

Mate choice in female convict cichlids (*Amatitlania nigrofasciata*) and the relationship between male size and dominance

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Abstract We examined how male size and fighting ability influence a female's mate assessment process and her eventual mate choice in the monogamous convict cichlid, *Amatitlania nigrofasciata*. Females always chose the larger of two males when they were allowed to see a larger male next to a smaller one and when a larger male defeated a smaller one in a fight. They did not differentiate between large and small males when they did not see the two males together nor did they choose a dominant over a subordinate male when both were the same size. We suggest that females select on the basis of male size because it is a better predictor of both direct and indirect benefits (i.e., future competitive interactions and foraging ability) than dominance behavior only. Despite selecting one male over the other early in the courtship period, females continued to visit both males until spawning. Our evidence suggests that this assessment behavior more closely resembles a bet-hedging tactic rather than the female's indecision as to which male will be her mate.

Keywords Mate choice · Mate competition · Intrasexual competition · Monogamy · Cichlidae

Introduction

In many systems, intra-sexually selected traits are typically reinforced by inter-sexual selection. That is, the traits which allow an individual to out-compete their own sex for access to resources are the same traits that attract mates (reviewed in Andersson 1994). Size is often such a trait; large individuals out-compete small ones for resources and large individuals are typically viewed as more attractive by the opposite sex (reviewed in Andersson 1994). Despite the advantage of larger size in these species, some studies have reported that when male–male competition is removed, females often do not prefer the largest of available males. For example, Peterson et al. (1999) observed that in brown trout (*Salmo trutta*) male–male competition often precedes over female mate preference for large adipose fins. Although large variegated pupfish (*Cyprinodon variegates*) males exclude smaller males from maintaining prime reproductive territories, females often mate with the smaller of the available males when male–male competition is removed (Draud and Itzkowitz 2004). Forsgren (1997) observed that dominance is based on size in male sand gobies (*Pomatoschistus minutus*) but when male–male competition is removed, females preferred superior parents regardless of whether they were the dominant or subordinate male. Similarly, in water striders (*Aquarius remigis*), larger males are able to compete for access to females but females prefer smaller males (Sih et al. 2002). These studies suggest that traits which allow males to out-compete other males for access to females can oppose the traits that females prefer (for review see Qvarnström and Forsgren 1998).

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This seemingly paradoxical relationship between intra and inter-sexual traits may be caused by obscuring the female's trait-selection process. For example, removing male–male competition might remove the importance of male size to females thus causing females to mate randomly or select an alternative male trait. That is, females might only recognize the benefit of large males if they directly observe these males dominating smaller males. For example, in bearded tits (*Panurus biarmicus*), females appear to incite male–male competition in order to select the highest quality male (Hoi 1997). Here, using the convict cichlid fish (*Amatitlania nigrofasciata*), we test the relative importance of male size and competitive ability on female mate choice.

Within convict cichlids (as with most teleosts) size is directly correlated to fighting ability (Koops and Grant 1993). Most studies on convict cichlids also verify that females benefit from mating with a larger male. For example, under field conditions, Wisenden (1994) observed that large pairs raise a higher percentage of young to independence than small pairs, suggesting that larger size incurs an advantage. Gagliardi-Seeley and Itzkowitz (2006) further observed that it is the size of the male that determines the ability of a pair to clear its territory of offspring predators. Although larger males do confer a benefit, there is contradictory evidence regarding whether or not females select males based on size. In two relatively similar designs, Noonan (1983) and Santangelo (2005) tested female choice by presenting a female with the choice of spawning with one of two visually isolated males (i.e., the female had at least visual access to both males and males were unable to see one another). Noonan (1983) observed that females choose the larger of two males while Santangelo (2005; see also Santangelo and Itzkowitz 2004) found that females did not. Although there were several differences among these two designs (see “Methods”), one difference seems especially important; Noonan (1983) used males that differed in size to a greater extent than in Santangelo (2005). For this reason, here we used the same design as Santangelo (2005) but used size differences comparable to Noonan (1983).

