

Original Article

Context-dependent male mate choice: the effects of competitor presence and competitor size

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Differences in the intensity of male–male competition for high- and low-quality females affect their value as mates. This can favor the evolution of mating preferences that vary with inherent male competitiveness and/or context-dependent mate choice. In the eastern mosquitofish (*Gambusia holbrooki*) we investigated how a male's choice of mate is influenced by his absolute size when alone (baseline mating preference) and by the presence and relative size of a competitor (context dependent). In standard 2-choice mating trials, we compared the time in association with the larger of 2 females in: 1) the absence of a rival; 2) the presence of a same-sized rival, and 3) the presence of a different-sized rival. We predicted which female the focal male would choose based on his estimated reproductive success. In all 3 social contexts, large and small focal males spent significantly more time with large females, but large males had a stronger association bias, indicating an effect of male size (competitiveness) on male mating preference. In contrast, neither the presence of a competitor nor his relative size affected the time the focal male spent with the large female. There was therefore no evidence that males facultatively adjust mate choice decisions to avoid competitors. This suggests that males do not maximize their expected reproductive success in the context of the current social setting. *Key words:* eastern mosquitofish, *Gambusia holbrooki*, male–male competition, mating preferences, sexual selection. [*Behav Ecol*]

INTRODUCTION

Mate choice involves a trade-off between a lower mating rate (potential mates are rejected) and an increase in the value of those individuals that are accepted as mates (Jennions and Kokko 2010). Males often prefer to mate with larger more fecund females in experimental studies (Bonduriansky 2001). In general, however, male mate choice is not selected for when the interval between encounters with receptive females is long compared to the time until a male is able to mate again (e.g., replenish sperm) because choosiness sharply reduces a male's mating rate (Jennions and Kokko 2010). In contrast, when several mates are simultaneously available, being choosy does not lower a male's mating rate, and male mate choice is readily favored if females vary in their value as mates (Barry and Kokko 2010). Studies that offer males a simultaneous choice of females can therefore address how males assess the relative value of potential mates. It is difficult for a male to determine a female's value if she does not immediately fertilize eggs once chosen. Her value partly depends on how many additional competitors she will attract, as competitors reduce the likelihood of gaining fertilizations (Servedio and Lande 2006). This devaluation should, however, vary among males according to their ability to achieve fertilization under male–male competition, or to bear associated costs (e.g., risk of injury; Venner et al. 2010).

Theoretical models for the evolution of male mating preferences predict that selection will rarely result in all males exhibiting the same preferences because the mean value of a female declines with how many males she attracts (Servedio and Lande 2006; Servedio 2007). The available models predict a range of possible relationships between male competitive ability and the strength and/or direction of male mating preferences for larger females (models: Fawcett and Johnstone 2003; Härdling et al. 2004, 2008; Härdling and Kokko 2005; Rowell and Servedio 2009; Venner et al. 2010). The predicted relationship depends on the extent of variation in male competitive ability and female fecundity/quality, the interval between mate choice and fertilization, the mate encounter rate, population density, and the details of the models' underlying assumptions. The only consistent principle is that males should exhibit “prudent choice”, balancing the inherent profitability of mating with a given female against the likely effect of competition on their share of paternity per unit of mating effort (e.g., investment in guarding, courtship, or ejaculate). Consequently, even when several females are simultaneously available, solitary males might still show different mating preferences if males vary in competitive ability. In short, many models predict the evolution of context-independent (sometimes called “innate”) male mating preferences.

Variation in the immediate level of competition for specific females might also favor context-dependent mate choice (Rowell and Servedio 2009; Venner et al. 2010). Males can show phenotypic plasticity in mate choice in response to the actual presence of rivals (e.g., Candolin and Salesto 2009; Wong and McCarthy 2009; Franceschi et al. 2010). Many studies investigate how male–male competition alters female choice (Wong and Candolin 2005), far fewer test whether male choice changes in the presence of rivals and the effect of their relative competitiveness.

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The numerous assumptions underlying male choice models and logistical constraints on confirming them create a challenge when empirically testing specific models (Barry and Kokko 2010, p. 167). Simply showing that mate choice differs between males varying in competitive ability (usually measured as body size) is inadequate due to the many predicted outcomes. It is, however, still worthwhile testing whether males make choices that maximize their fitness in the immediate social context. This requires a system where one can estimate the relative number of offspring that a male will sire with each available female given the presence of rivals.

