect male mate choice. Specifically, it is largely unknown whether facultative mate choice is influenced by the relative competitive ability of rivals or differs depending on the immediate presence (direct physical threat) or earlier presence (greater likelihood of sperm competition) of competitors. For example, although Wong and McCarthy (2009) showed that a male mating preference for large females is reduced by the earlier presence of competitors, they did not investigate the effect of the relative size of the focal and competitor males or whether the effect was greater if the competitor remained present during actual male mate choice.

Study species

The mosquito fish, *G. holbrooki*, is an ideal species to investigate how male–male competition affects male mate choice. They occur at high densities and simultaneous male choice among different-sized females that vary in the number and size of males associating with them is a biologically realistic scenario. Female size varies considerably and is strongly correlated with fecundity (Deaton 2008a). Fertilization is internal and males transfer sperm through a modified anal fin, called the gonopodium (Constantz 1989). Males do not court and engage in coercive “sneak” copulation attempts that involve gonopodial thrusting (Bisazza 1993; Bisazza and Marin 1995). Males relentlessly pursue females (e.g., up to 20 copulation attempts per minute; Wilson 2005). Sperm competition is high because females store sperm (Constantz 1989) and broods exhibit high levels of multiple paternity (Zane et al. 1999). Larger males are better physical competitors (Hughes 1985; Bisazza et al. 2001), gain a greater share of copulations when 2 males compete for a female (Bisazza and Marin 1995), and have larger sperm reserves (Locatello et al. 2008). This suggests that a smaller male will be more adversely affected by the past or current presence of a larger competitor near a larger more valuable female. However, when alone with a female, smaller males have a higher insemination rate than larger males (Pilastro et al. 1997), and there is no relationship between male size and sperm quality (Locatello et al. 2008). This suggests that the previous presence of a solitary small

rather than large male near a female might be a cue that the absolute level of sperm competition will be higher.

We conducted 2-choice mate experiments with 3 “choice” stages in which the level of perceived competition for preferred females differed. We predicted that:

1. Males will choose large females in a no cost situation and that this preference will not depend on focal male size.
2. Males will switch to choosing a nonpreferred female after seeing a competitor near a preferred female (i.e., when the value of the preferred female is reduced).
3. The switch in male choice will depend on the relative competitive ability of the focal male, and the type of competition (sperm vs. sperm and physical competition) with larger males less likely than small males to switch their mating preference, especially if there is direct physical competition.
4. Males will spend more time associating with an originally nonpreferred females when the presence of a competitor near the initially preferred female is ongoing (i.e., due to greater risk of direct physical contest and sperm competition) than when only having seen a competitor near the preferred females before testing (i.e., only greater sperm competition)

MATERIALS AND METHODS

Juvenile *G. holbrooki* were collected from southwestern Sydney, Australia (New South Wales Department of Primary Industry Permit # P06/0147). In the laboratory, fish were reared in groups of 12 at 26 °C in 9 l plastic aquaria until they could be sexed. They were then moved to single sex tanks and kept at the same density. Communal rearing allowed for natural dominance interactions among males. Fish were fed live *Artemia* and food flakes ad libitum. Throughout the experiment, fish were maintained on a 14:10 photoperiod. The interval between field capture and the start of experiments was 3 months as we had to wait for fish to mature and then had to measure them prior to setting up the experiment.

All mating trials were conducted in a plexiglass tank (63.8 × 45 × 10 cm) divided into 3 compartments illuminated overhead by fluorescent tubes. The 2 end compartments (each 7.2 × 45 × 10 cm) housed test females and competitor males. The focal male whose mate choice was quantified was placed in the central compartment (45.6 × 45 × 10 cm; see Figure 1). The compartments were separated by plexiglass so there was only visual contact between the focal male, test females, and competitor males. The outer sides of the tank were covered in black plastic. Observations were made through a small opening in a blind so that the observer did not disturb the fish while recording choice behavior.

