



Natural versus sexual selection: predation risk in relation to body size and sexual ornaments in the green swordtail

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In general, we assume that natural (predation-mediated) and sexual selection have opposing effects on the evolution of characters that serve as ornaments. Males of most swordtail fishes (genus *Xiphophorus*) have an elongation of the caudal fin known as the sword that is used to attract females, as it increases apparent body size of males. By increasing apparent body size, the sword may also attract the attention of predators or decrease the likelihood that a predator will attack. Using the green swordtail, *Xiphophorus hellerii*, we evaluated separately the effect of body size and the presence of the sword on the likelihood of being attacked by a predator. We conducted preference tests using a sympatric cichlid, *Thorichthys ellioti*, as a predator. For the effect of body size we used live pairs of male swordtails of different sizes without swords (surgically removed) as stimuli, and for the effect of the sword we used videos of male swordtails with and without their sword (digitally removed). We found no effect of body size, but the cichlid predators directed more bites towards individuals with swords. Despite their benefits in terms of attracting mates, the sword seems to increase the risk of being attacked by a predator and thus represents a trade-off between natural selection (mediated by predation) and sexual selection.

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Predation is a major selective force in the evolution of morphological and behavioural adaptations in animals (Sih 1985). The evolution of traits related to avoiding and reducing predation risk is favoured because individuals that exhibit these traits can invest more time and energy on other critical activities or traits (Lima 1998). Endler (1995) found that these morphological and behavioural adaptations have the effect of decreasing conspicuousness or attractiveness to predators of individuals that carry them. Therefore, many organisms experience a conflict between different ecological demands, as they must optimize foraging and reproduction, while avoiding being attacked by a predator (Johnson & Agrawal 2003).

The effects of predation depend, among other things, on how the size of prey affects their risk of being caught and eaten (Juanes 1994; Juanes & Conover 1994). If the risk is greater for small individuals, selection should favour the allocation of resources to somatic growth, resulting in delayed maturation and reproduction at larger sizes; we would expect the opposite if the risk is greater for large individuals (early maturation and reproduction at smaller

sizes; Charlesworth 1980). Several studies have shown that predation can be directed to both smaller sizes (e.g. Werner et al. 1983) and larger sizes (e.g. Lafferty 1993). In predator–prey systems of cichlids and guppies (*Crenicichla saxatilis*–*Poecilia reticulata*), predation favours small prey (Reznick et al. 1990; Winemiller et al. 1990), while in cichlid–platy and cichlid–swordtail systems, predation may favour larger sizes (Basolo & Wagner 2004). In those cases where natural selection favours larger sizes (less predation), there may be body structures that increase the apparent size of the fish without requiring investment of greater resources in body growth (Fuiman & Magurran 1994).

Another mechanism that may favour the development of exaggerated structures is sexual selection, which promotes the evolution of structures and elaborate displays that usually occur in males (Andersson 1994). Elaborate structures of males can be used during competition for access to females, thus increasing the chances of success in contests and thus mating (intrasexual selection). In mating systems with elaborate courtship displays, elaborate structures can evolve as a result of selection by females since they may reflect the benefits that males can offer to females and their progeny (intersexual selection). These ornaments may be maintained in populations because they increase the reproductive success of males that exhibit them, and because females that choose matings based on these attributes can derive direct benefits (e.g. better territories and/or resources in the territory, care and

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protection to the female and her offspring, higher fertility, lower risk of predation) or indirect genetic benefits (e.g. hatchlings inherit the father's appeal, and/or regardless of sex, the offspring could inherit the father characteristics associated with greater viability; Andersson 1994).

In general, we expect the costs of producing a large trait to increase proportionally to the benefits obtained by the increment of the trait (Kotiaho et al. 1998). The costs resulting from such increment in size of a sexual trait may be direct (e.g. predation) or physiological (e.g. greater energy expenditure). Because both viability and mating success affect the fitness of a male, a trait may be expected to have a detrimental effect by decreasing viability through natural selection and to have a beneficial effect through sexual selection by increasing mating success (Kotiaho et al. 1998). Therefore, we expect the expression of a sexual trait to reflect a balance between natural and sexual selection (e.g. Reznick & Endler 1982; Andersson 1994); however, the evidence for natural selection balancing this trade-off is often not conclusive. In summary, natural and sexual selection often act in opposite directions, because the former tends to favour organisms that are less conspicuous to predators (Reznick & Endler 1982; Zuk & Kolluru 1998), while the latter promotes the evolution of conspicuous traits that tend to maximize matings (Houde 1987; Houde & Torio 1992). The goal of this study was to assess whether these selective forces are opposing or complementary in the green swordtail fish, *Xiphophorus hellerii* (e.g. Jennions et al. 2001).

Males of most species in the genus *Xiphophorus* have an elongation of the lower rays of their caudal fin, forming a structure called a sword (Rauchenberger et al. 1990). Previous studies have shown that females prefer males with a sword (i.e. intersexual selection; Basolo 1990a) because it increases apparent body size (Rosenthal & Evans 1998), and larger males may be better at defending a territory (Magnhagen & Kvarnemo 1989), may suffer less predation (Scharf et al. 2000), and if it is a heritable condition, their offspring may develop larger bodies (Reynolds & Gross 1992). When food is abundant, male green swordtails invest in both body and sword growth; however, with a reduction in food availability, males shift their growth strategy and invest more heavily in sword growth (Basolo 1998). This shift in strategy may maintain a constant growth in lateral projection area (LAP; i.e. body and fin area seen from the side; MacLaren & Daniska 2008; MacLaren & Fontaine 2012) during low resource conditions.

