



Sexual selection on the multicomponent display of black morph male *Girardinus metallicus* (Pisces: Poeciliidae)



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ABSTRACT

Sexually selected displays often include suites of integrated traits. Black morph males of the poeciliid fish *Girardinus metallicus* perform courtship and aggressive displays that exhibit their conspicuous yellow and black coloration. Body size, gonopodium size and ventral black area are correlated with intermale aggression, which is key for access to mates. A previous study showed that females may prefer dominant males prior to watching them fight; however, that result was obtained in trials that allowed for male-male interactions across partitions, and to date no study has uncovered the traits important in female choice. We performed a more comprehensive investigation of the multicomponent sexual display including measures of male yellow hue, saturation and brightness. We examined the behavior of size-matched males paired to maximize the difference in yellow saturation, and measured female choice exclusive of male-male interactions and chemical cues. We found no female preference for any traits in the multicomponent sexual display. Males with brighter and more saturated yellow coloration were more likely to be dominant, and dominant males courted and attempted copulations more. Our results suggest that yellow coloration is sexually selected; however, the courtship display requires further investigation because we did not identify targets of female preference, and we discuss possible explanations for this finding.

1. Introduction

Morphological and behavioral traits are often integrated into multicomponent sexual displays, a phenomenon that has received much attention in the literature (reviewed in Møller and Pomiankowski, 1993; Candolin, 2003; Hebets and Papaj, 2005; Lozano, 2009; Bro-Jørgensen, 2010; Rios-Cardenas and Morris, 2011). Although the production and assessment of sexual signals is costly (e.g., Zuk and Kolluru, 1998), possible explanations for the evolution of adaptive multicomponent displays include: 1) they constitute multiple messages with each trait signaling different, and sometimes conflicting (Rios-Cardenas and Morris, 2011), aspects of condition (Møller and Pomiankowski, 1993) or signaling quality to different receivers (Andersson et al., 2002); 2) they together indicate quality synergistically or redundantly, as backup signals (Jennions and Petrie, 1997); 3) different traits are important under different environmental conditions (Candolin, 2003; Cole and Endler, 2015); and 4) different traits reflect condition at different life history stages during an individual's lifetime (Møller and Pomiankowski, 1993). Given these multiple, sometimes competing hypotheses, understanding the functional significance of a

multicomponent sexual display requires examination of the integrated phenotype and its role in intra- and intersexual selection (Møller and Pomiankowski, 1993).

An investigation of sexual selection on multicomponent displays should involve assessment of mate choice independently of intrasexual competition, because the two processes may favor the same or different traits as described above, and because male-male competition may impact female choice. For example, male aggression may disrupt the ability of females to choose mates by promoting forced copulations, reducing courtship activity and decreasing the ability of females to view courtship displays (Wong and Candolin, 2005; Hibler and Houde, 2006; Miller and Svensson, 2014). Furthermore, if the males preferred by females are less successful in male-male competition, they may have reduced access to females (Kodric-Brown, 1992; Jennions and Petrie, 1997; Miller and Svensson, 2014), although this may be ameliorated by cryptic female choice (e.g., Pilastro et al., 2004; Firman et al., 2017). If male-male competition hampers the ability of females to assess male quality, then multicomponent displays may assist females in assessment by giving them more types of traits from which to choose (Candolin and Reynolds, 2001; Wong and Candolin, 2005; Miller and Svensson, 2014).

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Moreover, because males successful in competition are not necessarily of high quality in other ways, females may prioritize signals of other aspects of male quality over signals of competitive ability (Lozano, 1994; Jennions and Petrie, 1997; Candolin, 1999, 2003). Alternatively, male-male competition may facilitate female choice by allowing females to choose dominant males because they are of higher quality (Kodric-Brown, 1993; Berglund et al., 1996; Hunt et al., 2009; Miller and Svensson, 2014), or avoid very aggressive males to minimize harmful repeated mating attempts (Bierbach et al., 2013).

Girardinus metallicus is an endemic Cuban poeciliid with male-specific polymorphism: “normal morph” males are abundant, drably colored and sneak copulations without performing a courtship display (Farr, 1980; Kolluru et al., 2015), whereas black morph males are rare, conspicuously colored (black and yellow) and almost always perform a courtship display prior to attempting copulation (Lorenzen, 1996; Kolluru et al., 2014, 2015; Dadda, 2015). The courtship display consists of the male swimming beside or below the female while holding the gonopodium away from the body, expanding the dorsal fin and raising the head (Lorenzen, 1996; Kolluru et al., 2014). Males also display to each other during aggressive encounters, by holding the gonopodium away from the body and expanding the dorsal fin, but without raising the head (Kolluru, G.R., pers. obs.).

