COURTSHIP BY SUBORDINATE MALE SIAMESE FIGHTING FISH, BETTA SPLENDENS: THEIR RESPONSE TO EAVESDROPPING AND NAÏVE FEMALES

by

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Summary

In a social environment, a communication signal may provide information to individuals other than those interacting with the signaler. Eavesdropping is gathering information without being directly involved in the communication interaction. Female Siamese fighting fish, *Betta splendens*, choose the winner of male-male aggressive interactions based upon information she extracts from eavesdropping. Naïve females, those that have not witnessed the interaction, show no consistent preference for either male. This suggests that losers would be more successful in courting a naïve female. We conducted two sets of trials: one set tested the losers' courting preference of eavesdropping females or naïve females whereas the other tested the winners' courting preference. We found that losers displayed gill cover erection, a courting behaviour, significantly more towards the naïve female than towards the eavesdropping female whereas the winner showed no preference. These results suggest that male *B. splendens* can moderate their response to an audience in ways more complex than previously appreciated. Our data support the suggestion that communication can serve as a network that reaches beyond the immediate signaler and receiver. Understanding the complexity of communication networks will enable us to broaden our ideas about the mechanisms of sexual selection.

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Introduction

In most social environments communication often takes place in the context of a community, a network of several signalers and receivers. Individuals other than those in the signaling interaction may gain information from communication signals (*e.g.* Bradbury & Vehrencamp, 1998; McGregor & Peake, 2000; Earley & Dugatkin, 2002). As our understanding of the influence of individuals not directly involved in a signaling interaction increases so does the potential implication of information transfer in these complex networks. A network model of communication provides a context for strong selection on honest communication signals. Selective forces not only act on signalers and receivers, but on audiences as well. This has been widely recognized in the context of predator-prey interactions when a predator uses communication signals from prey to locate them (*e.g.* frogs *Physalaemus pustulosus* and bats *Trachops cirrhosus*, Ryan *et al.*, 1982; fireflies *Photurus* sp. and *Photinous* sp., Lloyd, 1975).

In a communication network, through eavesdropping, an audience may gather information from communication signals of conspecifics. By eavesdropping, individuals are able to gather information about fighting ability, relative quality, motivation and condition without being directly involved in the interaction (*e.g.* McGregor & Peake, 2000; Mennill *et al.*, 2002). This information can be acquired at little cost, and at small risk (*e.g.* McGregor, 1993; Johnstone, 1998). Several studies have shown that eavesdropping is important in the assessment of opponents (nightingales *Luscinia megarhychos*, Naguib & Todt, 1997; green swordtails *Xiphophorus helleri*, Earley & Dugatkin, 2002; Siamese fighting fish *Betta splendens*, Oliveira *et al.*, 1998) and male quality by females (great tits *Parus major*, Otter *et al.*, 1999; black-capped chickadees *Poecile atricapilla*, Mennill *et al.*, 2002; Siamese fighting fish *Betta splendens*, Doutrelant & McGregor, 2000). While individuals use information gained from eavesdropping to direct their behaviour (McGregor & Peake, 2000), the presence and the sex of eavesdroppers, in turn, affects the behaviour of the signaler (Doutrelant *et al.*, 2001; Matos & McGregor, 2002).

Female Siamese fighting fish, *Betta splendens,* use information gained from eavesdropping in mate choice (Doutrelant & McGregor, 2000). Male *B. splendens* defend territories that provide access to females (Bronstein, 1984; Doutrelant & McGregor, 2000). In order to maintain a territory, a

male must be able to win male-male aggressive interactions (Robertson & Sale, 1974). The territorial behaviour of *B. splendens* provides a context for intense signal selection and honest displays (Bronstein, 1994; Halperin *et al.*, 1998). Male displays include the conspicuous and stereotyped signals of fin spread, tail beats, and gill cover erection, used for both courtship and aggression, and bites, used solely in aggressive interactions (Robertson & Sale, 1974; Doutrelant *et al.*, 2001). The frequency and duration of aggressive displays are reliable predictors of the winner (Bronstein, 1994). Eavesdropping females, based upon male displays, will in the initial stages of mate choice display more towards the winner of a male-male aggressive interaction (Doutrelant & McGregor, 2000). Naïve females, that have not seen males display during a male-male aggressive interaction, show no preference for the winner or loser (Doutrelant & McGregor, 2000).