Here we investigate male mate choice for 2 simultaneously available females that differed in size, hence fecundity, in the eastern mosquitofish (*Gambusia holbrooki*). We initially ran trials in the absence of a rival to measure “baseline” male mating preferences (“innate” preferences in theoretical models). We then tested for context-dependent male choice by introducing a single superior, inferior, or matched competitor to see if this affected the focal male’s mate choice.

The study system

G. holbrooki occur at high densities and males incessantly attempt to inseminate females (e.g., Wilson 2005). It is common for several males to be exposed to several simultaneously available females that are all potential mates (Zulian et al. 1995). Previous studies suggest that solitary males preferentially associate with larger females (Bisazza et al. 1989; Hoysak and Godin 2007; Mautz and Jennions 2011). Males do not court, instead they “sneak mate” by swimming behind a female and then rapidly thrusting their gonopodium (a modified fin) toward her gonopore. Fertilization is internal and females mate multiply (Constantz 1989; Zane et al. 1999). When 2 or more males compete for a female, most mating attempts are by the largest male who is socially dominant (Hughes 1985; Bisazza and Marin 1995; Pilastro et al. 1997; Bisazza et al. 2001). The relative insemination success per mating attempt is, however, dependent on the male to female size ratio, which favors smaller males (Bisazza and Marin 1995; Pilastro et al. 1997).

In the current study, we estimated a focal male’s relative reproductive success when a rival is present by first estimating his relative share of mating attempts and then multiplying this by his estimated success per mating attempt. Male size differences were such that the larger male always gained the bulk of paternity if 2 males competed for the same female.

MATERIALS AND METHODS

Adult *G. holbrooki* were collected from Lake Burley Griffin, Ginnindera, and Bruce Ponds in Canberra, Australia. We used male association time in 2-choice trials to measure male mating preferences. This predicts actual mating attempts in *G. holbrooki* as males incessantly attempt to copulate (Wilson 2005; Agrillo et al. 2006; Dadda et al. 2008).

We compared how long a focal male spent in association with the larger of 2 females in: 1) the absence of a rival (“unconstrained mate choice” trials); 2) the presence of a same sized rival (“equal competitor” trials); 3) the presence of a different sized rival (“unequal competitor” trials). Individuals were categorized as either small (females: <25.7 mm, males <19.8 mm) or large (females >36.1 mm, males >25.5 mm). These thresholds are ~1 standard deviation (SD) below or above the mean for each sex based on 1787 wild-caught males and 2209 females (males: 18.1 and 24.7 mm; females: 25.2 and 37.3 mm).

In the equal or unequal competitor trials, we predicted the optimal mate choice by the focal male if males maximize their reproductive success in the current social context. To do this, we estimate the focal male’s offspring production if he competed

with the rival for a share of paternity in the brood of the more fecund female or, instead, relinquished this female and solely mated with the less fecund female. First, we estimated each female’s fecundity using data from wild-caught females (brood size = $1.164 \times \text{female standard length} - 15.96$, $F_{1,177} = 25.77$, $P < 0.001$, $n = 178$; 2 outliers were excluded: standardized residuals >4 SD). Second, if one male was large and the other small, we assumed that the large male would make 93% of all mating attempts when both competed for the same female (see Table 1 in Bisazza and Marin 1995). If both males were in the same size class, we assumed that they made the same number of mating attempts when competing for a female. (The alternate assumption that the slightly larger male made the majority of mating attempts did not change our predictions; see below.) Third, to estimate the proportion of mating attempts that were successful for each male, we used a regression from Bisazza and Marin (1995) that explained 77% of variance in insemination success with the male to female body size ratio. We assumed that a male’s share of successful mating attempts determine his relative share of paternity as male body size is unrelated to ejaculate size (Locatello et al. 2008). Fourth, we then predicted how many offspring the focal male would sire if he stayed with the larger female and shared paternity or switched to the smaller female and obtained complete paternity (i.e., we assumed that if one male associated with the smaller female, the other would stay with the larger female). The data on male reproductive success is presented as though females were virgins but is equivalent to assuming that the paternity assigned to previous mates is equivalent for small and large females.

