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Male mate preference and size-assortative mating in convict cichlids: A role for female aggression?



A.N. Bloch^{a,*}, V.J. Estela^a, J.M. Leese^b, M. Itzkowitz^a

- ^a Department of Biological Sciences, Lehigh University, Bethlehem, PA, USA
- ^b Department of Natural Science, DeSales University, Center Valley, PA, USA

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ABSTRACT

Many monogamous species demonstrate size-assortative mating patterns within natural populations. To better understand the role of intersexual selection in this process, we examined the effect of male preference for female body size in the convict cichlid (*Amatitlania siquia*). We provided males with a choice between females that differed in size, relative to each other and in relation to the focal male. Based on previous work, we expected males to prefer the largest available female mates across all treatments. Surprisingly, males spent more time near the smaller of two available females, but only when the other female was larger than the male. Additionally, males spent little time with either of two potential female mates when both females were larger than the male. We hypothesized that while males might prefer the largest of available females, female behavior might limit males from acting on this preference. To test this, males were force paired with a smaller or larger female. Pair formation only occurred when the female was smaller than the male, and females that were larger than their male counterparts showed significantly more aggression when compared to smaller females. Together, these data suggest that in the absence of intrasexual competition, male mate preference for large females in convict cichlids might be limited by female aggression.

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1. Introduction

Assortative mating by size, defined as a positive correlation between male and female sizes of mate pairs within a population (Arnqvist et al., 1996; Crespi, 1989; Rowe and Arnqvist, 1996), is a common non-random mating pattern in nature (Crespi, 1989; Ridley, 1983). Because size-assortative mating affects genetic demographics (Coyne and Orr, 2004), it can profoundly impact a population's evolution (Arnqvist et al., 1996; Coyne and Orr, 2004; Crespi, 1989). Despite numerous descriptions of this pattern across a wide range of taxa (e.g. arthropods: Crespi, 1989; reptiles: Shine et al., 2001; amphibians: Lu et al., 2009; crustaceans: Bollache and Cézilly, 2004; birds: Helfenstein et al., 2004; mammals: Preston et al., 2005; fish: Rowland, 1989), it remains unclear how the mechanism of assortative mating acts to organize mate pairs (Arnqvist et al., 1996; Ridley, 1983).

To examine the process leading to size-assortative mating, we used the serially monogamous convict cichlid fish (Amatitlania siquia). This species forms pairs with males almost uniformly being larger than the females, in both the laboratory (Beeching and Hopp, 1999; Beeching et al., 2004; Santangelo, 2005; but see Leese et al., 2010) and the field (McKaye, 1986; Perrone Michael, 1978; Wisenden, 1994). This mating pattern seems to be influenced by both intrasexual competition and intersexual selection. Regarding the former, cichlid fish are highly aggressive, and within-sex conflicts prior to pair bond formation are common. Size has been shown to be an important factor in determining the outcome of these contests (Haley 1987), with the result being that the largest individuals of each sex generally win contests and are thus available to mate. If these contests are the main factor influencing pair formation, the observed size-assortative pairing in convict cichlids may occur simply because males have a larger maximum body size than females. As competitions occur, the largest male and largest females win contests leading to the formation of a pair bond, with the next largest of each sex doing the same, and the pattern continues throughout the population. In this scenario, intrasexual completion alone could drive size-assortative mating.

^{*} Corresponding author at: Department of Biological Sciences, Lehigh University, 111 Research Drive, Bethlehem, PA 18015, USA.

E-mail address: anb212@lehigh.edu (A.N. Bloch).

