



Sexual difference in signal-receiver coevolution

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Abstract. The responses of males and females to a male signal were compared between two sister species, one in which the signal is present and one in which the signal is absent. The signal is a pattern of vertical bars found on males throughout the northern swordtail fish, genus *Xiphophorus*. In *X. multilineatus*, the bars function both to attract females and deter rival males. Males in *X. nigrensis*, the sister species to *X. multilineatus*, do not have bars. *Xiphophorus nigrensis* males did not respond differently to males with bars compared with males without bars, but *X. nigrensis* females were more attracted to males with bars than males without bars. Thus, the male response to bars is congruent in both taxa: male response was present when the male trait was present (in *X. multilineatus*) and absent when the male trait was absent (in *X. nigrensis*). The female response to bars, however, was congruent in *X. multilineatus* but incongruent in *X. nigrensis*: female response was present but the male trait was absent in *X. nigrensis*. This pattern suggests that of the three components of the communication system, (male response, female response and male signal), the signal and male response coevolved more closely than did the signal and female response.

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The evolution of extravagant male traits can be viewed from a conventional animal communication standpoint, in which male traits are signals and the males and females that respond to those traits are receivers (Boake 1991; Zahavi 1991; Zuk 1991; Harper 1992). It has been assumed that the evolution of a signal requires some type of coordination between signal and receiver; otherwise, changes in the signal would not be perpetuated (Alexander 1962; Butlin & Ritchie 1989). A growing number of studies, however, report cases in which female preference for a specific male trait is not congruent with the male trait. For example, female preference for male traits have been detected in taxa where males do not possess the trait (Ryan & Wagner 1987; Basolo 1990, 1995; Ryan & Rand 1993; Hill 1994). Patterns of signal-receiver coevolution have been of interest because they suggest the degree to which communication systems evolve as integrated and coordinated units, as in the case where the genetic bases for the signal and response are pleiotropic (Alexander

1962), as opposed to evolving more independently, as in the case of sensory exploitation where pre-existing preferences provide the selection that favours the evolution of certain signals (Ryan 1990, 1994; Ryan et al. 1990a).

Male traits can evolve under sexual selection as signals used not only in attracting mates but also in deterring rivals. The idea that some male signals serve a dual function is not new (Tinbergen 1953) and has been demonstrated in numerous cases, such as visual signals in fish (Rowland 1989) and birds (von Schantz et al. 1989) and acoustic signals in frogs (Gerhardt 1994), birds (Catchpole & Slater 1995) and mammals (McComb 1987). In most sexual selection studies, however, the interaction between the male trait and the female preference, a dyad, is often investigated without reference to the male response to that signal (Boake 1991; Andersson 1994). If a signal influences both female and male responses, then studies of the function and evolution of the communication system should encompass the entire communication triad: the signal, the female's response and the male's response. By comparing all three components between taxa, the degree of coevolution of female response and male trait can be compared with the degree of coevolution of

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male response with the same male trait. Within a taxon, signals and receivers are 'congruent' if the response and signal are either both present or both absent (Hill 1994), and 'incongruent' if either the response or the signal is found in the taxon without the other. When characters are found to be congruent in the same taxa where other characters are incongruent, it suggests that the congruent characters have coevolved more closely. The comparisons of communication triads between taxa can be used to test predictions concerning the evolutionary outcome of differential selective pressures on the male signal–female receiver dyad and the male signal–male receiver dyad. For example, if mating with the wrong species is more costly than threatening the wrong species (Searcy & Brenowitz 1988; Harper 1992), then the male trait and female response might be expected to coevolve more closely (more often congruent) than the male trait and male response (more often incongruent).

In this study, we compared the coevolutionary patterns of female responses and a male signal with male responses and the same male signal between taxa to determine whether the male responses were as congruent with the signal as the female responses. Our comparison was between two species and therefore does not suggest character states for the ancestor shared by these two species. The ancestral states could be used to determine which trait was lost or gained to produce the pattern of congruence or incongruence. Because the male signal is present in one species and absent in the other, however, we were able to determine whether the responses of females and the responses of males remained congruent with the signal when it changed, regardless of which trait was lost or gained to do so.