We predicted that in “equal competitor” trials, the focal male would, on average, spend less time with an otherwise preferred larger female. In 36 of 40 trials, the fitness return was greater from the smaller female than sharing paternity in the larger female’s brood (Figure 1a,b). This prediction held whether the decision to switch was random (i.e., either male switches to the smaller female) or made by the smaller male (as the focal male was slightly smaller in 22 of 40 trials). In sum, we predicted focal males would mainly associate with the smaller female in about half the trials.

In “unequal competitor” trials, we predicted that a large male would always associate with the larger female because even if the small male only associated with her, the large male would still sire more offspring than if he only sired all those of the smaller female. We therefore predicted that a small focal male would always associate with the smaller female (estimated 15.3 ± 2.8 vs. 2.9 ± 0.6 offspring, $n = 20$), while a large focal male would always associate with the larger female (estimated 21.5 ± 4.4 vs. 15.3 ± 2.8 offspring, $n = 20$). Summary statistics are presented as mean \pm SD.

We have framed our predictions about male association patterns as if a male should exclusively associate with 1 female. Even if males move between females, however, they still apply if modified to become predictions about the relative amount of time spent with the larger female. A small focal male should still avoid a large competitor to maximize his insemination rate.

Experimental procedure

Fish were initially housed in single-sex 200 l tanks (15–20 individuals/tank). Three days before mating trials, males and females were individually housed in 1 l containers. Choice trials were conducted in a $58 \times 45 \times 10$ cm glass tank divided into a central compartment ($22 \times 45 \times 10$), where test males were released, and 2 end compartments ($18 \times 45 \times 10$) each housing a female. The outer walls were lined with black plastic to minimize disturbance. The inner dividing walls were clear Plexiglass to allow visual contact between the sexes. The tank was lit with an overhead light.

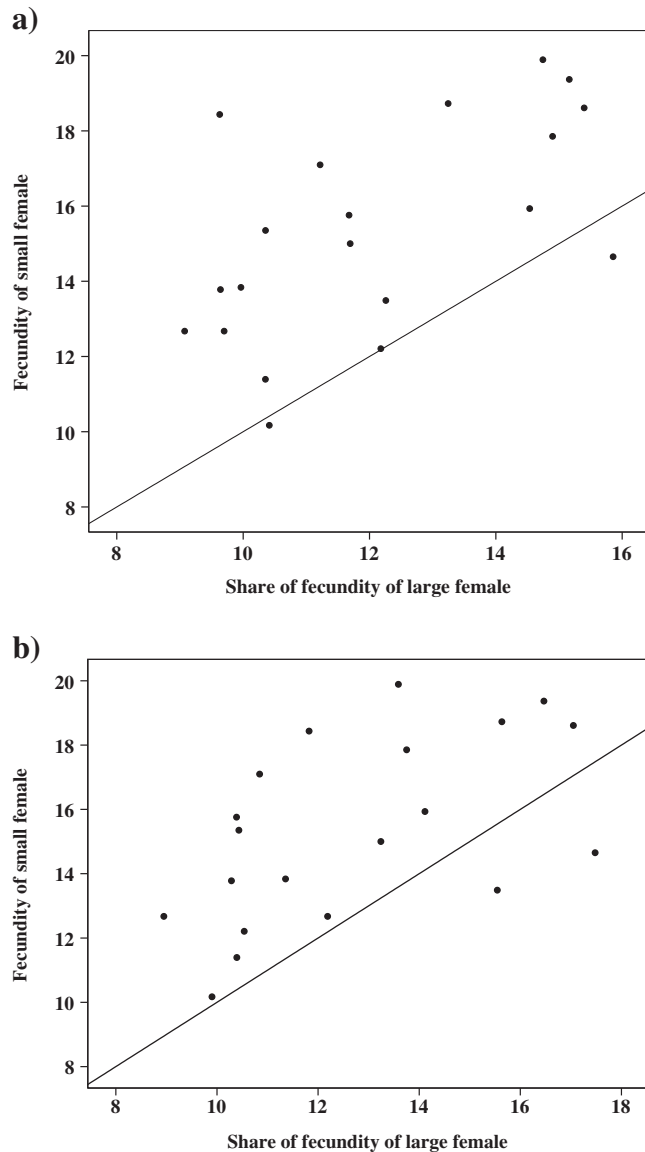


Figure 1
The expected fecundity of the focal male when he stays with the larger female and shares paternity with the competitor or switches to have exclusive access to the smaller female when the focal and competitor male are both (a) large or (b) small. These estimates of reproductive success were based on data from Bisazza and Marin (1995).