Each mate choice trial consisted of three 10-min mate choice stages during which data were collected (see below for stage details). On first introducing a focal male to the test tank, there was a 10-min “acclimatization” periods prior to stage 1 during which the male was placed in an opaque plastic tube in the center of the tank. There was a second acclimatization period between stages 1 and 2 and a third between stages 2–3. All trials were therefore 60 min in length. The acclimation period between stages was provided for 2 reasons: 1) competitor males were added or removed between stages, and this might disturb females. Poeciliid females, however, only require a few minutes to return to normal behaviors after a disturbance (see Aspbury and Basolo 2002; Royle et al. 2008; Wong and McCarthy 2009); 2) during this period, males had 10 min to observe a competitor near the preferred female as part of the experimental design to see how this affected their mating preference in the next choice stage (see also Wong and McCarthy 2009).

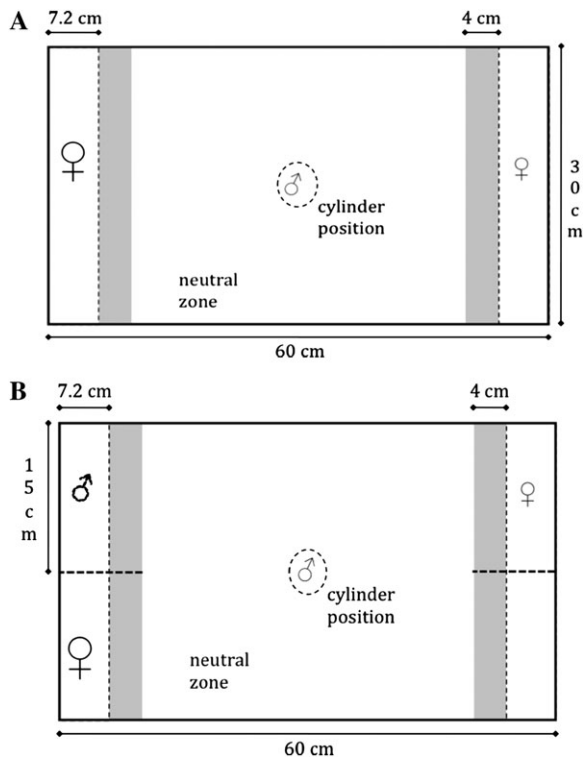


Figure 1
Experimental aquarium layout showing an example setup of test subjects. Solid lines: opaque barriers, dashed: transparent. Shaded areas: female-association zones. (a) Setup during initial mate choice (stage 1). (b) Setup after exposure to competitor male (whether present/absent) near preferred female (stages 2 and 3). Locations of both females and competitor male were randomized across stages/trials.

Males generally return to normal behaviors almost immediately after being handled (Mautz BS, personal observation). For example, Wilson (2005) noted that all males actively pursue females with 2 min of being introduced to a new tank. We are therefore confident that males were sexually interested in test females. The focal male and stimulus females were not directly handled during a trial (i.e., caught with a dip net). At the end of each stage, we simply lowered a transparent open-ended plastic tube over the focal male and then slowly moved the vertical tube back to the center of the test arena and left the male there for 10 min until the tube was raised to start the next choice stage. Females were not swapped between end compartments between stages. This was a biological consideration as we felt that any disruption caused by transfer of females was not worthwhile given that a side bias is unlikely in a highly symmetric test arena. A simple side-bias test confirmed that, on average, focal males spent equal time associating with females on both sides of the tank ($t_{76} = 1.146$, $P = 0.147$).

To determine any influence of male body size on mate choice, focal males were divided into 2 size classes: large males (>21.3 mm) and small males (<18.5 mm) were, respectively, at least 1 standard deviation (SD) above or below the population mean for the cohort of lab-reared males.