We also examined whether females select dominant males independent of any size difference. In other species, females apparently derive little benefit from mating with dominant individuals and thus it is not surprising that these females do not select the dominant male when given the opportunity (see review by Wong and Candolin 2005, but see Shapiro and Dewsbury 1986). Some studies imply that when females do select dominant males, they choose based on signals correlated with dominance, not the competitive ability directly. Logically, when females do not choose dominant males, their preferences should be for traits unrelated to male dominance (e.g., Peterson et al. 1999;

Stapley 2008; also see Forsgren 1997). In convict cichlids, van Breukelen and Draud (2005) observed that females are more likely to “divorce” (i.e., switch mates after establishing a pair bond) after seeing their mate physically interact with a larger male. However, male size in the absence of this brief interaction did not influence divorce rate, suggesting that size as a cue alone is not enough for a female to judge competitive ability. For this reason, we examined the role of male dominance on female choice with and without a substantial size difference between males.

Finally, we examined how male size and dominance influenced female mate assessment behavior. Santangelo (2005) observed that when given a choice convict cichlid females quickly show a preference for one of two males but continue to visit the rejected male until spawning. He proposed that this was a bet-hedging tactic that gave the female a readily available mate in case her selected male became unavailable. If bet-hedging is a mate-choice tactic in this system, we hypothesize that females will continue to visit rejected males at a rate independent of any difference between males. For example, if females show a clear preference for a larger male while showing no preference for a dominant male, she should continue visiting a smaller male and a subordinate male at the same rate. Alternatively, if visiting these other males is caused by indecision (e.g., the size differences between the males are too small for the female to decipher), increasing the differences among males should cause females to reduce the visits to less preferred males (Luttbeg 1996). Few empirical studies have examined how male differences influence female assessment behavior but Kvarnemo and Simmons (1999) observed that male bushcrickets (*Kawanaphila nartee*) more quickly reject females with increasing differences perhaps indicating that our alternative hypothesis is more likely.

Methods

All replicates for this experiment were conducted at Lehigh University. The fish used in this study were a combination of individuals purchased from local pet suppliers and individuals bred in the laboratory. Previous studies have shown that there are no discernable behavioral differences between the populations from these pet suppliers and natural populations (Bockelman 2004). All fish were housed in same-sex groups in 473-l aquaria that were maintained at 20°C ($\pm 2^\circ\text{C}$). All fish were on a 14 L:10 D photoperiod and fed daily with commercial trout food.

Experimental tanks (265 l) were divided into three equal sized areas (Fig. 1). The center area was designated as the “neutral area” while the two side areas would eventually

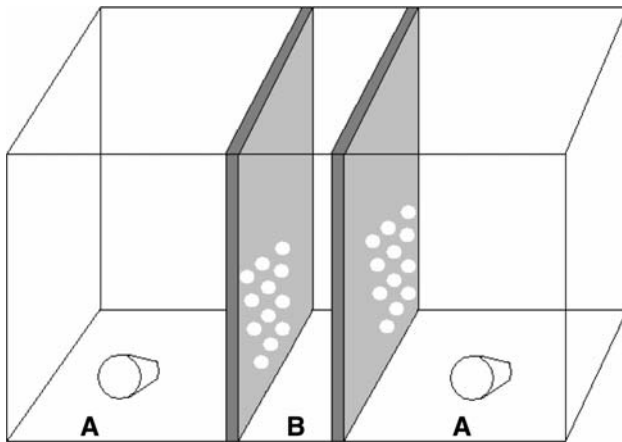


Fig. 1 Diagram of the female choice experimental tank. *A* indicates the male compartments and *B* is the neutral area

receive one male each. Opaque dividers separating the neutral area from the male compartments contained small holes that allowed a female to enter each male compartment but prevented the males from leaving their respective areas. For this reason, females were between 50 and 62 mm in total length, all small males were between 60 and 72 mm, and all large males were between 80 and 92 mm. Females were always 10 mm (± 2 mm) smaller than the smallest male in a given choice test. Each male compartment contained a flowerpot for a breeding site and an air stone.

This study contained four different treatments:

- no visual comparison: large versus small male;
- visual comparison: large versus small male;
- status comparison: equal size dominance versus subordinate male; and
- status comparison: large dominant versus small subordinate male.

