



Male–male competition and the sword in male swordtails, *Xiphophorus helleri*

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Male green swordtails, *Xiphophorus helleri*, express a secondary sexual trait, the sword, which is favoured by female mate choice. However, the role of the sword as a signal in male–male competition has received little attention. We studied the effect of both male body size and sword length on the outcome of male–male competition. Although body size and natural sword length were positively correlated, only body size had a significant effect on competitive success. To examine the independent effect of sword length on competitive success, males were matched for body size and natural swords were replaced with plastic caudal attachments simulating swords. The attachments were of equal size but were painted to approximate swords of different lengths. When matched for body size, males with longer apparent swords won significantly more contests than males with shorter apparent swords. These data suggest that, controlling for body size, longer-sworded males experience greater competitive success. Thus, in green swordtails, it appears that both male–male competition and female choice may have played a role in the evolution of longer swords.

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Sexually dimorphic traits can arise due to natural selection, where males and females experience different selective regimes (Lande 1980; Merilaita & Jormalainen 1997), or due to sexual selection (Darwin 1859), where the traits possessed by individuals affect their success in obtaining mates. The role of sexual selection in the origin and maintenance of sexual dimorphism has received considerable attention (for review, see Andersson 1994). Both intersexual selection, or mate choice, and intrasexual selection, competition in one sex for mating access to the other sex, are important in the exaggeration and maintenance of traits in males (Davies & Halliday 1978; Wagner & Sullivan 1995). Here, we focus on the role of intrasexual competition via male–male competition in the maintenance of a sexually dimorphic trait.

Male–male competition can result from differences between males in their searching abilities (Wiklund & Fagerström 1977; Carroll & Salamon 1995) as well as in their success in direct competitive interactions. Competitive interactions between males have been studied in numerous

taxa (see review in Andersson 1994), and in many cases, specific male characteristics have been found to influence male competitive success, which in turn affects male mating success (Parker 1974). For example, size can directly affect the outcome of male–male contests (Davies & Halliday 1978; Arak 1983), as can a number of other morphological traits. Although some traits that males use in competition are weapons, such as antlers in deer (Clutton-Brock 1982), sexually dimorphic traits need not be exclusively valuable as weapons to influence contest success (Berglund et al. 1996; Härdling 1999). Even when not used as weapons, males with more exaggerated traits can experience greater contest success (Davies & Halliday 1978), because the traits serve as signals of intent (Maynard Smith 1982), past success (Parker 1974), vigour (Zahavi 1977), size (Parker 1974), feeding success (Karino & Haijima 2004) or age (Burk 1988). By allowing evaluation of prospective competitors without direct contact, these signals may allow males to avoid unnecessary injury, unnecessary energy expenditure or increased predation risk incurred during fighting (Maynard Smith & Parker 1976; Maynard Smith & Brown 1986). Thus, signalling in competitive interactions in a sense can be beneficial to prospective losers and prospective winners, in that both benefit by reducing or avoiding direct contests if they are disparate in abilities (Parker 1974).

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Traits favoured by females in a mate choice context may also be favoured by male–male competition, and males and females may use the same traits to evaluate males as prospective mates or competitors. For example, both male and female dragonflies use the same attributes to evaluate males (Moore 1990). In other circumstances, either males and females use different traits, or they weigh the importance of traits differently when making assessments (Warner & Schultz 1992; Wiltenmuth 1996). A male trait that appears to be important in female mate choice is the sword in green swordtails, *Xiphophorus helleri*. The sword in male green swordtails consists of a set of long, multicoloured fin rays that can extend far beyond the caudal margin. Both sword length (Basolo 1990) and sword colour pattern (Basolo & Trainor 2002) have been found to influence female mate choice in swordtails. In a study in which sword length and sword coloration were controlled, female green swordtails also showed a preference for body size, preferring larger males to smaller males (Basolo 1998b). Male body size also appears to influence the outcome of male–male competition, because larger males win contests more often than smaller males (Beaugrand et al. 1991); sword length, however, was not controlled for in this study. While male swords appear to be favoured by female mate choice, sexual selection via male–male competition could also have contributed to the evolution of the sword.