Stage 1: initial male mating preference

A single focal male was placed in the opaque tube in the middle of the central compartment. A large (mean \pm SD: 28.1 ± 1.47 mm) and a small female (22.6 ± 1.73 mm) were haphazardly chosen from 1 of 2 stock tanks and individually placed in

opposite end compartments. The trial began after 10 min when we lifted the opaque tube allowing the focal male to observe both females and swim freely in the central compartment. We then monitored the time the focal male spent in association with each female for 10 min. We defined the male as associating with a female if he was <5 cm from the barrier separating him from the female and directly oriented toward her. It was obvious based on this criterion if males were sexually interested in females. Association time generally predicts the likelihood of copulation attempts in freely associating Poeciliids (e.g., Walling et al., 2010). The proportion of time spent with the preferred (i.e., longer association time) female was determined as “time with preferred female/time with both females.” For a trial to proceed to Stage 2, the focal male had to spend $>55\%$ of his total association time with 1 female. This criterion increased the likelihood that a female was classified as preferred due to active male choice rather than by chance (sampling error). In 92 of 95 trials, the focal males spent $>55\%$ of their time with 1 female.

Stage 2: influence of viewing a competitor on male mate choice

After Stage 1, the focal male was captured in a transparent open-ended plastic tube that was then moved to the center of the mate choice arena. Each end compartment was then divided in half with clear Perspex, and a competitor male was placed in the compartment next to the focal male’s preferred female. The competitor was either larger (4.14 ± 0.83 mm) or smaller than the focal male (4.11 ± 0.57 mm) (mean difference \pm SD). Males were randomly assigned a large/small competitor before use in experiments. The focal male was then allowed to observe the competitor near his preferred female for 10 min (see also Wong and McCarthy 2009). The competitor was then either removed or remained alongside the preferred female. The decision to remove or retain the competitor was randomized. We then again measured the focal male’s association time with his originally preferred female using the same criteria as in Stage 1. A change in preference is attributed to the addition of the competitor (for alternate explanations, see DISCUSSION).

Stage 3: influence of competitor presence/absence on male mate choice

After stage 2, the focal male was again placed in a transparent plastic tube in the central compartment and allowed to view the same competitor next to his originally preferred female for 10 min. (If the competitor had been removed during Stage 2, he was returned). Following this, the focal male received the opposite competitor presence/absence treatment to that in Stage 2. Each focal male therefore received both treatments. We then measured his association time with his originally preferred female.

Focal and stimulus fish were always taken from a different stock tank so that they could not observe each other before use.

Repeatability

A subset of 30 focal males was retested 14 days later (second trial). The order of the presence/absence treatment in stages 2 and 3 from a male’s first trial was reversed for his second trial. The experimental design was therefore fully balanced, although the actual data were not because some males did not complete their second trial. We ensured that for a given focal male, we used different females and competitor male in the 2 trials.

Statistics

The 2 main dependent variables were “proportion of association time with the preferred female” or “with the larger female.” Both proportions were arcsine square root transformed to achieve normality. To facilitate interpretation, we ran a series of “orthogonal” linear mixed models. Each model reported included all test terms and, depending on the number of fixed factors, all 2-way and 3-way interactions between categorical fixed factors. For each model, we tested whether any significant terms became nonsignificant when nonsignificant effects were excluded from the model. We followed the model simplification approach of (Crawley 2005): starting with higher order interactions, we removed nonsignificant terms from the model until only significant main effects were present. This procedure had no effect on any of the terms that were significant in the full model, and for completeness, we therefore present full models.