The signal we examined is a pattern of dark vertical bars found in many species of the genus *Xiphophorus* as well as other poeciliid fishes (Fig. 1). The bars are present in *X. multilineatus* and absent in the sister taxon *X. nigrensis* (Rauchenberger et al. 1991; Meyer et al. 1994). Vertical bars, along with several allozyme differences, distinguish these two allopatric species (Rauchenberger et al. 1991). In *X. multilineatus*, the bars have a polygenic basis with a Y-linked component (Zimmerer & Kallman 1988). The bars of *X. multilineatus* males intensify when males interact (Franck 1964; Zimmerer & Kallman 1988) and when males court females, and

they function in both deterring rival males and attracting females (Morris et al. 1995b). The goal of this study was to compare the relative degrees of coordination between signal and response based on the sex of the receiver by determining whether the response of the receiver (of either sex) was temporally decoupled from the signal. We compared male and female responses to the bars between two sister species, *X. multilineatus* and *X. nigrensis*, because we know that the bars changed (i.e. were either lost in *X. nigrensis* or gained in *X. multilineatus*) during the time period that these two species differentiated.

METHODS

We tested *X. nigrensis* males and females with the same pairs of *X. multilineatus* males previously used to examine the function of the bars in *X. multilineatus* (Morris et al. 1995b). All of the fish used in these experiments were either wild-caught or raised in large outdoor communal tanks and therefore had previous experiences with other males and females. We matched pairs of *X. multilineatus* stimulus males for size (within 0.5 mm) and treated them with the anaesthetic MS222 before manipulations, in accordance with animal care guidelines. One male from each pair of stimulus males had his bars removed by freeze-branding (Raleigh et al. 1973) and was the barless male. As a control, the other male of the pair was freeze-branded between the bars, but kept his bars ('barred control male'). Pigmentation in the branded areas faded 2–3 days after branding, and the colour of the branded area was similar to the overall colour of the fish. Behaviour patterns of the males did not appear to be affected by the branding.

Test of Female Response

Prior to testing female response to the bars, stimulus males and females were separated for at least 1 week. The test aquarium (45 × 90 × 41 cm) was divided into five equal sections. The sections at each end were separated from the three central sections by Plexiglas. One male from each pair of stimulus males was placed at each end of the test tank. We placed a female in an opaque cylinder in the centre of the test tank and allowed all fish to acclimate for 10 min. When we removed the



Figure 1. (a) Vertical bars on a large *X. multilineatus* male; (b) *X. nigrensis* males do not have vertical bars.

opaque cylinder, we recorded the time the female spent in each of the sections near the males for 20 min. Tests in which one or both males did not interact with the female were excluded. The males were then switched end to end, and we repeated the entire test to control for side bias.

We compared the mean time that *X. nigrensis* females spent with the barless versus the barred males to determine whether females were attracted to barred males. We also compared the mean difference in the time *X. nigrensis* females spent with barless versus barred males to the mean

difference in the times *X. multilineatus* females spent with the same pairs of males to determine whether there was a difference in preference for the bars between the species. *Xiphophorus nigrensis* females prefer large males over small males (Ryan et al. 1990b). Although we controlled for male size in each female preference test by matching stimulus males for size, male size might have influenced the strength of the preference for bars. Therefore, we also compared the differences in the times female spent with the barred males versus the barless males to the respective sizes of

the stimulus males. We used linear regression to determine whether the slopes of the resulting regressions were significantly different from zero, and an analysis of covariance to determine whether the slopes were significantly different between species.

Female mating preferences in many fish are difficult to assess directly. Our studies with *X. nigrensis* have shown that the results from preference tests like those described above (preference for large males over small males, Ryan et al. 1990b) are consistent with the results from three other types of studies: those that measured the receptive behaviour of females placed in a tank with one male (females behaved more receptively with large males than with small males; Morris & Ryan 1993), studies of male access to females in the field (large males had greater access to females than small males; Morris et al. 1992), and paternity analysis using genetic markers of male reproductive success in nature (large males produced more offspring than small males; Ryan et al. 1990b).