In the no visual comparison: large versus small male treatment, each male was placed directly into the side male compartments of the experimental choice tank (Fig. 1). These males differed in size by 20 mm (± 2 mm). To avoid side bias, the sides in which the large and small males were placed were alternated for each replicate.

The visual comparison: large versus small male treatment began with the two different sized males being placed each in their own transparent box within the neutral area. Males were placed side by side with opaque black plastic separating them so they could not see each other; however, the female was able to see both males at the same time. After 4 h, the males were removed from their boxes and each placed in a side compartment (Fig. 1).

The status comparison: large dominant versus small subordinate male treatment began with placing the female in a transparent box in the neutral area and two males, one

2 cm larger than the other, also placed in the neutral area. Invariably, aggression occurred between the two males. We considered an individual a dominant male when he chased his opponent eight or more times without retaliation. Once a dominant male was determined, we separated the males into the side compartments as described above.

In the equal size: dominance versus subordinate male treatment, males were less than 5% different from each other in total length, because previous work has shown that less than 7% total length difference in convict cichlids can be considered equal size competitors (Leiser and Itzkowitz 1999). Similar to the large dominant versus small subordinate male test, two males placed in the neutral area were allowed to interact. Females again observed these fights from inside a clear box. When a dominant individual was declared, the males were placed in separate side compartments (Fig. 1).

Once males were confined to their own compartment, we recorded the number of days it took for the female to spawn with a male. As in previous experiments using the “Santangelo Design”, if the female did not make a choice within 21 days, the trial was terminated and the female was designated as not making a choice. In addition, prior to the female making her choice, we recorded her location in the experimental aquaria about five times a day. From these data, we calculated the percentage of times we observed the female in each compartment.

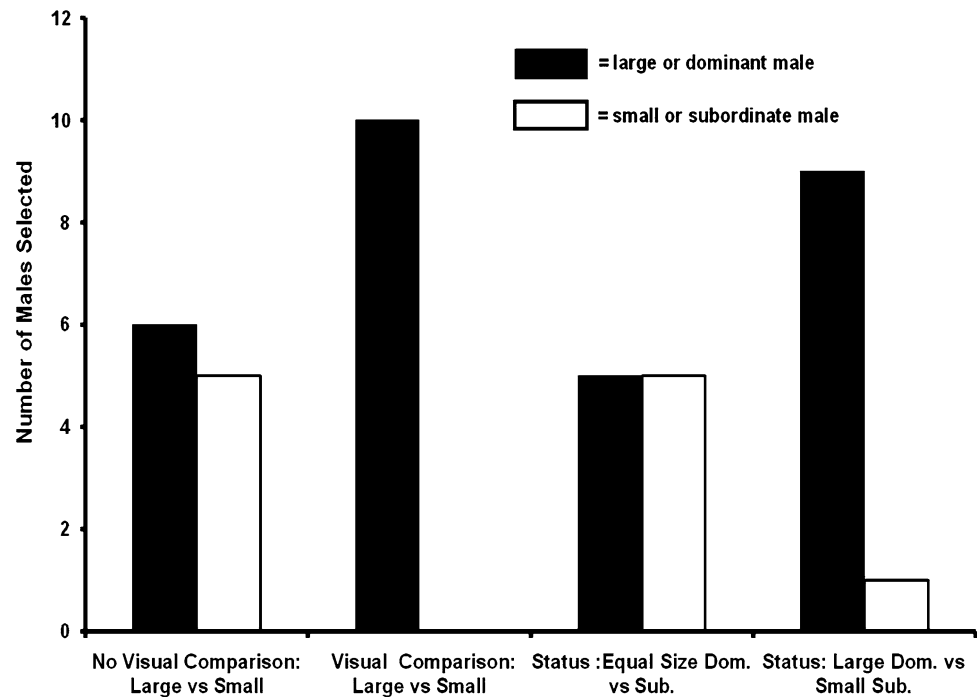
Statistics

Non-parametric tests were used due to the departures from parametric assumptions by the data. A binomial test was used to test the frequency with which large or small males were chosen (Zar 1999). The Wilcoxon matched-pairs test was used to test for differences in the frequency with which the female was observed to be with selected males versus rejected males in all circumstances. Finally, the Kruskal–Wallis ANOVA test was used to determine if rejected males were visited equally under all conditions. All statistical tests were conducted using the computer program Statistica.

