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Conflicting preferences within females: sexual selection versus species recognition

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Preferences for mates within and between species are often harmonious, as traits that females prefer are usually more developed in conspecifics than heterospecifics. This need not be the case, however. When it is not, conflict between these arenas of mate choice can be resolved if females attend to different cues for each task. But this raises the potential for correlations among preferences to limit the opportunity for these two processes to operate independently. Here, we show that, within individual female pygmy swordtails (*Xiphophorus pygmaeus*), directional preferences for conspicuous ornamentation are inversely associated with discrimination against a sympatric heterospecific, *Xiphophorus cortezi*. Thus, mate choice among and within species need not be separate, independent processes; instead, they can be mechanistically intertwined. As a consequence, different arenas of mate choice can constrain one another, even when females assess multiple cues.

Keywords: mate choice; reproductive character displacement; Xiphophorus; *Poeciliidae*

1. INTRODUCTION

Mate choice depends on the evaluation and integration of multiple perceptual cues produced by potential partners. These cues, and their concomitant preferences, are often redundant, acting in concert to signal both within-species attractiveness as well as species identity [1]. Under some circumstances, however, sexual selection and species recognition can be in direct conflict. There are numerous examples of reproductive character displacement of both male traits and female preferences among sympatric species (reviewed in [2]). Several studies have shown that directional preferences for elaborate male traits can be lost or reduced in populations where these traits are shared by sympatric heterospecifics [3–5].

When such a trade-off arises in a single trait, females can avoid a conflict between intra and interspecific mate choice by attending to multiple cues [6,7]. For example, females in a population of pygmy swordtails, *Xiphophorus pygmaeus*, prefer males of larger size [8]. Indeed, females show a preference for the sympatric *Xiphophorus cortezi* when species-typical vertical bar patterns and pheromone cues are experimentally removed; however, females show strong preferences for conspecifics when presented with these additional traits. By attending to multiple cues, therefore, females avoid a compromise between sexual selection and species recognition.

Female responses to multiple cues, however, may be constrained by phenotypic correlations among multiple preferences [9]. Correlations among female responses across contexts could be owing to any number of factors, including pleiotropic effects of the same genetic locus, linkage disequilibrium among underlying loci, sensory trade-offs or cognitive limits on attention. The magnitude and the direction of these correlations are critical to the evolutionary relationship between species recognition and sexual selection [10].

In this study, we addressed these correlations by examining individual variation in female preferences in the pygmy swordtail *X. pygmaeus*. In this species, males are usually small, inconspicuous and lack courtship, in contrast with the large, ornamented, courting males of other swordtail species. Nevertheless, females show preferences for sexually dimorphic visual traits that have been secondarily lost in their own species, choosing large, courting *Xiphophorus nigrensis* males over conspecifics [11]. It is important to note here that *X. pygmaeus* and *X. nigrensis* are allopatric.

Xiphophorus pygmaeus is sympatric with another large, courting and ornamented swordtail, *X. cortezi* [12]. Females avoid *X. cortezi* males on the basis of multiple cues [7,13]. We sought to ask if 'hidden' preferences for traits of large size and courtship exhibited towards allopatric *X. nigrensis* could confound discrimination against large, courting sympatric *X. cortezi*. Specifically, we determined if hidden preferences for allopatric heterospecific males are negatively correlated with discrimination against sympatric heterospecific males. To do so, we quantified, within individual females, the strength of preference for *X. nigrensis* versus discrimination against *X. cortezi*.

2. MATERIAL AND METHODS

All fishes used were from stocks maintained in large outdoor tanks at the Brackenridge Field Laboratory, University of Texas, Austin, TX. Females had no prior experience with heterospecifics, either sympatric or allopatric ones. *Xiphophorus pygmaeus* were wild-caught or first-generation offspring of individuals collected at three localities (figure 1; about 30 adult individuals per locality per year) on the Río Huichihuayán, San Luis Potosi (SLP), Mexico; *X. nigrensis* males were from individuals collected at sites on the Río Choy, SLP and *X. cortezi* were from populations sympatric with *X. pygmaeus*. Fish were maintained in large, semi-natural populations at the Brackenridge Field Laboratory, University of Texas at Austin. To acclimatize fishes to the laboratory and to standardize sexual motivation [8], 30 days prior to testing, fishes were housed in groups, segregated by sex and species, in 40 l aquaria.

