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The effect of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens*

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The evolution of signals has mainly been considered in the context of an emitter–receiver dyadic interaction. However, communication usually occurs in the presence of individuals (an audience) that are not directly involved in the communication interaction, and it is more realistic to assume that signal evolution occurs in a network. Several types of information could be available to an audience, and, therefore, the presence of an audience could have effects on the behavior of the communicating animals and on signal evolution. We investigated whether the presence of an audience of conspecifics affected intrasexual aggressive communication in male fighting fish. We found that if the audience was a female, males increased the intensity of conspicuous displays that can be used in communication with both males and females and decreased highly aggressive displays that are solely directed to males. If the audience was a male of similar size, there was no significant change in the way in which males displayed. These results suggest that the presence of an audience could be one reason that many long-range and conspicuous signals are often shaped to transmit information to both males and females. *Key words:* aggression, audience, *Betta splendens,* communication, signal evolution. *[Behav Ecol 12:283–286 (2001)]*

Traits that are specialized for the purpose of communication (signals and displays) are the products of natural selection and the results of coevolution between receiver and emitter. Some signals are directed toward mainly one individual (e.g., many aggressive interactions), whereas others may be directed toward several individuals (e.g., many mate attraction signals). The evolution of signals is often considered in the context of an emitter–receiver dyadic interaction. However, as many signals are conspicuous and/or long range, even signals directed toward one individual can be received by several individuals (e.g., Wiley, 1983; Zahavi, 1980), and signal evolution should occur in a network context (McGregor, 1993; McGregor and Peake, 2000).

Animals other than those directly involved in an interaction have been called an ‘‘audience’’ (e.g., Evans and Marler, 1984). Several types of information could be available to an audience, and therefore the presence of an audience would constitute a selection pressure for signal evolution. For example, eavesdropping has been defined as a way of extracting information by monitoring interactions between other individuals (McGregor and Dabelsteen, 1996). Eavesdropping can give information on quality of potential mates or potential opponents (Doutrelant and McGregor, 2000; Naguib and Todt, 1997; Oliveira et al., 1998; Otter et al., 1999). Consequently, signaling behavior could change in the presence of an audience.

Many studies have investigated how the presence of predators influences the evolution of color traits or behavioral displays (e.g., Magnhagen, 1991), but few studies have investigated the effects of an audience of conspecifics on signal evolution (alarm signals are an exception; e.g., Evans and Marler, 1984; Gyger et al., 1986; Marler and Evans, 1996). The aim of our study was to investigate if the presence of male or female conspecifics modified intrasexual communication in male fighting fish (*Betta splendens*).

Breeding fighting fish are territorial, defending an area around a nest of mucus-coated bubbles floating on the water surface. They are a good species in which to study the effects of an audience because their aggressive displays are highly stereotypic, conspicuous, and well documented (e.g., Baenninger, 1984; Bronstein, 1985; Evans, 1985; Galizio et al., 1985; Halperin et al., 1992; Robertson, 1979; Wallen and Wojciechowski Metzlar, 1985). Fighting fish are also the only species of fish in which both males and females have been shown to eavesdrop (Doutrelant and McGregor, 2000; Oliveira et al., 1998).

Aggressive displays in *B. splendens* have been shown to be an honest indicator of male condition and/or motivation (Evans, 1985; Halperin et al., 1998; Simpson, 1968). Robertson and Sale (1974) showed that gill cover erection and tail beats are used in male–male interactions and in male–female interactions. In contrast, they found that biting is a behavior used only in male–male interactions and that males add bubbles to the nest in male–female interactions. Time in gill cover erection has been shown to predict fighting capacity and is correlated with behavioral dominance (Evans, 1985); number of bites and number of tail beats have been shown to be energetic and reliable signals of male quality (Halperin et al., 1998). We would predict a change in the intensity of these behaviors if an audience modifies male–male intrasexual communication.

MATERIALS AND METHODS

We obtained 28 males and 4 females from several local wholesalers. We measured distance between the mouth and base of