First, we examined initial mating preferences prior to exposure to a competitor (i.e., Stage 1) to test whether 1) males spent more time with larger females, 2) this effect depended on male body size, and 3) whether the strength of the preference was greater when the females were more disparate in size. The proportion of time with the larger female was the response variable, with focal male size and the absolute difference in female size as fixed factors and male identity as a random factor. The null hypothesis was tested using the intercept value (i.e., was the proportion of time spent with the larger female = 0.5). A mixed model was used to account for repeated measures as some males were tested twice. Second, we tested for a difference in time spent with the originally preferred female before and after viewing a competitor (i.e., stage 1 vs. 2 + 3). Trial (first or second) and male size were treated as fixed factors and male identity as a random factor. Third, we tested whether the presence or absence of a previously observed competitor affected mate choice for the originally preferred female (i.e., only Stages 2 and 3). We ran a linear mixed model with competitor present/absent (2 levels), focal male size, relative competitor size (i.e., bigger or smaller than the focal male), and test order (4 levels, i.e., trial 1, stage 2 = 1 . . . trial 2, stage 3 = 4) as fixed factors and male identity as a random factor. We report parameters estimates and associated *P* values from the full models. We also calculated mixed models that included an interaction between male identity and one of the fixed factors (i.e., random slopes models; see Schielzeth and Forstmeier 2009). Including these interactions did not change the results.

Proportional data should be analyzed using a binomial error distribution, however, there are sometimes issues with the reliability of models using binomial error distributions (Crawley 2005). We present our analysis using arcsine transformed proportions as this provided a better fit to the data than using untransformed data. For completeness, however, we also presented the results based on a model with binomial error in Supplementary Material, Supplementary Appendix 1. The results are qualitatively almost identical: A single marginally nonsignificant results become significant in the reanalysis.

Finally, we calculated the repeatability of the strength of a male's mating preference for the preferred females across trials that were 14 days apart. We report the intraclass correlation (r_i) for each of the 3 stages (Lessells and Boag 1987). Stages 2 and 3 differed between trials in whether or not the competitor was present. We therefore also report r_i for trials that differed in temporal sequence but where competitor presence or absence was the same in both trials. We test for a statistical difference in the r_i when the competitor was presence and absence following Zar (1999).

All tests were 2-tailed with $\alpha = 0.05$. Summary statistics are presented as mean \pm SD. Models were run in S-Plus 7.0.

RESULTS

Initial preference

In Stage 1, males spent significantly more time in association with the larger of the 2 females ($t_{30} = 4.105$, $P < 0.001$; 95% confidence interval: 59.3–75.8%) (Figure 2). The proportion of time spent with the larger female did not depend on the absolute size difference between the 2 females ($F_{1,29} = 0.189$, $P = 0.667$), or the focal male's size ($F_{1,45} = 0.418$, $P = 0.521$). There was therefore no evidence for a size-dependent male mating preference in the absence of competitors.

The effect of viewing a competitor

After the focal male viewed a competitor, there was a significant decline in the proportion of time he spent with his originally preferred female ($F_{1,180} = 5.792$, $P = 0.017$; Figure 3). This result is not readily attributed to a general temporal decline in choice for an initially preferred female. First, there was no difference in the time spent with her in the first and the second half of Stage 1 (mean difference: “Trial 1”: 73.1 ± 58.6 s, $t_{31} = 1.25$, $P = 0.222$; Trial 2: 65.8 ± 82.0 s, $t_{28} = 0.45$, $P = 0.657$). Second, the strength of preference did not decline over the 14 days between the first and second trial ($F_{1,180} = 0.647$, $P = 0.422$). After viewing a competitor, there was a weak but significantly positive relationship between male size and the proportion of time spent with an initially preferred female ($F_{1,45} = 4.08$, $P = 0.049$; Figure 3).