Male green swordtails have well-studied competitive interactions. In laboratory tests, size and previous contest success were important determinants of current contest success (Beaugrand et al. 1991). In past experimental manipulations of the sword, males behaved more aggressively towards males with full swords than to males with experimentally shortened swords (Hemens 1966; Franck & Hendricks 1973), suggesting that males do attend to the swords of their competitors.

Intersexual selection and intrasexual selection may either favour the same traits or favour different traits. We investigated how two male traits that are important in female mate choice, male body size and sword length, affect the outcome of male–male competition between green swordtails. First, we conducted a correlational study to investigate the importance of body size and natural sword length as determinants of competitive success in pairwise contests. However, a relation between sword length and competitive success could result from some genetically or phenotypically correlated effect, and not from variation in sword length, so we conducted a sword manipulation experiment in which body size was controlled. Pairs of males were matched for body size and given artificial sword attachments of different lengths. Thus, in these contests, only the length of the swords differed systematically between partners.

METHODS

The Study Organism

Green swordtails, *X. helleri* (Haeckel), are live-bearing fish in the family Poeciliidae and are widespread in the

Atlantic tributaries of northern Central America (Rosen & Bailey 1963). Male green swordtails possess a composite morphological trait, the sword. This composite trait consists of a specific set of lower caudal fin rays with melanophore pigmentation along the lower margin, a stripe of coloration ranging from green (pterins) to orange or yellow (carotenoids) above the lower stripe, and a second black stripe above the green/carotenoid coloration, which extends from the insertion of the rays to beyond the caudal margin (for further details, see Rauchenberger et al. 1990; Basolo 1996).

Test subjects were male descendants of green swordtails collected from Savannah Stream near Mile Marker 28, Western Highway in Belize under permits issued to A.L.B. by the Belize Fisheries Ministry. Fish were housed in treated water (deionized water treated with Novaqua, Hayward, California, U.S.A., Instant Ocean, Mentor, Ohio, U.S.A., and Start Right, Cibolo, Texas, U.S.A.) and maintained at approximately 26°C, on a 14:10 h light:dark cycle. Fish were fed live brine shrimp (*Artemia* sp.) in the morning, liver diet at noontime, and Tetra-Min (Melle, Germany) flakes in the afternoon.

Male test subjects originated from colony tanks or from tanks with two siblings. All subjects were housed with females prior to assignment to this experiment. During the experiment, subjects were housed individually in 6-litre tanks with gravel, plant matter and several snails. Tanks were covered with opaque plastic lids. Males were periodically housed with females; at intervals of 5–9 days, the females were moved to the next subject's tank. This procedure provided all subjects with periodic exposure to females. Males with recent exposure to females respond more appropriately to conspecifics (Franck & Hendricks 1973).

Male size was determined from digital images. The lateral aspect of each male was videotaped at the front of a glass tank (20 × 20 × 20 cm, filled to 10 cm, 4 litres). The resulting images were digitized using Adobe Premiere and Photoshop software. NIH-Image was used to measure standard length (anterior of head to distal margin of caudal peduncle), the length of the natural sword (from the distal margin of the caudal peduncle to the distal tip of the sword), total length (anterior of head to distal margin of caudal fin excluding the sword extension), and lateral area (body area only, excluding the sword extension, caudal fin and dorsal fin) from each image.

Preliminary Observations

We conducted preliminary observations to examine the duration of contests, the characteristics of male behavioural interactions, and to determine how to measure male competitive success. We conducted taped observation trials with 32 pairs of males in a test tank measuring 30 × 26 × 30 cm (23.4 litres) to quantify male–male interactions. Males were randomly paired and introduced to the tank between 1600 and 2000 hours on the evening before the test. A perforated opaque divider separated males from one another during the acclimation period. The following morning at 1000 hours, the divider was

removed and males were videotaped for 1 h. Casual observations of each pair continued for approximately 1–80 h after taping to examine additional behavioural sequences of competitive interactions and to determine the stability of contest outcome. The males were returned to their home tanks after the last observations. In competitive interactions, males displayed the following behaviours: chase (one male swims rapidly at the other while the other retreats) (Hemens 1966; Beaugrand et al. 1984) and avoidance behaviour (slow movement out of the path of the other fish).