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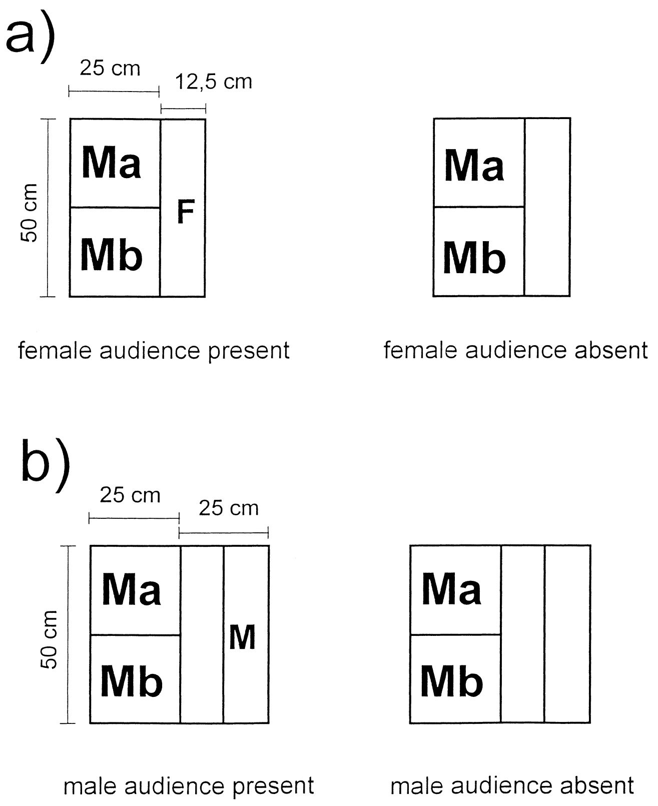

Figure 1
Top view of the experimental setup designed to investigate the effect of an audience on male-male (Ma, Mb) interactions. F, female audience; M, male audience.

tail (standard length) on each fish. All interacting males were matched in size and color (red or blue). Males ranged in size from 3.5 to 4.1 cm (mean ± SD, 3.8 ± 0.15). Fish were maintained on a 12 h:12 h light:dark cycle at 25–27°C and were fed twice daily using Tetramin flake food and live food (*Daphnia pulex*) or frozen *Tubifex*. Aquaria were filled with aged tap water, and 10% of the water was changed every 10 days. Males were held in isolation in aquaria 25 × 25 × 30 cm (length × width × height). Each fish was introduced into its aquarium 24 h before the interaction occurred.

Experiment 1: Female audience

Interactions between the male subject (Ma) and another male (Mb) occurred in aquaria 50 × 25 × 30 cm divided in two by a removable, opaque partition and a fixed transparent partition (Figure 1). This aquarium was flanked by an aquarium 50 × 12.5 × 30 cm that could contain a female (the audience; Figure 1).

There were 20 subjects, each of which interacted twice with the same male for 10 min on each occasion. One interaction was in the presence of a female (audience), the other was in the absence of a female (no audience). Two hours separated the two interactions. The order of these interactions was balanced over the experiment (i.e., each type of interaction was the first to be presented on an equal number of occasions). Each male acted as a subject in one trial (i.e., two interactions) and also as the other male in a trial with a different male.

For the trial with an audience, males were allowed to see the female for 3 min before the male–male interaction began. Males immediately began displaying to one another through the transparent partition after the opaque partition was removed. We measured the following displays of the subject from video recordings: time with erect gill cover, number of bites, number of tail beats, and time at less than one fish length to the partition separating the two males. We analyzed these behavioral measures with Wilcoxon matched-pair signed-ranks tests.

Experiment 2: male audience

We used the same experimental design as for experiment 1 with a male audience. The same behavioral measures were collected. Twelve of the 20 subjects had been subjects in the first experiment, but they interacted with a different male in this experiment. The aquarium holding the male audience differed from that holding the female audience in that the male was placed in the outer part to prevent the male subjects from interacting with the audience rather interacting with one another (Figure 1b). Because of this difference in design, we did not statistically compare the results obtained for male and female audiences.

RESULTS

In the absence of a female audience, males behaved significantly differently from the way they behaved when a female audience was present for all the four measures collected (Table 1). Significantly more males performed more tail beats, spent more time with gill cover erect, interacted farther away from the other male, and performed fewer bites with a female audience than without.

We found no significant differences in the same four measures in the presence of a male audience compared with the absence of an audience (Table 1). However, the difference in time spent within one fish length of the partition separating the interacting males approached significance. The tendency was that more males performed more tail beats, spent more time with gill cover erect, interacted farther from the other male, and performed more bites with a male audience than without. The statistical power of detecting an effect of a male audience with our sample size of 20 is approximately 0.7 (Zar, 1999).