Results

There was no difference in the number of days it took females to make a choice between the four experimental groups (ANOVA, $df = 3$, $F = 1.63$, $p = 0.19$). On average, it took females 14.2 (± 1.09) days in the no visual comparison: large versus small treatment ($n = 11$), 15.6 (± 1.06) days in the visual comparison: large versus small treatment, 11.8 (± 1.8) days in the status comparison: equal size dominant versus subordinate treatment ($n = 10$), and

Fig. 2 The number of males chosen by a female for each experimental treatment



11.7 (± 1.9) days in the status comparison: large dominant versus small subordinate treatment ($n = 10$).

Figure 2 illustrates that females did not choose large males more often than small males (no visual comparison: large versus small, $x = 6$, $n = 11$, $p > 0.99$) unless they observed both males together (visual comparison: large versus small, $x = 10$, $n = 10$, $p = 0.0019$). Females did choose large dominant males over small subordinate males after observing the fight (status comparison: large dominant versus small subordinate, $x = 9$, $n = 10$, $p = 0.021$). They did not differentiate between equal-sized dominant males and subordinate males (status comparison: equal size dominance versus subordinate, $x = 5$, $n = 10$, $p > 0.99$) after observing the fight.

Similar to the assessment patterns described in Santangelo and Itzkowitz (2004) and Santangelo (2005), females showed their mate preference by spending more time with their eventual mate. This preference usually appeared within a few days of establishing the replicate, although spawning often occurred many days later. Figure 3 gives the percentage of observations of the female with the selected and rejected males in all tests and illustrates that the female always spent more time with the male she selected (no visual comparison: large versus small: $N = 11$, $T = 1.5$, $z = 2.8$, $p = 0.005$; visual comparison: large versus small: $N = 10$, $T = 0.00$, $z = 2.80$, $p = 0.005$; status comparison: large dominant versus small subordinate: $N = 10$, $T = 2.00$, $z = 2.59$, $p = 0.009$; status comparison: equal size dominance versus subordinate male: $N = 9$, $T = 3.0$, $z = 2.31$, $p = 0.02$). There was also no significant effect of treatment on the amount of time

females spent with rejected males (Kruskal–Wallis ANOVA: $H = 1.40$, $df = 3$, $N = 40$, $p = 0.705$). Thus, females did not spend more or less time with any of the different types of rejected males.

Discussion

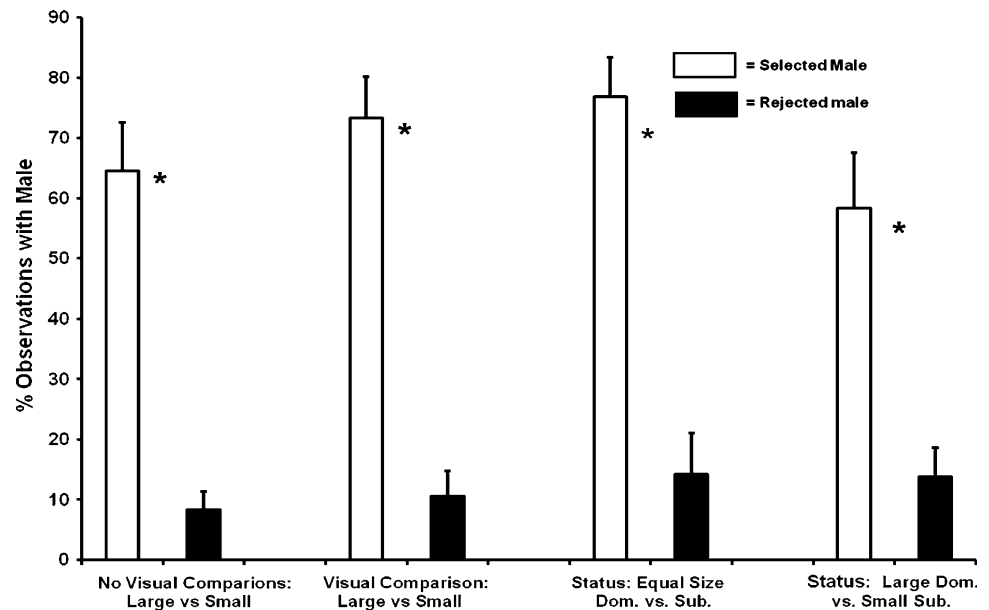
In convict cichlid fish, females do benefit from mating with the larger of available males. For example, previous studies have shown that pairs with larger males are:

1. superior competitors for breeding sites (e.g., Itzkowitz et al. 1998);
2. more effective at repelling offspring predators (e.g., Gagliardi-Seeley and Itzkowitz 2006); and
3. raise more offspring to independence (Wisenden 1994).

Given these benefits, it is not surprising that females preferred to mate with the large male after he dominated a smaller male. We disproved the hypothesis, however, that females were selecting for the more dominant male, because females did not preferentially select the dominating male when he was similar in size to the one he subordinated.

Although size is correlated with ability to win fights in teleosts, particularly convict cichlids (Koops and Grant 1993), size might be indicative of other characteristics important to the female. For example, females that select on the benefits of dominance and not size require that the dominant individual keep encountering the same subordinates and/or continue defeating new opponents. Convict

Fig. 3 The mean percentage number of observations (+SE) of the female with the selected and rejected male. The *asterisk* indicates significant difference. See “Results” for further details



cichlids live in streams with hundreds of individuals making repeated encounters with only the same subordinates unlikely. Some studies have shown that prior aggressive interactions can influence the outcome of subsequent interactions (i.e., winners keep winning; for review see Jackson 1991), but this may be time-sensitive. In pumpkinseed sunfish (*Lepomis gibbosus*), winners of an aggressive encounter were more likely to win their next encounter only if it happened within the next 15 to 60 min (Chase et al. 1994). This would limit the benefit of selecting solely on the basis of winning a single encounter, especially when pair bonds are prolonged, as in the convict cichlid. Perhaps such direct benefits (i.e., resource defense or acquisition) are of lesser importance than the indirect benefits (i.e., good genes) gained from mating with the largest available male. That is, large size may be indicative of a male's ability to avoid predation and find sufficient food, and thus suggests superior quality. In a recent review on mate choice, Kokko et al. (2003) discuss that, even in systems where males provide direct benefits, it is likely that indirect benefits also have a role.

Our results also illustrate that the critical factor for a female selecting a large male was seeing him alongside a smaller one, not necessarily dominating the smaller male. This suggests that the size assortative mating seen in convict cichlids is not due to females preferring males of a given size class (e.g., based on her own size). It is unclear why she would need to see the two males in close proximity before consistently selecting the larger male but this may reflect the need to select the largest male that is immediately available. In Costa Rican streams, females are often found in large heterosexual groups (personal observation) and thus a female may not have the opportunity to return to males that were inspected previously. Instead,

they may assess males that are immediately available and initiate courtship and pair formation among these males. This may explain the differences between the Santangelo design (e.g., Santangelo 2004, 2005) and the Noonan Design (Noonan 1983). Although both designs appear to allow for sequential assessment, the Noonan Design allowed females to quickly swim back and forth while viewing both males while the Santangelo design required that females enter each male's compartment and spend time physically interacting with that male. This delay in assessing each male may have interfered with the female's ability to judge size differences resulting in her choosing males based on other characters.

We found no support for the hypothesis that females continue to visit rejected males based on female indecision. We predicted that, if females were repeatedly visiting rejected males because of indecision, this indecision should be reduced when females were offered a male that was clearly preferred by all females versus males who possessed traits that did not influence female choice (e.g., dominance in the absence of a size difference between males). In all four experiments, there was no significant difference in the proportion of time females spent with a rejected male. For this reason, the bet-hedging hypothesis remains a viable explanation.

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