We used the number of chases as an indicator of contest outcome; males that gave the greatest number of chases were designated the winners for each pair, similar to the criteria in Beaugrand et al. (1984). Although we videotaped only for 1 h, we found that contests generally took more than 1 h to be resolved, but the apparent winner of the contest always chased more than the other fish. Contest outcome was also indicated by behavioural and morphological differences between the competitors. The loser of the contest was typically characterized by darker coloration and the appearance of facultative vertical stripes, folded fins, head-down posture, and a position at the periphery of the tank. The contest winner in *X. helleri* usually had spread fins, no darkening or vertical stripes, and moved freely about the tank. We noted no circumstances where the contest outcomes changed, and green swordtail contest outcomes have been found to be quite stable (Beaugrand & Beaugrand 1991).

Correlational Study

We conducted a correlational study of the relations between sword length, body size and competitive success. Males were randomly assigned to pairs with the restriction that males were not matched either with siblings or with males with whom they had had previous experience. Some of these males had been used for the observation trials. Lateral area (i.e. size) of males ranged from 2.78 to 4.84 cm² ($\bar{X} \pm \text{SE} = 3.69 \pm 0.63$). These pairs were created randomly, and lateral area differed between members ($\bar{X} \pm \text{SE}$ difference = 0.69 ± 0.66 cm²). Pairs of males were tested in gravel-lined 12-litre plastic tanks (approximately half the size of the test tank used in observation trials) with opaque barriers on three sides. Contest durations can exceed several hours, so rather than capture the entire contest, we selected a videotaping regime that would maximize our ability to determine the winner. Pairs were videotaped for five 10-min intervals spaced approximately 80 min apart. To confirm that all contests were resolved and the outcomes stable in the smaller test tank, we initially left pairs together overnight ($N = 8$ pairs). However, extended interactions in these smaller tanks were found to be harmful to the health of some test males. Therefore, the remaining 20 pairs were separated and returned to their home tanks the same day. We used Stress Coat (Chalfont, Pennsylvania, U.S.A.) to replenish the slime coat on the males when we removed them from the contest tanks.

We counted all chases by each male in the 50 min of taped behaviour (five 10-min intervals). The male that

had chased most often was deemed the contest winner. In all cases, our casual observations of contest outcome on the day of the contests (based on coloration and posture) were consistent with the outcome determined using the chasing criterion. We used S-Plus 6.1 (MathSoft, Seattle, Washington, U.S.A.) for all of our statistical calculations. The correlation between sword length and lateral area led us to use multiple logistic regression to examine the independent effects of differences in sword length and in lateral area on contest success.

Sword Manipulation Experiment

To examine the relation between sword length and competitive success, apart from any genetically or phenotypically correlated effects, we manipulated the swords of males that were matched for lateral area (range 3.52–4.83 cm², $\bar{X} \pm \text{SE} = 4.07 \pm 0.24$ cm²). We matched 12 pairs of males for similar lateral area, removed their natural sword extension, and surgically attached plastic swords (Basolo 1998a). The artificial swords received by members of a pair were identical in size and shape, but were coloured with two black stripes and a yellow stripe to simulate swords differing in apparent length; one attachment was painted to appear equal in length to the mean standard length of the pair and the other was painted to appear equal in length to one-half the mean standard length of the pair (anterior half painted as a sword, posterior half remained clear plastic). Differences in lateral area between competitors were minimized ($\bar{X} \pm \text{SE} = 0.026 \pm 0.003$ cm², $N = 12$). Assigning swords of different length was quasirandom, in that we counterbalanced for small differences in body area. That is, the randomization regime ensured that, in six cases, the larger male would receive the longer attachment, and in the other six cases, the smaller male would receive the longer attachment. All males were given at least 7 days for post-surgery recovery. Tests were conducted and videotapes were scored as described in the correlational study. Artificial sword attachments were removed after testing. Chi-square analysis was used to determine whether males with larger body size, longer natural sword length or longer artificial sword length won significantly more often than expected by chance. We used the chasing criterion to determine the winner of each contest.