The courtship display of black morph *G. metallicus* appears to exhibit the ventral surface and gonopodium to the female, and the ventral black coloration is the most conspicuous difference between male morphs (to human eyes), leading Kolluru et al. (2015) to investigate sexual selection on ventral black area. They found no evidence for female preference based on ventral black area, although males with greater ventral black area had higher mating activity in the second of two direct interaction trials. Interestingly, males that females associated with in dichotomous choice tests went on to have greater mating activity when the fish were allowed to interact with each other directly. Because males that exhibited greater mating activity were also dominant, these results suggest either that females were able to assess dominance based on cues that were not measured, that males signaled to each other during the dichotomous choice tests (males were on opposite sides of the arena and could see each other through barriers that admitted chemical cues), or that females influenced male dominance status during the dichotomous choice trials. It appears that male-male aggression in the form of chases and bites is the key to mating success in *G. metallicus*, a finding also supported in the normal morph (Farr, 1980). Kolluru et al. (2014, 2015) demonstrated that males with larger body and gonopodium size and with greater ventral black area exhibit higher levels of mating activity via aggressive monopolization of females. However, neither study was able to uncover which traits are important in female choice, despite the intense courtship activity of the black morph males (Kolluru et al. 2014, 2015).

Black morph males also exhibit yellow body coloration (Lorenzen, 1996; Greven, 2005) which should be favored by sexual selection because yellow and orange coloration are often honest indicators of male quality in poeciliid fishes, as they are produced using carotenoid pigments. Carotenoid pigments contain beneficial antioxidants that are difficult to acquire and process for deposition in the skin (Lozano, 1994; Grether, 2010). Ventral black coloration may also serve as an amplifier of the yellow, facilitating female assessment of quality by enhancing the visibility of the yellow body region (Hasson, 1989, 1990; Grether et al., 2004; Brooks, 1996). Given this, yellow rather than ventral black may be the direct target of female choice.

To investigate female choice and male-male competition on the integrated suite of morphological traits we identified independent axes of morphological variation that included yellow coloration, paired size-matched males differing in yellowness, subjected each pair to female choice tests that excluded male-male interactions, and then allowed the males and the female to directly interact with each other. Under the hypothesis that female choice and male-male competition favor yellow body coloration because it is indicative of male quality (e.g., Morris

et al., 2007; reviewed in Berglund et al., 1996; Rios-Cardenas and Morris, 2011), we predicted that females would spend more time associating with the yellower of the males within a pair, and that those males would subsequently be more likely to aggressively monopolize access to females.

2. Materials and methods

2.1. Animal husbandry

We maintained stocks of captive *G. metallicus* in the Kolluru laboratory at California Polytechnic State University. These fish originated from a founder population that has been housed in captivity for approximately thirty years. Our colony was initiated using several hundred individuals from this captive stock via David Reznick's lab, which we obtained in two batches (one in 2010 and the other in 2015).

We housed the fish in mixed-sex 38-liter stock tanks under controlled temperature conditions ($25 \pm 0.5^\circ\text{C}$) at a 12:12 L:D lighting schedule using a mixture of full-spectrum fluorescent and LED bulbs. We fed the fish high-quality flake food (TetraMin Plus Tropical Flakes®, Tetra, Spectrum Brands, Inc.) before the experiment and frozen brine shrimp (*Artemia* sp.) during isolation.

We isolated adult males ($n = 46$) in 7.5-liter ‘home isolation tanks’ before photography to ensure that each male had access to high quality food without competition and to reduce variation in baseline coloration levels. The vast majority of males ($n = 39$) were isolated for 23 to 25 days prior to photography; a subset of males died and had to be replaced ($n = 7$), and these males were therefore only isolated for 2 to 4 days prior to photography. Home isolation tanks contained gravel and Java moss and were visually isolated from each other with opaque barriers. We isolated adult females in similar ‘home isolation tanks’ for 11 to 49 days prior to the start of behavior trials. For practical reasons we were unable to use virgin females or females that had recently given birth to ensure sexual receptivity (Houde, 1994); however, isolating females prior to testing is a standard technique used to increase female motivation to mate in poeciliids (e.g., Plath et al., 2004; Wong et al., 2011; Calabrese et al., 2014) including in a prior study of *G. metallicus* (Bertram et al., 2016).

2.2. General overview

We photographed each male and analyzed the images to obtain average hue, saturation and brightness (HSB) values of homologous points on the lateral surface of the fish (Fig. 1) and to obtain a series of morphological measures as described below. To pair the males, we minimized the difference in standard length while maximizing the difference in yellow saturation (using the factor 2 scores described below; Supplement 1). We then assigned a different female to each pair, ensuring that all three fish within a group ($n = 23$ groups) came from different housing tanks, such that they had never seen each other. We performed behavioral trials between 2 and 6 weeks post photography; males were fed frozen brine shrimp twice daily throughout this period. We performed female choice tests in which we measured the time the female associated with each male in the pair. Because our focus was on visual signals (i.e., coloration), we placed males and females in different tanks to ensure that female association time was based on visual and not other cues; because the males did not have the ability to visually or chemically detect each other, we assessed female choice independently of male-male competition. To assess intersexual selection with chemical and tactile cues present and to assess intrasexual selection, we then performed a direct interaction test with all three individuals in the same aquarium. We performed all experimental trials in a black-curtained area lit by full-spectrum fluorescent and LED lights, and the conditioned water in the observation tanks was replaced between pairs. We covered three sides of the observation tanks with brown paper and observed from the front. We performed all trials blind with respect to the yellow

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