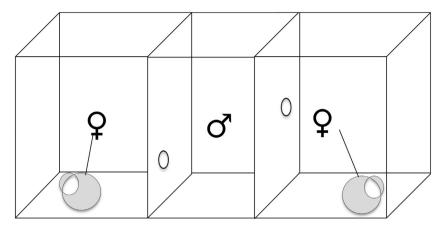


Fig. 1. Diagram of the male choice tank. On each side, a female was tethered to a small flower pot and were unable to leave their compartment. The central compartment ("neutral" compartment) initially held the male. The male had free-access into both female compartments via a small hold placed in the opaque dividers. See Methods for further details

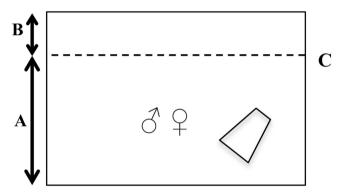


Fig. 2. Diagram of tank used in Experiment II. (A) The male/female (σ^n/Q) focal compartment (22.8 cm) with flowerpot. (B) intruder compartment (7.6 cm). (C) clear divider.

Intersexual selection, i.e. mate choice, has been shown to influence size-assortative mating in convict cichlids (Noonan, 1983; Beeching et al., 2004; Gagliardi-Seeley et al., 2009). Studies have primarily focused on female preference for large body size in males, but male preference for female body size has also been explored. Beeching and Hopp (1999) observed that convict cichlid males prefer to associate with the largest of available females, even if the female size exceeded their own, suggesting that male preference alone would not be responsible for male-larger size-assortative mating patterns in nature. This study, however, observed male preference when males could view females through a clear partition, which prevented individuals from physically interacting and reverse-size assorted pairs (i.e. female-larger) from actually forming. Whether the interaction and/or behavior of one or both individuals would impede or completely prevent female-larger pairs from forming is unclear. Leese et al. (2010) suggested this might be the case by demonstrating low rates of pair bond formation in convict cichlids when males were placed with females that were larger than themselves.

To more thoroughly examine these interactions in the convict cichlid, we observed male preference for potential female mates by allowing males to visit and physically interact with females in the

absence of direct intrasexual competition. We provided males with one of three treatments: (1) two females that differed in size, with the smaller female being size-matched to the male and the larger female being larger than both (2) two females size-matched to each other, but both larger that the focal male, and (3) two females size-matched to each other and the focal male. If intrasexual competition alone is responsible for pair formation (sensu Haley, 1987), we predicted that males would show a time-based preference for the larger of two females available, when females differed in size. When given the choice between size-matched females, we predicted that males would still show a preference, albeit a weaker one, for one female over another, and that this would occur regardless of whether females were larger than the male or not. If males did not show a clear preference for the larger of two females, when the female was larger than the male, or showed differences in preference patterns, when females were size-matched to each other but larger than the focal male, it might suggest that female behavior toward a male smaller than herself could impact or limit a male's preference.

To further explore this possibility, we also examined the behavioral interactions between males and females (*sensu* Leese et al., 2010) in a second 'no-choice' experiment. We placed a single male with a female that was either larger or size-matched together in a tank. We monitored aggression levels of the females in the pair to see if larger females treated males differently than size-matched females. We know from previous work that female-larger pairs are less likely to form, but this was the first attempt to determine if female behavior contributed to this result. We also observed whether male aggression levels were different when the female was smaller or larger.

2. Methods

The fish used in this study were a mixture of fish that were wild-caught and purchased through a distributor. All fish were separated by sex and maintained at $25\pm3\,^{\circ}$ C, on a 14:10 light:dark cycle. To avoid pseudoreplication, all fish were tested only once. All experimental procedures were conducted in accordance with Lehigh Institutional Animal Care and Use Committee protocol #176.

Table 1Mean total length of focal males and stimulus females for all treatments. Different letters within each treatment indicate significant differences (*p* < 0.05).

	Treatment 1A			Treatment 1B			Treatment 1C		
Total Length (mm)	Small Female	Male	Large Female	Large Female 1	Male	Large Female 2	Small Female 1	Male	Large Female 2
	63.76 ^a	63.76 ^a	73.88 ^b	71.72 ^b	61.74 ^a	71.78 ^b	64.2ª	64.2 ^a	64.2 ^a

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