We tested 20 small (19.7 ± 1.0 mm) and 20 large (25.7 ± 1.0 mm) focal males. In each trial, one end compartment housed a small female (26.9 ± 2.4 mm) and the other, a large female (34.9 ± 4.1 mm). To start a trial, a focal male was placed in a clear container in the middle of the central compartment and allowed to acclimatize for 10 min (see Houde 1997; Langerhans et al. 2005; Deaton 2008b). The focal male (and, if present, his rival) was then remotely released. We videotaped males for 10 min and noted the association time with each female (time spent <5 cm from the front of her compartment).

Each focal male was used in a repeated measures design with 3 social treatments whose order was randomized. Each male was only tested once per day. The end housing the large female was alternated between trials. Each focal male was tested with the same female pair in all 3 trials. Each female pair was

used in 6 trials: 3 with a large and 3 with a small focal male. The large females were $30 \pm 12.4\%$ larger than the small females (range: 9–60%), corresponding to an estimated fecundity of 24.7 ± 4.6 versus 15.3 ± 2.8 ($N = 20, 20$).

Treatment 1: “unconstrained mate choice” trials

Only the focal male was present in the central compartment.

Treatment 2: presence of a small competitor

Each competitor male was used in a single trial. The mean size of competitors was 20.1 ± 0.6 mm (size matched to within 1 mm of the small focal males; 19.7 ± 1.0 mm) in “equal competitor” trials and 20.2 ± 0.8 mm in “unequal competitor” trials ($N = 20, 20$). Competitor males were wild-caught fish that were housed in the same way as focal males prior to trials. During the 10-min acclimatization period, both males were placed in the release container but were physically separated by a clear plastic divider. Both males remained free swimming in the tank for the entire trial.

Treatment 3: presence of a large competitor: as for treatment 2

The mean size of large competitors was 25.5 ± 1.4 mm in “equal competitor” trials (size matched to large focal males; 25.7 ± 1.0 mm) and 24.6 ± 1.0 mm in “unequal competitor” trials ($N = 20, 20$).

Statistical analysis

The key response variable is the relative time spent with the larger female (time with larger female/total time with females), arcsine square root transformed to meet parametric assumptions. We used a general linear mixed model (GLMM), with focal male and female pair identity as random factors and social treatment, focal male size class, order, and the female size ratio (large/small) as fixed factors. We initially fit a model that included all interactions between fixed terms, and then sequentially removed nonsignificant higher interactions to generate a final model (Crawley 2002). For ease of presentation, we retained all 2-way interactions and main effects regardless of their significance. The final model with only significant terms produced almost identical results. Random terms were retained as part of the experimental design (Crawley 2002). We ran 2 a priori planned orthogonal comparisons to test whether male preferences differed in the presence/the absence of a competitor (treatment 1 vs. 2 and 3) and whether it depended on the relative size of the competitor (treatment 2 vs. 3). We also ran a GLMM with total time spent associating with both females as the dependent variable using the same approach. If total time does not differ between treatments then tests for variation across treatments in the proportion of time and the total time spent with the large female are equivalent.

To test whether focal and competitor males independently associated with females, we ran a GLMM with a third dependent variable: the difference between the observed and expected proportion of the trial spent together in association with a given female. The expected value is the product of the proportion of the trial spent with a given female by each male (i.e., if the position of one male does not affect that of the other male). The model was run as described above except that female size class was a fixed factor. The key test is whether the intercept is greater than zero (i.e., observed time together is greater than expected).

4 of 120 trials were excluded from analyses as their standardized residuals were >3 SDs from predicted values in all 3 analyses. In these trials, a male (3 focal, 1 competitor) spent $<2\%$ of his association time with the larger female. The next lowest value was 16% ($N = 200$ males). Models were run in SPSS 17.0 with $\alpha = 0.05$ and two-tailed tests.