Test of Male Response

We tested the responses of males using the same pairs of stimulus males used to test the responses of females. Most of these pairs were tested in female choice tests first, but some were tested in the male response tests first. We examined the responses of males to the bars by comparing the fight intensity of unmanipulated focal males in contests with barless and barred stimulus males. Focal males were always smaller than the pair of stimulus males they were tested against, so stimulus males won all contests (i.e. were dominant). The behaviour patterns of the focal males (the losers) determined when the contest was over (see below).

We kept all males isolated in individual 2.5-litre tanks throughout the testing period. Tests were conducted in a 45 × 60 × 41-cm tank. We placed one focal male and one stimulus male on either side of an opaque partition that divided the test tank into two equal parts. After 24 h, we removed the partition and recorded the number of bites delivered by each male, the length of the contest and the winner of contest. We measured contest length as the time from the first approach to the time when one male became dominant. A male was considered to be dominant in a contest when

the other male lowered his dorsal fin and retreated when approached (Franck 1964). The following day, the same focal male was tested against the other stimulus male from the matched pair. To control for any influence of prior fighting experience (Franck & Ribowski 1987), we randomly determined the order in which we tested the barless versus the barred males against the focal males.

We used bites per minute as an indicator of fight intensity (Morris et al. 1995a). Fight intensities of focal males in contests with barless males were compared with fight intensities of the same focal males in contests with barred males to determine whether the focal males responded differently to barless males. For both contest types (stimulus male barless or stimulus male barred), we also compared total fight intensities (bites/minute by focal male + bites/min by stimulus male) for contests with *X. nigrensis* focal males with total fight intensities for contests with *X. multilineatus* focal males to determine whether the responses of males to the bars differed between species.

Fight intensity decreased as the size between the opponents decreased in contests between *X. multilineatus* focal males and the barless stimulus males (Morris et al. 1995b). In this study, we determined whether there was a significant relationship between fight intensity and size difference in contests between the *X. nigrensis* focal males and the barless stimulus males. Then, to compare this relationship between the species, we regressed difference in fight intensity on difference in size, and compared the slopes of the regressions for the two species with an analysis of covariance. We calculated difference in fight intensity by subtracting fight intensities of contests in which the stimulus male was barred, from fight intensities of contests in which the stimulus male had no bars, which strengthens the comparison between species by removing variation due to differences between focal males.

RESULTS

Test of Female Response

Female *X. nigrensis* spent significantly more time with the barred males ($X \pm SD = 947.29 \pm 210.57$ s, $N=8$) than with the barless males (473.29 ± 324.33 s, $N=8$; Wilcoxon signed-ranks test, $z = -2.2$, $P=0.03$; Fig. 2a).

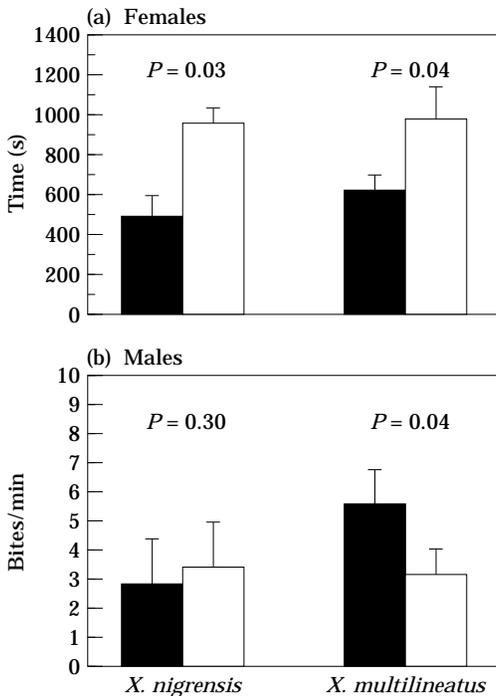


Figure 2. The responses of (a) females and (b) males to barred stimulus males (□) and barless stimulus males (■) across sister species (*X. nigrensis* males have no bars, *X. multilineatus* males have bars).