In the green swordtail, the average size of males and females is greater in populations with piscivorous fishes than in populations without these predators (Basolo & Wagner 2004). Based on this correlation, Basolo & Wagner (2004) suggested that because larger individuals might be more difficult to capture and manipulate, a large body size may avoid predation in this species. We suggest that by increasing apparent body size (by the increase in LPA due to the enlargement of the caudal fin; MacLaren & Daniska 2008; MacLaren & Fontaine 2012), the sword may also be reducing predation, a hypothesis that has not been tested. Using the green swordtail, we sought to determine the effect of body size and the presence of the sword on the likelihood of being attacked by a predator. A previous study examined the effects of UV coloration expressed on the sword of *Xiphophorus nigrensis* males on predator preferences (Cummings et al. 2003). However, to our knowledge this is the first experimental study looking at the effect on predation of body size and presence of the sword (two sexually selected traits) in *X. hellerii*.

Given that body size in *X. hellerii* could affect the probability of being attacked by a predator, because larger individuals may be more difficult to capture and handle, we suggest that smaller individuals may be more likely to be attacked by predators. The male sword is a trait that is also likely to be related to the

probability of being attacked by a predator; if the sword affects body size perception (makes swordtails appear larger), then swordless males may be more likely to be attacked by a predator. Alternatively, if the sword attracts predators, then swordless males may be less likely to be attacked by a predator.

METHODS

During the rainy season, we collected *X. hellerii* individuals from the Pixquiaco River (19°29'57.46"N, 96°56'47.08"W, $N = 28$) near the town of Coatepec in the state of Veracruz, Mexico, and from a creek (19°19'47.29"N, 96°43'25.57"W, $N = 42$) that flowed into La Antigua river near the town of Apazapan, Veracruz, Mexico. We selected these sites based on the abundance of the species and the proximity to our laboratory. We captured animals using funnel traps and electrofishing (BADGER-1 Backpack Electrofishing Unit, Version Monocanal, 0–600 V). We only collected mature males and females. Mature males are distinguished by the presence of a sword and a well-developed gonopodium (modified anal fin used to transfer sperm). Mature females are distinguished by the presence of a brood spot (pigmentation of tissue surrounding the female reproductive organs). We transported collected fishes to the laboratory where we placed them in 54-litre tanks (60 × 30 × 30 cm) for storage and maintenance. We filled tanks with tap water treated with a chlorine-removal solution (API Stress Coat, Mars Fishcare, Inc., Chalfont, PA, U.S.A.). Fish appeared to acclimate well to this type of water, as we did not notice any unusual behaviour during the duration of the study. We fed the fish three times a day ad libitum with commercial flakes (Basic Flakes, Wardley Essentials, Hartz Mountain Corp., Secaucus, NJ, U.S.A.).

Collection sites were 30 km apart; however, there was no significant difference in standard length (SL), the distance from the anterior tip of the mouth to the end of the caudal peduncle ($t_{68} = -0.922$, $P = 0.36$; mean ± SE: Pixquiaco: 45.37 ± 1.20 mm; Apazapan: 46.74 ± 0.90 mm), or sword length (adjusted to SL, see Basolo & Wagner 2004 for calculations; $t_{64} = -1.93$, $P = 0.06$; mean ± SE: Pixquiaco: 21.84 ± 0.98 mm; Apazapan: 26.77 ± 1.33 mm) among individuals from these localities. To determine whether the sample size used in these analyses could have influenced the probability of detecting an effect of the independent variable (if it existed), we determined the effect size and its respective confidence intervals, CI (Cumming & Finch 2001). Our analyses revealed that the effect size of body size ($r = 0.111$, $CI = -0.127, 0.337$) and sword length ($r = 0.234$, $CI = -0.0079, 0.4509$) did not differ significantly from zero, suggesting that there was no real effect given by the source population. Therefore, in subsequent analyses, we combined males from both localities without distinction.

We used *Thorichthys ellioti* to act as the predator, because it is an omnivorous cichlid whose diet includes fish (Valtierra-Vega & Schmitter-Soto 2000) and it is sympatric with *X. hellerii*. In addition, among all sympatric cichlid species, *T. ellioti* showed a clear response to *X. hellerii* individuals in a preliminary study. Furthermore, in the laboratory, *T. ellioti* eagerly consumed small (juvenile) *X. hellerii* individuals. Finally, an analysis of gut content of *T. ellioti* ($N = 28$) indicated that fishes made up about 38% of identifiable gut material (A. Hernandez-Jimenez, unpublished data). We used electrofishing to collect the predators (23 individuals) from the Apazapan population (see location above), where they coexist with *X. hellerii*. We placed predators in individual tanks (see size above) where we fed them three times daily ad libitum with commercial pellets (Cichlid Floating Pellets, Wardley Essentials) and sporadically with zebrafish, *Danio rerio* guppies, *Poecilia reticulata*, *X. hellerii* juveniles and other unidentified small poeciliids so they would continue to eat live food. We used a calliper to measure the

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