Male *B. splendens* increase biting and decrease time spent near the opponent, during aggressive interactions in the presence of an eavesdropping male. With a female audience, male interactions are less aggressive (*i.e.* less biting) and take longer to escalate. This suggests that males visually distinguish between male and female audiences and adjust their behaviour accordingly (Matos & McGregor, 2002). Following male-male aggressive interactions, the loser may exhibit submissive colouration and behaviours that communicates his subordinate status and terminates aggression from the winner (Robertson & Sale, 1974).

Given that female *B. splendens* choose to mate with winners, we compared the losers' courting behaviour to an eavesdropping female versus a naïve female. We expected that the loser of a male-male aggressive interaction, when given a choice between courting an eavesdropping female or a naïve female, would prefer the naïve female. Choosing to court a naïve female, a female that has no prior information about his inferior quality, should increase his likelihood of mating.

Methods

Twelve male *B. splendens*, variable in colour and size, and three females, equal in size and colour display, were used to investigate a loser's courting behaviour towards an eavesdropping or naïve female. Each *B. splendens* was kept isolated in a 7.5 L tank (30.25 × 15.0 × 20.5 cm) at room temperature. Removable opaque partitions placed between all of the tanks allowed us to control visual contact between fish and to prevent interactions prior to the experiment.

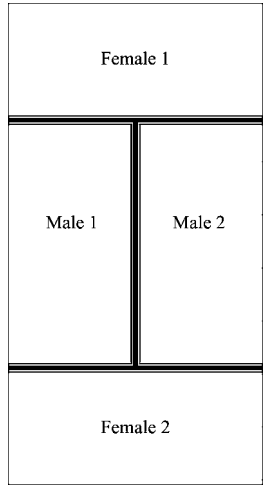

Fig. 1. The experimental tank set-up. Male and female *B. splendens* were located in adjacent tanks separated by removable opaque partitions indicated by bold lines.

We ran eleven trials in which each male was tested as a loser only once. The experimental set-up consisted of four tanks as shown in Fig. 1. Two males and two females, all chosen randomly, were placed in adjacent tanks separated by removable opaque partitions. The partition between one of the female tanks and the two male tanks was removed. Each male was able to interact with this eavesdropping female for 3 minutes to ensure that the males were aware of the female's presence. Next, the partition between the two males was removed to initiate male-male aggressive interaction for 15 minutes. The duration of gill cover erection and the number of bites clearly directed to the opponent, were documented for each male. The male with the longest duration of gill cover erection and the greatest number of bites was determined as the winner of the interaction (Bronstein, 1985). Partitions were then replaced to visually isolate the winner. Plastic inserts were placed in female tanks to contain them in full sight of the loser at all times. The partition between the naïve female and loser was then removed to allow him to interact with eavesdropping and naïve females for 10 minutes.

The duration of gill cover erection and number of bites performed in the sections of the tank nearest the eavesdropping and naive females were recorded. In addition, the duration of time each male spent in the section near the eavesdropper, the middle or neutral section, and the section near the naive female, all in equal thirds of the tank (approximately two fish lengths), was recorded. The construction of a bubble nest was also observed but not recorded since there was only a single nest associated with each male and we could not clearly determine if the behaviour was directed toward the eavesdropping or the naïve female.

Eleven separate trials were run to determine a winner to test his response to the eavesdropping and naïve female. We followed the same procedure used for the loser. These trials were performed to rule out an alternative hypothesis that the naïve female was preferred as a novel stimulus. Thus, each male was tested once as a loser and once as a winner. Females were chosen randomly; female A was naïve 12 times, female B, 5 times, and female C, 5 times. Female A was an eavesdropping female 10 times, female B, 6 times, and female C, 6 times.

One-tailed Wilcoxin signed rank tests were used to determine if significant differences existed between behaviours directed towards the eavesdropping or naïve female by male *B. splendens*. Means ± standard errors are reported.

Results

The loser spent significantly more time with gill cover erection toward the naïve female (mean ± SE, 22.0 ± 4.3 sec) than towards the eavesdropping female (11.0 ± 3.2 sec) (Fig. 2, $T = 0$, $p = 0.004$, $N = 11$). Eight out of the eleven losers spent more time in the third of the tank closest to the naïve female (264.0 ± 26.9 sec), than to the eavesdropping female (194.0 ± 18.9 sec) or in the neutral section (144.0 ± 26.9 sec). There was a strong tendency for the loser to spend more time closest to the naïve female, however, this difference was not statistically significant (Fig. 3, $T = -16$, $p = 0.065$, $N = 11$).