DISCUSSION

Our experiment showed that a female audience caused males to change the nature of male–male interactions. One reason for this change is that females may not use the same signals as males when assessing male quality. Signals used in intrasexual communication are thought to contain information on male motivation or male strength. Intersexual signals may attract females directly through sensory exploitation, indirectly by acting as indicators of genetic quality of males, and/or may be honest indicators of current quality (for a review, see Andersson, 1994). Therefore, in the presence of a female audience, interacting males could use a different combination of signals than in the absence of females. The nature of the difference we found supports this interpretation. In the presence of a female audience, males performed fewer of the aggressive displays that are used only in male–male interactions (bites and close-range interactions) and more of the displays that are considered more conspicuous (i.e., tail beats) and that are used in the presence of both sexes (i.e., time with erect gill cover; Robertson and Sale, 1974). This interpretation supports a role for an audience in the evolution of conspicuous and general signals.

A motivational explanation for the effect of an audience (e.g., males could be more motivated to display in the pres-

Table 1
Male behavior during male–male interaction in presence or absence of an audience

	Female audience				Male audience			
Behavior	Present	Absent	z^a	p^b	Present	Absent	z^a	p^b
Time (s) <1 fish length from the partition separating the two males								
Mean ± SE	237 ± 46	343 ± 51	−2.2	.028	273 ± 41	319 ± 44	−1.9	.06
Median	186	334			299	384		
Lower quartile	90	148			67	154		
Upper quartile	348	581			466	479		
No. of tail beats								
Mean ± SE	68 ± 14	50 ± 12	−2.9	.003	74 ± 15	70 ± 14	−1.0	.29
Median	62	38			64	57		
Lower quartile	14	1			16	14		
Upper quartile	102	90			114	118		
Time (s) with gill cover erection								
Mean ± SE	166 ± 21	139 ± 21	−2.1	.03	243 ± 36	229 ± 36	−0.7	.48
Median	164	124			241	225		
Lower quartile	85	74			92	79		
Upper quartile	218	204			378	357		
No. of bites								
Mean ± SE	24 ± 7	40 ± 10	−2.4	.016	22 ± 6	20 ± 7	−1.1	.28
Median	13	20			10	8		
Lower quartile	0	3			1	0		
Upper quartile	38	74			38	16		

[a] z, Wilcoxon matched-pairs signed-ranks test.

[b] p values are two tailed; $n = 20$.

ence of an audience than in its absence) is a different, but complementary, level of interpretation; it is not an alternative (Tinbergen, 1963). An explanation of our results that is closely related to this motivational explanation is that males were placed in a conflicting situation (display to the female audience or to the interacting male) and alternated displays toward the male with displays toward the female. We can exclude these explanations for a number of reasons. First, there was no evidence of a male–female interaction: males did not perform displays known to be only directed at females (adding bubbles to the nest), neither did females perform displays toward the males (e.g., vertical stripes, gill cover erection). Second, in three cases, the opponent stopped displaying and lay on the aquarium bottom displaying submissive coloration. In these cases the male approached to less than one fish length from the partition separating male and female and started an interaction with the female. This suggests that males direct attention to their male opponent and only switch attention to the female when the opponent is considered beaten.

There are several explanations for the lack of an effect of a male audience. One explanation is that displaying males use honest signals of quality, and therefore they cannot change the intensity of their display in the presence of an audience. Second, the signals to a male audience would be the same as those used in the male–male interaction; therefore we would not expect different displays to be used in the presence of a male audience. Third, if signal intensity is related to relative differences in features such as size (R. F. Oliveira, unpublished observation), the fact that the three males in each trial (two interacting males, one male as audience) were closely matched for size and color (see Methods) would minimize the effect of a male audience.

The fact that the male audience could not approach closer than 12.5cm (approximately 3 fish lengths) to the interacting males may have contributed to the failure to find an effect of the male audience. Two factors make this rather unlikely. First, there was often a considerable distance between the interacting male and the audience because the interactive males moved back and forth along the partition between them. This movement by the interacting males could add up to 25 cm (about 6 fish lengths) to the distance separating the male or female audience and the interacting males. Second, on the occasions when the opponent male did not display actively or moved to its end of the tank, the subject immediately approached to within one fish length of the partition and directed displays toward the audience regardless of the behavior of the audience. This suggests that the subject was aware of the audience throughout the trial.

To conclude, we found that the effect of a female audience was that males used more conspicuous and generalist signals (i.e., signals used for either male–male or for male–female interactions) in male–male interactions. This audience effect could explain why many long-range or conspicuous signals, such as bird song (e.g., Catchpole and Slater, 1995), are generally used both for inter- and intrasexual communication. As a result, their structure often reflects a trade-off between intrasexual selection and intersexual selection functions. Our results, together with others on audience effects and eavesdropping (reviewed by McGregor and Peake, 2000), emphasize the importance of considering communication in the context of networks for a better understanding of signal evolution.

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