Female preference for barred males in *X. nigrensis* (474.0 ± 347.8 s, $N=8$) was not significantly different from female preference for bars in *X. multilineatus* (364.0 ± 373.1 s, $N=8$; Mann-Whitney U -test, $z = -0.23$, $P=0.82$; Fig. 2a). The relationship between male size and the strength of the female's preference for barred males was not significant in either species (*X. nigrensis*, $R^2=0.135$, $df=6$, $P=0.42$; *X. multilineatus*, $R^2=0.013$, $df=7$, $P=0.79$). There was no significant difference between the slopes of these regressions for the two species ($F=0.35$, $P=0.57$). Females of both species preferred barred males regardless of whether conspecific males have bars; thus female response and male signal were congruent in *X. multilineatus* but incongruent in *X. nigrensis*.

Test of Male Response

Xiphophorus nigrensis focal males did not respond significantly more aggressively to the

barless males ($X \pm SD = 2.75 \pm 4.9$ bites/min, $N=9$) than to the barred males (3.42 ± 4.7 bites/min, $N=9$; Wilcoxon signed-ranks test $z = -1.13$, $P=0.3$, Fig. 2b). The mean response of *X. nigrensis* focal males to barred males (6.0 ± 5.2 bites/min, $N=9$) was not significantly different from the mean response of *X. multilineatus* focal males to the same barred males (6.1 ± 5.6 bites/min, $N=9$; $t=0.07$, $P=0.9$). However, *X. multilineatus* focal males were more aggressive to the barless males (10.58 ± 7.5 bites/min, $N=9$) than *X. nigrensis* focal males (4.15 ± 6.2 bites/min, $N=9$; $t=2.08$, $P=0.05$).

With *X. nigrensis* focal males, the relationship between size difference and fight intensity in contests with barless males was negative (Spearman $r = -0.69$, $P=0.05$, $N=9$). The difference in fight intensities between the two contest types was not significantly correlated with size difference in *X. nigrensis*, but it was significantly different from the positive correlation for the same relationship in *X. multilineatus* (Fig. 3). Although male interactions in *X. multilineatus* were mediated by the presence or absence of bars, this signal did not appear to influence male interactions in *X. nigrensis*, which lacks bars. Therefore, the male response and male trait were congruent in both species.

DISCUSSION

The three components of a communication triad (male response, female response and male signal) were compared between two closely related taxa to determine whether signal-receiver congruence differed depending on the sex of the receiver. We showed that the signal and male response are congruent in both taxa, but the same signal and female response are congruent in only one taxon. Therefore, these results suggest that over the same temporal scale, male response and a male signal have coevolved more closely than female response and the same male signal.

Previously we demonstrated that the vertical body bars function both to attract females and deter rival males in *X. multilineatus* (Morris et al. 1995b). The comparison of the responses of *X. multilineatus* males with those of *X. nigrensis* males provides a broader context for interpreting the responses of *X. multilineatus* males to the bars. Fight intensity between focal *X. multilineatus* and

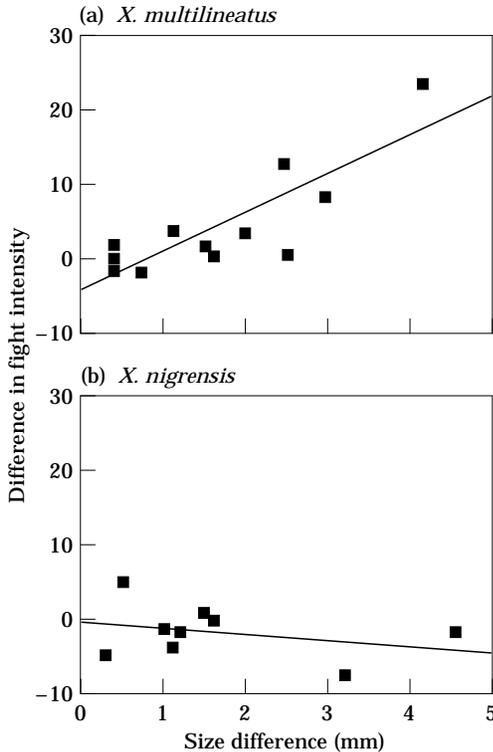


Figure 3. Difference in fight intensity (bites/minute) for focal males in contests with barless stimulus males compared with contests with barred stimulus males, plotted as a function of the size difference between the opponents. The relationship was significant in *X. multilineatus*, (a) ($r^2=0.69$, $P=0.0008$, $N=12$; Morris et al. 1995b), but not in *X. nigrens*, (b) ($r^2=0.09$, $P=0.44$, $N=9$). The slopes of the regressions were significantly different between species ($F_{1,19}=16.1$, $P=0.0009$).