Presence/absence of a competitor

The proportion of time spent with the originally preferred female did not depend on whether the competitor male was larger or smaller than the focal male ($F_{1,53} = 1.40$, $P = 0.243$) or on whether the competitor was still present during the choice trial ($F_{1,53} = 1.65$, $P = 0.204$). There were no also interaction between competitor presence and the relative size of the competitor ($F_{1,53} = 2.65$, $P = 0.109$). No other 2-way or the 3-way interactions were significant (all $P > 0.12$). There was also no effect of treatment order on the proportion of

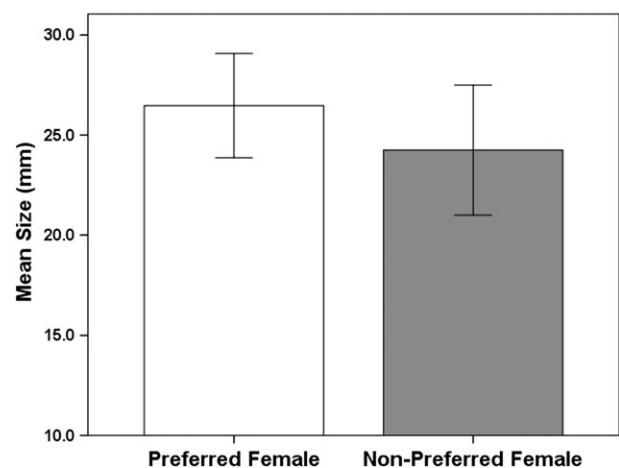


Figure 2

Mean size (\pm SD) difference between preferred and nonpreferred females (Preferred size: 26.5 ± 2.6 mm; Nonpreferred: 24.3 ± 3.26 mm; $P < 0.001$).

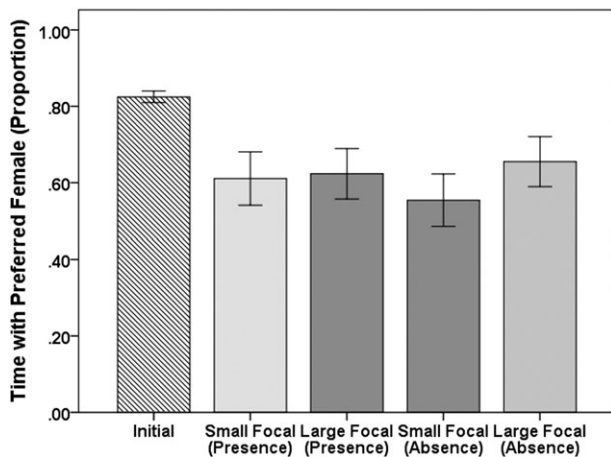


Figure 3
Proportion of time spent with initially preferred female (hatched bar) and then after exposure to a competitor who was either present or absent during the choice trial. Figure is for illustrative purposes only. Bars represent mean (\pm standard error) of raw data and do not take into account repeated measures. Light gray bars represent small focal males, and dark gray bars represent large focal males.

time spent with the originally preferred female ($F_{3,53} = 1.365$, $P = 0.264$).

Repeatability of male choice

The strength of a male's initial mating preference prior to viewing a competitor was significantly repeatable between trials that were 14 days apart ($r_T = 0.349$, $F_{46,30} = 1.885$, $P = 0.034$). After viewing a competitor near the preferred female, however, there was no repeatability of the strength of a male's mating preference for the originally preferred female in either the second ($r_T = -0.204$, $F_{46,30} = 0.726$, $P = 0.839$) or third stage of a trial ($r_T = 0.206$, $F_{45,30} = 1.410$, $P = 0.162$). The same lack of repeatability occurred if we analyzed mate choice after having viewed a competitor when the competitor remained present ($r_T = -0.045$, $F_{46,30} = 0.929$, $P = 0.596$) or was absent ($r_T = 0.426$, $F_{46,30} = 1.74$, $P = 0.056$). In the latter case, the repeatability is only marginally nonsignificant, and the 2 measures of repeatability differ significantly ($Z = 2.196$, $P = 0.028$).