RESULTS

Time with larger females and social treatment

On average, large and small focal males both spent significantly more than 50% of their association time with the larger female (model estimates: small male: 57–73%, large male: 68–82%; range is 99% confidence interval [CI] so $P < 0.01$), but larger males had a stronger preference than small males ($F_{1,82} = 5.588$, $P = 0.020$). The proportion of time spent with the large female also increased significantly with a greater size difference between the 2 females ($F_{1,18} = 13.436$, $P = 0.002$), strengthening the claim that males attend to female size. In this, and all other analyses, trial presentation order and all 2-way interactions were nonsignificant.

Contrary to our predictions, the proportion of time spent with the larger female did not differ among the 3 social treatments ($F_{2,82} = 1.369$, $P = 0.260$; Figure 2). Specifically, the proportion of time the focal male spent with the larger female did not decrease in the presence of a competitor ($F_{1,87} = 1.871$, $P = 0.175$), nor did it depend on the competitor's relative size ($F_{1,65} = 1.171$, $P = 0.283$; Figure 2).

There was also no effect of social treatment on the total time the focal male spent associating with females ($F_{2,60} = 1.161$, $P = 0.320$). Neither the presence of a competitor ($F_{1,68} = 1.998$, $P = 0.162$) nor his relative size ($F_{1,27} = 0.181$, $P = 0.674$) had an influence. The size difference between females did, however, have a marginally nonsignificant positive effect on the total time spent with females ($F_{1,18} = 4.281$, $P = 0.053$). Finally, large focal males spent significantly more time than small focal males associating with females ($F_{1,16} = 12.087$, $P = 0.003$; 99% CI: large males: 503–563 s; small males: 450–509 s).

Male–male association

Males did not avoid each other and they actually spent significantly *more* time together associating with the same female than expected by chance ($F_{1,32} = 54.311$, $P < 0.001$; expected $39.5 \pm 15.5\%$ of the trial, observed: $49.1 \pm 17.6\%$; $N = 80$ trials).

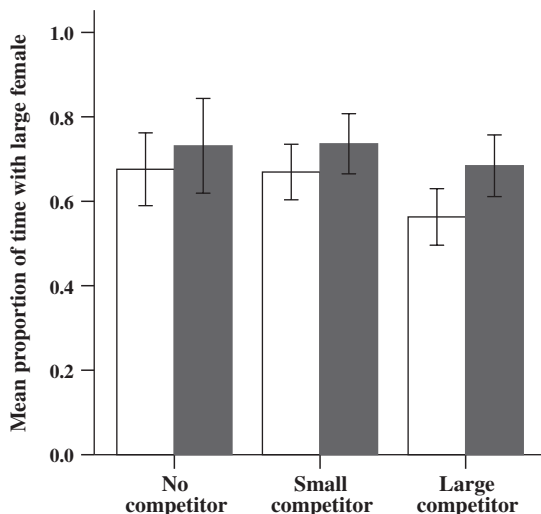


Figure 2

Raw data showing proportion of time spent in association with large females for small (white bars) and large (gray bars) males across each of the 3 social treatments; 1) competitor absent, 2) in the presence of a small competitor, and 3) in the presence of a large competitor. Error bars represent 95% CI.

DISCUSSION

Baseline male mating preferences

Both large and small male *G. holbrooki* preferentially associated with larger females. This is corroborated by the strong positive relationship between the proportion of time spent with the larger female and the magnitude of the difference in female body size. Presumably, males can better distinguish between more disparate sized females (see Bisazza et al. 1989), and increased discrimination is also favored due to the greater difference in fecundity-related value of the 2 females. Our results support previous studies showing that male *G. holbrooki* prefer larger females (Bisazza et al. 1989; Hoysak and Godin 2007; but see McPeck 1992). This male preference has also been reported in other poeciliids (references in Hoysak and Godin 2007; Deaton 2008a; but see Ala-Honkala et al. 2010). There was, however, evidence that the strength of this preference varied with male size. Larger male *G. holbrooki* spent significantly more time than smaller males with the larger of 2 females (see also Mautz and Jennions 2011; for another example in poeciliids, see Basolo 2004). A weaker preference for large females by smaller, less competitive males is consistent with the predictions of several theoretical models. Such a finding does not, however, offer strong support for any specific model because almost every possible relationship between male competitiveness and strength of preference for larger females has been predicted depending on the model parameter settings (e.g., Härdling and Kokko 2005). Even so, our findings support the broader assumption that male competitiveness affects their baseline mating preference for females that differ in fecundity. The obvious next step is to test whether smaller males have greater reproductive success when they mate with smaller rather than larger females when the sexes interact at natural densities.