barless stimulus males was greater than the fight intensity of contests with *X. nigrens* focal males and barless or barred stimulus males (Fig. 2b). Because we do not know the fight intensity of the ancestor of these two species in the same situations, however, we do not know whether the response of *X. multilineatus* to males without bars has increased in intensity or the response of *X. nigrens* males to males without bars has decreased in intensity. Studies of the responses to the bars of other species in this group could distinguish between these two alternatives.

Fight intensity increases in many species as the size between the opponents decreases (Archer 1988). In contests between unmanipulated *X. nigrens* males and in contests between

unmanipulated *X. multilineatus* males, fight intensity increased as size between the opponents decreased (Morris et al. 1995a). This relationship, however, was reversed in contests between *X. multilineatus* focal males and barless stimulus males, which suggests that the role the bars played in male–male interactions in *X. multilineatus* is influenced by body size (Morris et al. 1995b). Although the fight intensity of *X. nigrens* focal males in contests with the barless stimulus males increased as the size difference between males decreased, the relationship was not statistically significant. Therefore, removal of the bars did not appear to change the relationship between size difference and fight intensity in *X. nigrens*. The two species did differ significantly, however, in the influence of differences in body size on the responses of focal males to the barless stimulus males, further suggesting that the bars play a role in male–male interactions in *X. multilineatus* but not in *X. nigrens*.

The patterns detected in this study have two important implications for the evolution of communication systems and sexual selection. First, this study adds to the growing number of examples of opportunities for sensory exploitation (Ryan 1990, 1994; Ryan et al. 1990a). If male *X. nigrens* evolved bars, this trait would be favoured by sexual selection, because female preference for bars already exists in this species. Further studies of preference and bars in sword-tails, in which both traits are mapped onto a phylogeny for *Xiphophorus*, could be used to determine whether the preference was maintained when the bars were lost as opposed to having evolved in the absence of the bars.

Second, the signal and receiver showed different degrees of congruence between the two taxa depending on the sex of the receiver. We suggest two reasons for this sex difference. First, this difference could result from differences in strength or the presence of a genetic correlation between signal and receiver, depending on the sex of the receiver. Female responses and male signals can become genetically correlated, if females with the strongest responses mate with males with the strongest signals (Fisher 1958; Heisler 1984). Indeed, several sexual selection models rely on a genetic correlation between female preference (response) and male trait (signal) for the evolution of female preferences (Kirkpatrick & Ryan 1991). Although male responses and male signals can

not become genetically correlated by this mechanism, both male and female responses could become genetically correlated with male signals by other mechanisms (Falconer 1981). Selection experiments could determine whether genetic correlations exist between male responses and male sexually selected traits.

The sex difference we detected could have also resulted from differences in selective regimes to which the sexes were exposed. In other words, the tighter evolutionary coordination between male signal and male response might suggest stronger selection against responding incorrectly to this signal as a rival than as a mate. Although the bars could currently be used to distinguish between a conspecific and heterospecific, they probably do not function in this respect, because *X. multilineatus* and *X. nigrensis* are allopatric. In addition, these two species will produce hybrid offspring in the laboratory that are both viable and fertile (Kallman 1989). Therefore, the standard cost associated with mating with the wrong species may not apply to a choice between males of these two species.

Further studies of the congruence of male responses and female responses to the bars are necessary to determine whether the pattern we detected can be generalized to the evolution of the bars in this genus. The evidence presented here, however, suggests that studies of the evolution of female preferences that examine only female responses to a signal may be missing an important evolutionary component: the responses of males.

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