DISCUSSION

Male mate choice has potentially large effects on male fitness and is an important selective force on females (Clutton-Brock 2009). In agreement with our first prediction, we showed that males preferentially associate with larger females under a no cost scenario. This mating preference is consistent with earlier studies of mosquito fish (*G. holbrooki* or *G. affinis*) (e.g., Bisazza et al. 1989; Hoysak and Godin 2007; Deaton 2008b; Wong and McCarthy 2009). As female fecundity is positively correlated with female body size (Bisazza et al. 1989; Deaton 2008a), this preference is likely adaptive. However, if several males and females are simultaneously available as mates, it is difficult to explain why all males would prefer larger females: Greater competition for larger females should eliminate the potential fecundity benefits. This directly selects against the evolution of a uniform male mating preferences for more fecund females (Servedio and Lande 2006; Servedio 2007). Our subsequent finding that competitor presence leads to facultative shifts in mate choice helps to explain why this does not happen.

The influence of male–male competition

It is possible for all males to prefer larger females in a cost-free situation (i.e., no competitors and simultaneous choice). A preference for large females can also be maintained if it is facultatively modified based on cues about the likely level of competition for specific females and enhanced by male self-assessment of his relative competitiveness (e.g., Candolin and Salesto 2009; Fawcett and Bleay 2009). In support of our second prediction, we found that male *G. holbrooki* spent significantly less time with preferred (generally larger) females when associating with these females increased exposure to competition. Our results are qualitatively similar to 2 other recent studies (Wong and McCarthy 2009; Ziege et al. 2009). This change in preference presumably reflects a perceived increase in the level of direct mating competition for these females and/or that the intensity of sperm competition will be higher after mating. Although male mosquito fish experience intense competition for mates, and show size-based dominance (Hughes 1985; Deaton 2008a), the observed changes in male choice in response to competitors were equivocal with respect to effects of the focal male's absolute or relative body size. When comparing male mating preferences with initial preferences (stage 1 vs. stage 2 + 3), we detected a significant effect of male body size. Male size did not initially influence the time focal males spent near preferred females, but after viewing a competitor, larger males spent more time than smaller males associating with their preferred female. However, this size-based mating preference was not detected when comparing across stages (stage 2 vs. 3) after exposure to a competitor. In this case, neither focal nor competitor male size influenced the time spent with an originally preferred female. Given a larger sample size, these slightly contradictory results probably translate into a weak size-based male mating preference. Size-based variation in the strength of a male's mating preference for large females might be related to larger males being socially dominant (Hughes 1985; McPeck 1992; Wilson et al. 2010). Larger males have higher mating rates when 2 males compete for a single female (Bisazza and Marin 1995). This makes it less costly for a larger male to compete with another male for access to a female.

Surprisingly, only a handful of empirical studies, mostly in fish, have investigated how increased competition influences male mate choice (Bel-Venner et al. 2008; Candolin and Salesto 2009; Wong and McCarthy 2009; Ziege et al. 2009). Only one other study has experimentally investigated the effects of relative size on mating patterns (Franceschi et al. 2010). Theoretical models of male mate choice often predict the circumstance under which size/quality-based assortative mating occurs due to size-dependent male mate choice given male–male competition (e.g., Venner et al. 2010). There is some empirical support for this prediction from studies showing facultative shifts in mate choice based on presence of competitors (e.g., Bel-Venner et al. 2008; Candolin and Salesto 2009).

Given male size predicts social competitiveness, we predicted that males would continue to associate with their preferred female in the presence of a smaller competitor, but switch to the other female when exposed to a larger competitor. This did not happen so our third prediction was not supported. An initial male preference for large females that disappears when its expression leads to greater male–male competition has been reported in some species (e.g., Wong and McCarthy 2009) but not in others (e.g., Franceschi et al. 2010), and more studies are needed. There are at least 2 possible explanations for the lack of an effect of relative competitor size in our study. First, smaller male *G. holbrooki* are better at inseminating females when alone (Pilastro et al. 1997). This insemination

advantage might elevate the perceived intensity of sperm competition when mating with a preferred female seen with a smaller male. The effects of greater sperm competition and reduced social competitiveness might therefore cancel out. Second, focal males might be unable to assess their relative competitiveness or size based solely on visual cues. For example, Agrillo et al. (2008) showed in 2-choice trials that male *G. holbrooki* did not preferentially approach a mixed-sex group containing males that were smaller rather than larger than the focal male.