We used standard dichotomous choice tests [14] to evaluate whether responses to sympatric heterospecifics were correlated with preferences for large-size within-individual females. We used a 220 l aquarium, 120 × 32 cm and filled to a depth of 40 cm. The aquarium was divided along its length by Plexiglas dividers into two flanking sections 21 cm wide and a central section. This central section was further subdivided into left and right 'preference' areas 27 cm wide and a neutral area 23 cm wide. We placed males in opposite flanking sections and placed the female in a 12 cm diameter cylinder in the centre of the aquarium. We allowed animals to acclimatize for 10 min prior to testing. The cylinder was then lifted, allowing the female to move freely about the central section. A small clump of Java moss (*Vesicularia dubyana*) was provided for

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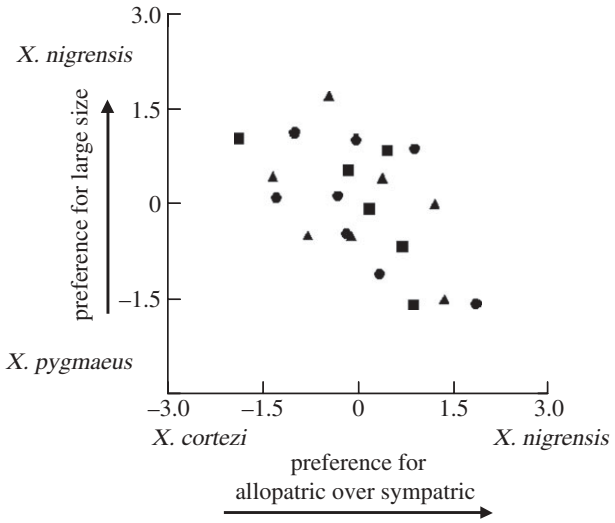

Figure 1. Individual female preferences for *X. nigrensis* versus *X. cortezi* and versus *X. pygmaeus*. Filled circles, Nacimiento; filled squares, Huichihuayán; filled triangles, Y-griega.

cover in the centre of the aquarium. The female's position (left, centre or right) was recorded for 10 min using a computer event-recording programme. A female was operationally defined as present in a section if her eye appeared in that section. The males were then switched to control for side biases, after which we repeated the acclimatization and testing periods.

We presented females with a choice between live *X. cortezi* and *X. nigrensis* males courting matched for size (standard length). Immediately before or afterwards, we presented the same *X. nigrensis* versus a smaller *X. pygmaeus* male. To correct for interpopulation variation in preference, we standardized each female's net preference as the *z*-score with respect to her population. We computed the Spearman rank correlation coefficient between net preferences in the two trials.

3. RESULTS

There was a significant negative correlation between preference for *X. nigrensis* over *X. cortezi* and preference for the same *X. nigrensis* over *X. pygmaeus* ($n = 21$, Spearman rank correlation coefficient $= -0.522$, $p < 0.01$; figure 1). Untransformed net preferences are shown in the electronic supplementary material, figure S1. We did not detect a difference in net preference among the populations for *X. nigrensis* over *X. pygmaeus* ($n = 21$, Kruskal–Wallis test statistic $= 0.303$, $p = 0.86$) or for *X. nigrensis* over *X. cortezi* ($n = 21$, Kruskal–Wallis test statistic $= 3.89$, $p = 0.14$). There was no effect of order on preference (paired *t*-test on preference for *X. nigrensis*: $n = 21$, $t = 0.10$, $p = 0.92$).

4. DISCUSSION

Species preferences and body-size preferences were correlated within females. Individuals that avoided *X. cortezi* relative to other heterospecifics showed a weakened preference for body size; that is, they were less likely to prefer the larger *X. nigrensis* over the smaller *X. pygmaeus*. At both population and individual levels, females that discriminated more against *X. cortezi* versus *X. nigrensis* were thus less attracted to the larger male *X. nigrensis* versus *X. cortezi*.

The genetics [9] and psychological mechanisms [6,15] underlying female response to multiple cues are key determinants of how between- and within-species preferences can interact. In *X. pygmaeus*, female assessment of multiple cues allows for rejection of sympatric heterospecifics despite directional biases for more-ornamented males [7]. Nevertheless, directional preferences covary with responses to heterospecifics. The ancestral bias for large size in *Xiphophorus* [16,17] compromises rejection of sympatric congeners with respect to allopatric ones, even when body size itself is uninformative; perhaps females with a strong-size bias simply fail to attend to other traits.

Secondary loss of directional preferences [16,17] may provide an opportunity for females to attend to more subtle and more complex cues in mate choice. In our study, a broadly permissive [16] preference for body size appears to be supplanted by a more refined assessment probably based on a combination of olfactory cues and higher order visual cues such as motor patterns, body shape and vertical bar morphology. Counterintuitively, the loss of a strong preference along one axis can lead to enhanced discrimination among complex signals (see [18]).

Within-individual covariation among behaviours, or 'behavioural syndromes', has garnered much recent attention [19]. Comparatively little attention has been paid, however, to how preferences for multiple traits covary among females [20]. Indeed, it is often assumed that preferences for different traits, especially in different modalities, are free to evolve independently. In evolutionary psychology, selection is often posited to favour domain-specific modules, specifically adapted to a particular task [21,22]; e.g. mate evaluation versus species recognition. Our results, however, suggest that choice behaviour is not independent across tasks, and that domain-general constraints may be important to behavioural evolution. Further studies of how individual females respond to suites of stimuli should prove fundamental to our understanding of how the psychological architecture of mate choice influences sexual selection and reproductive isolation.

The Institutional Animal Care and Use Committee of the University of Texas at Austin approved the experimental procedures.

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