RESULTS

Correlational Study

In all 28 pairs, chasing was recorded. Chasing was observed by both males in only four pairs. Winners were significantly larger than losers (21 of 28 pairs; $\chi_1^2 = 7.0$, $P = 0.008$; Table 1) and tended to have longer swords (19 of 28 pairs; $\chi_1^2 = 3.57$, $P = 0.059$; Table 1).

Sword length and body size were both strongly correlated ($r = 0.89$; paired t test: $t_{54} = 6.65$, $P < 0.001$) and we used multiple logistic regression to examine the independent contributions of these factors to contest success. When controlling for sword length differences, there

Table 1. Mean \pm SE number of chases, lateral area and sword length for winners and losers in the correlational study

	Winner	Loser
Number of chases	15.6 \pm 13.9	0.89 \pm 3.25
Lateral area (cm ²)	3.54 \pm 0.89	3.10 \pm 0.68
Sword length (cm)	3.72 \pm 0.75	3.55 \pm 0.62

was a significant positive relation between lateral area differences and competitive success (assigned 0 if losing, 1 if winning; multiple logistic regression: $t_{25} = 1.75$, $P = 0.048$). Differences in sword length, controlling for differences in lateral area, did not significantly account for variation in contest success (multiple logistic regression: $t_{25} = 0.228$, $P = 0.411$).

Sword Manipulation Experiment

Losers chased winners in only two of the contests, and the winner chased the loser in each trial ($\bar{X} \pm \text{SE} = 14.08 \pm 11.52$, $N = 12$). Analysis of contest outcome revealed that when males were matched for body size, males with longer apparent swords won significantly more contests than did males with shorter apparent swords (10 of 12 cases; $\chi^2_1 = 5.33$, $P = 0.02$; Table 2). Thus, sword length had a direct effect on contest outcome. Differences in lateral area did not significantly influence contest outcomes for the size-matched males ($\chi^2_1 = 0.07$, $P = 0.80$; Table 2). In addition, the original length of the natural sword did not affect contest outcome; for five of the 12 pairs, the contest winner had the longer natural sword prior to artificial sword attachments ($\chi^2_1 = 1.67$, $P = 0.20$; Table 2).

DISCUSSION

Male sword length appears to be a determinant of contest outcome in green swordtails if males are of similar size; males with longer artificial swords were significantly more likely to win contests than expected by chance. This result differs from that of an earlier experiment that failed to find a relation between artificial sword length and competitive success in the green swordtail (J. L. Nelson, unpublished data). However, in Nelson's study, males with artificial swords were tested immediately after surgical attachment, so the lack of recovery time could have influenced the results.

Our results also confirm a previously reported relation between body size and competitive success for green

swordtails. In previous studies in which the effect of sword length on male–male interactions was not controlled, small differences in body size (25 mm²) were found to be important in competition between green swordtails; larger males won more often than smaller males (Beaugrand et al. 1996). However, in our manipulative test, similarly small differences in body size were overwhelmed by the size of the artificial sword lengths, which dictated competitive success. Body size also appears to confer an advantage in male–male competitive interactions in other *Xiphophorus* spp., including *X. variatus* (Bisazza et al. 1996) and *X. cortezi* (Moretz 2003). Larger males also have a competitive advantage in many other taxonomic groups (see Andersson 1994). Thus, it is not surprising that larger male green swordtails had a competitive advantage.

When paired males differed in both body size and natural sword length, we did not detect a relation between natural sword length and competitive success when statistically controlling for differences in body size. These results do not preclude the possibility that swords are an important signal in competitive interactions, but they do suggest that size is more important than sword length. Our manipulative test results suggest that sword length is most important in contests when males are closely matched for size. Several studies have suggested that males of similar size could rely on multiple sources of information to assess the potential costs of escalating fights (Hurd 1997). When size is a determinant of fighting ability, males may assess the size of their competitors, but if size is similar between males, they may evaluate other attributes of their opponents (Adams & Caldwell 1990).