Our fourth prediction was not supported as we did not detect a greater reduction in focal male mating preferences when the competitor remained by the female during the actual choice trial. This implies that sperm competition risk is a greater factor in determining male mate choice than direct physical interactions with another male. Alternatively, earlier presence might be treated as a reliable cue that direct physical competition will occur. We did, however, detect a weak interaction between the presence/absence of competitors and focal male size ($P = 0.109$; which is statistically significant if the data are analyzed using a binomial error distribution: see Supplementary Material, Supplementary Appendix 1). This suggests that it will be worthwhile to investigate this effect more closely in a future study. It might indicate a weak but still biologically important effect of male size when considering the effect of physical male–male competition on male choice.

We have attributed the decline in the time males spent near the originally preferred females in stages 2 and 3 to a competitor effect. It is, however, possible that this arose due to a general temporal decline in preference for the larger female. Three lines of evidence argue against this interpretation. First, there was no decline in the time spent with the originally preferred female during the first and second half of stage 1 trials. Second, another study of *G. holbrooki* with a similar design to ours that included a “temporal control” found that males spent the same amount of time near preferred females in the equivalent of our first and third stage when not exposed to competitor males (Wong and McCarthy 2009) (i.e., males retained their original mating preferences for over 40 min). Third, we found no decline in time spent near the originally preferred females between stages 2 and 3.

Repeatability of mating behavior

We documented a significant repeatability ($r_T = 0.35$) in male mate choice before exposure to competitors. This supports the hypothesis that males maintain a preference for large females when there are marginal or no costs. Another study in *G. holbrooki* with 1 day between choice trials reported a lack of repeatability of male choice in a comparable visual choice test, but choice was repeatable when males directly interacted with 2 females (Hoysak and Godin 2007). Repeatability typically decreases rapidly with the interval between trials (Roberts and DeVecchio 2000; Bell et al. 2009) so the observed repeatability is noteworthy given the 14-day interval between measurements. Furthermore, female mating preferences generally show low repeatability (mean $r_i \approx 0.20$; Bell et al. 2009). Repeatability is an indicator of the maximum heritability of a trait (Boake 1989; but see Dohm 2002), suggesting that it might be more profitable to explore the quantitative genetics of male than female mating preferences. Importantly, however, after viewing a competitor, the repeatability of male choice for the originally preferred female was eliminated. The negative repeatability value for stage 2 is indicative of an increased variance in male mating preferences (Bell et al. 2009), or even a change in male preference toward the less preferred female.

Recently empirical studies have started to investigate how male–male competition shapes facultative changes in male mate choice (e.g., Wong and McCarthy 2009; Ziege et al. 2009) rather than simply assuming that males will avoid competitors. Our study showed that males make potentially adaptive facultative changes in mate choice based on an estimate of the future level of competition when attempting to mate with specific females. We found limited evidence that such mating preferences are related to male dominance status under competitive situations. In general, however, the predicted effects of size-based variation in male competitive ability on male choice were not observed (Barry et al. 2010; but see Franceschi et al. 2010). Our study highlights 2 issues. First, the need to better understand the exact form of competition between males, and the extent to which there are trade-offs between pre- and postcopulatory reproductive success (see Evans 2010). Differences in the direction on selection on male size driven by insemination rates, access to females, and sperm competitiveness could potentially confound the use of male size as a summary measure of male competitiveness. The assumption that larger males are superior competitors is, however, widespread in male mate choice studies. Second, although theoretical models predict facultative adjustment of male choice in response to competition, they make assumptions about availability of information to males. These assumptions might not apply in the field, especially in species where the local population composition varies so that the current and future level of competition for different quality females changes rapidly.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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