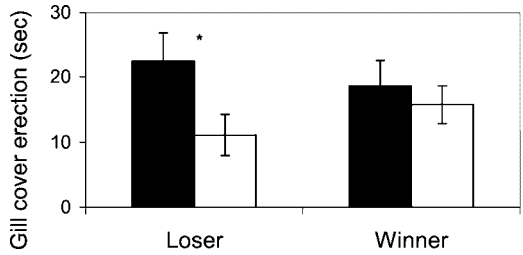

Fig. 2. Means and standard errors for the duration of gill cover erection by losers and winners while in the sections of the tanks closest to the eavesdropping (white bars) and naive female (black bars). * indicates $p < 0.05$.

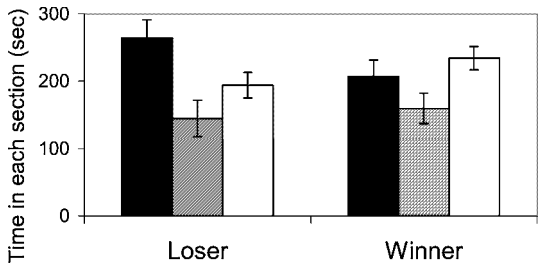

Fig. 3. Means and standard errors for time spent by losers and winners in the three sections of the tank; eavesdropper (white), neutral (gray), naive (black).

There were no significant differences in time spent with gill cover erection by the winner toward the naïve female (19.0±3.9 sec) and the eavesdropping female (16.0 ± 2.9 sec) (Fig. 2, $T = 22$, $p = 0.156$, $N = 11$). The winner spent 207 ± 24.4 seconds in the naïve section, 234 ± 17.3 seconds in the eavesdropper section and 159 ± 22.6 seconds in the neutral section (Fig. 3). This difference in time spent in tank sections by the winner was not significant ($T = 26$, $p = 0.267$, $N = 11$).

All male-female interactions consisted of courting behaviours; gill cover erection and construction of bubble nests. No solely aggressive behaviours (*i.e.* bites) were observed in any of the male-female interactions (Robertson & Sale, 1974).

Discussion

Losing male *B. splendens* courted the naïve female preferentially, while the winner of the male-male aggressive interaction showed no preference for either female. Losers performed significantly more gill cover erection toward the naïve female and demonstrated a strong tendency to spend more time in the section of the tank closest to the naïve female. Our results, that losers choose to court naïve females, suggests male *B. splendens* are able to assess the effect of their subordinate status and consequent low attractiveness to females. By courting naïve females, they increase their chance of being accepted by a female, while reducing the cost of courting females that will ultimately reject them.

Any differences seen in male behaviour were not due to variation in female behaviour. Both females exhibited horizontal stripes at the beginning of the trials showing that they were not sexually receptive (Robertson & Sale, 1974). Though it was not quantitatively recorded, both females appeared to direct their behaviours equally toward the male. Even though some females exhibited vertical stripes, indicating sexual receptivity (Robertson & Sale, 1974) for short periods (1-10 sec), there appeared to be no systematic differences between the eavesdropping and naïve females. Doutrelant & McGregor (2000) showed that although naïve females may visit the loser more often than the eavesdropping female at first, naive females do not spend significantly more time displaying to the loser. Overall eavesdropping females show preference for the winner while naïve females show no preference. If

female mate choice affected male mate choice, we would expect the winner to choose the eavesdropping females while the loser would show no preference. In contrast we found that winners showed no preference and losers preferred naïve females. This result also refutes the alternative hypothesis that losers prefer to court the naïve female because she is a novel stimulus.

In this study, losing male *B. splendens* courted naïve females rather than the eavesdropping females based upon the outcome of a male-male aggressive interaction. Signals emitted by male *B. splendens* during these interactions contained information on their relative quality (*e.g.* ability to defend a territory), which could be monitored and used by females in selecting a mate (Doutrelant & McGregor, 2000; McGregor, 1993). The effect of eavesdropping audiences on the behaviour of the signaling males has been demonstrated in several studies (*e.g.* Doutrelant & McGregor, 2000; Doutrelant *et al.*, 2001; Matos & McGregor, 2002). We believe we are the first to explore the effect of how the eavesdropper's potential choice affects the consequent behaviour of the original signalers. Further investigations of the role of eavesdropping in mate choice will help us to understand the effects of communication networks on the interactions between intra- and intersexual selection.

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