Although the sword manipulation experiment indicates that male sword length can affect the outcome of competitive interactions, precisely what types of information are conveyed by sword length has yet to be investigated. Sword size is determined in part by age since sexual maturity (Kallman 1984). While males grow little in body size after sexual maturity, the sword starts to develop as the male nears sexual maturity and continues to grow after sexual maturity; thus, sword length could indicate adult age. Sword length could also be indicative of male foraging history. Both body and sword size are affected by nutrition; males given more food grew larger and had longer swords than males given less food, although males receiving less food nearly compensated for sword growth differences after 8 months (Basolo 1998b). Although the heritability of sword length has not been directly studied in green swordtails, there is indirect evidence that sword length is heritable; the heritability of body size is 0.82 (Campton 1992), and body size and sword length are correlated in males in natural populations (Basolo & Wagner 2004).

While males appear to benefit from longer swords because females prefer them, and while longer swords positively affect fighting success, there are also costs of having longer swords. Shortened swords decrease both routine and courtship swimming costs, suggesting that there are metabolic costs associated with sword length (Basolo & Alcaraz-Zubeldia 2003). Male sword length is also shorter

Table 2. Lateral area, natural sword length and artificial sword length for winners and losers in the sword manipulation experiment

Factor	Larger won	Smaller won	χ^2	P
Lateral area	8	4	0.07	0.80
Natural sword length	5	7	1.67	0.20
Artificial sword length	10	2	5.33	0.02

in populations with predatory fish than in populations lacking predatory fish (Basolo & Wagner 2004), suggesting that longer swords result in higher predation risk. Increased predation risk in males with enhanced sexually selected traits has been reported in another poeciliid, the guppy, *Poecilia reticulata* (Endler 1987, 1988), as well as in other taxa (reviewed in Zuk & Kolluru 1998).

In green swordtails, sword length and body size are important in both male–male competition and in female mate choice. Males and females, then, appear to use similar traits to evaluate males. The sexes might, however, use the same signal to obtain different types of information, as has been suggested for mate choice in *X. helleri* (Basolo & Delaney 2001). Males and females use the same traits for evaluating males in other species (Cote & Hunte 1989; Lederhouse & Scriber 1996; but see Warner & Schultz 1992), but the relative importance of inter- and intrasexual selection can vary. Forsgren et al. (1996) reported that limited resource availability simultaneously increased the importance of male–male competition and decreased choosiness in females. The costs of longer swords in green swordtails could be examined relative to different indicators of male condition to better understand the value of the sword as an indicator in sexual selection (Kotiaho 2001; Cotton et al. 2004).

The sword can be adaptive as a signal in male competitive interactions only if mating success covaries with competitive success. There are at least two ways in which contest success can result in increased mating success. First, females might prefer competitively successful males. Females in a number of species have been shown to prefer males of greater competitive ability (Cox & LeBoeuf 1977; Forrest & Raspet 1994; Wiley & Poston 1996). Second, winning males could directly restrict the access of other males to females. In *X. montezuma* swordtails, larger males appeared to restrict access to females by smaller males when differences in sword length between paired males were controlled (M. Nootz & A. L. Basolo, unpublished data). Furthermore, increased mating success of winning males does not require direct interference competition, since winning males can restrict access to females by inducing behavioural changes in subordinate males, as has been observed in mice (D'Amato 1991).

As stated earlier, the sword appears to be important not only in female mate choice, but also in male–male competition in green swordtails. The relation between contest success and mating success has not been well explored, but in several systems, a link has been found (Andersson 1994). Additional studies of the relation between contest success and mating success will be important to understanding the role of the sword as a signal of competitive ability in green swordtails. Furthermore, the relative importance of intra- and intersexual selection may elucidate mechanisms for the origin and the maintenance of the sexually selected sword.

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