Context-dependent male mate choice

Focal males did not appear to maximize their reproductive success based on the current level of competition. Specifically, there was almost no decline in either the mean time or proportion of time spent with the larger female in the presence of a competitor, even when he was larger than the focal male and therefore would gain the bulk of paternity with her (Figure 2). The relative size difference between females had a marginally nonsignificant effect on the total time in association with females. This is probably because a greater size disparity makes it easier for males to identify the larger female so that they spent less time traveling between females. Intriguingly, males showed a significant tendency to stay together when associating with a female. This refutes our prediction that males will avoid competitors to maximize their reproductive success. Although nonsexual shoaling responses cannot be fully eliminated as an explanation for the observed association patterns, they do not alter our main conclusions for 3 reasons (also see Hoysak and Godin 2007). First, our results agree with studies showing that male *G. holbrooki* generally prefer larger females (Bisazza et al. 1989; Hoysak and Godin 2007; Deaton 2008a). Second, male *G. holbrooki* are continually sexually active (e.g., Wilson 2005, p. 1389) and, in our study, males performed characteristic sexual behaviors (e.g., extending their gonopodium downward). Third, even if male responses are partly based on shoaling preferences (i.e., associate with a rival to be in a larger group), males ultimately still attempt to mate with the females with whom they associate. Shoaling decisions are part of, rather than distinct from, context-dependent mating preferences. Interestingly, however, the benefit of being in a large group has not been considered in theoretical models of male mate choice.

To date, only a few appropriately designed experiments have tested whether male choice is facultatively adjusted in response to the immediate level of mating competition. Some studies show that competition affects mate choice (e.g., Candolin and Salesto 2009; Mautz and Jennions 2011), while others do not (e.g., Franceschi et al. 2010). More studies on a range of species are needed to identify those situations that favor plasticity in choosiness.

Why did competitors have no effect on male choice?

Males have been shown to adjust their mate choice in response to the current level of competition to maximize their reproductive success (e.g., fish: Candolin and Salesto 2009; Wong and McCarthy 2009; spiders: Bel-Venner et al. 2008). So why did neither relative competitor size nor presence affect male choice in *G. holbrooki*? Indeed, why did males often increase the level of competition by simultaneously associating with the same female? We offer 4 testable suggestions.

First, given temporal fluctuations in the number of competitors per female, the optimal male strategy might involve rules of thumb. This can lead to suboptimal mate choice when a specific mating context is viewed in isolation. This could include baseline preferences for specific female types so that males continue to court a female that has attracted competitors, rather than switch to a currently solitary female (Jordan A, Kokko H, personal communication). If the current number/identity of competitors is poorly correlated with the eventual level of competition to fertilize a female's eggs (see next point) then it is less likely to influence male mate choice. This can be tested by determining the repeatability of competition for a given female over time.

Second, when 2 males pursue the same female, this might increase their mean absolute insemination rate (Stoltz et al. 2009). Even if the smaller male gains a lower share of paternity, his absolute insemination rate might still be higher than when pursuing a female alone. Female *G. holbrooki* mate multiply and store sperm (Zane et al. 1999), so competition can extend beyond immediate competitors. This explanation can be tested by comparing the insemination success of solitary and paired males and, if necessary, revising predictions about reproductive success accordingly.

Third, factors other than the number of offspring sired might affect male fitness. For example, larger females often produce bigger offspring that might have greater reproductive value (Marshall et al. 2010). In *G. holbrooki*, larger females produce larger offspring (Livingston J, unpublished data). Similarly, large females might have greater survivorship thereby allowing a male to sire more offspring.

Fourth, other fitness components might be elevated due to benefits of being in a larger group (e.g., lower risk of predation; Krause and Ruxton 2002). A sufficiently strong trade-off between lower mating competition and higher mortality might favor males associating with competitors.

CONCLUSIONS

Theoretical models predict that male choice is strongly influenced by the level of male–male competition. Contrary to expectations, we found that male *G. holbrooki*, regardless of competitive ability, associated with larger females, irrespective of the presence of rivals. The generality of this finding will require tests on other species to investigate how the presence of rivals and relative social dominance affect male choice.

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