

# Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking

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Aggressive contests probably occur in networking environments where information about fighting ability is conveyed both to an opponent and to individuals peripheral to the fight itself, the bystanders. Our primary aim was to investigate the relative influences of eavesdropping and prior social experience on the dynamics of aggressive contests in *Xiphophorus helleri*. A bystander's ability to witness an encounter was manipulated using clear, one-way mirror, and opaque partitions. After watching (or not watching) the initial contest, the bystander encountered either the winner or loser of the bout. Treatment comparisons of bystander–winner or bystander–loser contest dynamics indicated the presence or absence of winner, loser, or eavesdropping effects. Winner and loser effects had negligible influences on bystander contest dynamics. Eavesdropping significantly reduced the bystander's propensity to initiate aggression, escalate, and win against seen winners regardless of whether the watched bout had escalated or not. Though eavesdropping had relatively little effect on bystander–loser contest dynamics, bystanders were less prone to initiate aggression and win against losers that had escalated in the witnessed bout. Thus, bystanders appear to preferentially retain and utilize information gained about potentially dangerous opponents (winners or persistent losers). Our data lend clear support for the importance of eavesdropping in visually based aggressive signalling systems.

**Keywords:** eavesdropping; aggression; social experience; communication network; *Xiphophorus helleri*

## 1. INTRODUCTION

Animals utilize an array of signals during aggressive contests to communicate information to conspecific opponents about physical prowess or willingness to escalate (see, for example, McGregor *et al.* 1992; Hughes 1996; Breithaupt & Atema 2000; Sparkes *et al.* 2000). Much work has focused on the evolution of signalling systems, in particular on conflicts of interest between the signaller and receiver, selective pressures that guide signaller and receiver behaviour, and the maintenance of honesty in such systems (Johnstone 1997). Common among these studies is the treatment of signalling interactions as 'two-animal games' involving only one signaller and one receiver. In fact, most game theoretical models of animal contests, and the supporting empirical tests, focus primarily on the dyad and on any individual attributes or assessment strategies that may influence a contestant's decision to continue to fight or flee (Enquist & Leimar 1983; Enquist *et al.* 1990; Marden & Rollins 1994; Mesterton-Gibbons *et al.* 1996; Mesterton-Gibbons & Adams 1998; Payne 1998).

Despite the important contributions of such a dyadic focus to our understanding of contest behaviour, it necessarily limits our view of how animals interact within their social environment. The social environment includes the two contesting animals and any additional individuals, the bystanders, that are peripheral to the interaction but within signal detection range. Extending the scope of aggressive contest research past the focal dyad and into the social milieu allows us to address the dynamics of 'n-animal games'. In these games, signaller behaviour may

be transmitted not only to one other individual but to multiple receivers, thereby creating a communication network (McGregor 1993; McGregor & Peake 2000; McGregor *et al.* 2000). These networks more accurately reflect the conditions under which signalling interactions may take place in group-living animals or those that establish contiguous territories and thus have several neighbours.

Indeed, a growing body of empirical evidence suggests that bystanders both influence and are influenced by aggressive interactions that occur within their social environment. As such, the communication network can be examined from the perspective of both the contestants and the bystanders. On one hand, if the individuals engaging in an aggressive contest change their behaviour in the presence of a bystander, then an audience effect is operating (Evans & Marler 1994). For example, male Siamese fighting fish (*Betta splendens*) increase the time spent in gill cover erection and decrease the number of bites directed towards a male opponent when a female bystander is present rather than absent (Doutrelant *et al.* 2001). On the other hand, bystanders may eavesdrop, or extract information from aggressive interactions between others, and subsequently modify their own agonistic response towards the monitored individuals (McGregor & Dabelsteen 1996). In fact, recent work on fighting fish and territorial songbirds suggests that the agonistic behaviour of a bystander is influenced by watching fights and is largely dictated by the identity of its subsequent opponent, i.e. perceived winner or perceived loser (McGregor *et al.* 1997, 2001; Naguib & Todt 1997; Oliveira *et al.* 1998; Naguib *et al.* 1999; Peake *et al.* 2001). Eavesdropping may provide useful information on the fighting ability of potential competitors without the observer itself having to expend energy or risk the costs of fighting (e.g. injury), and may be particularly advantageous when combat bears a high cost (Johnstone 2001).

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One concern with allowing the bystander to engage directly with the winner and loser it had watched is whether the effects of eavesdropping can be partitioned from the influence of the original combatants' prior social experience. Individuals that experience victory are more likely to win future duels while previous losers are more prone to be defeated in later encounters (e.g. Bakker *et al.* 1989; Schuett 1997; Hsu & Wolf 1999). Thus, interpreting the degree to which eavesdropping mediates contests between a bystander and a previous winner or loser may be confounded by the prior social experience of the initial contestants.

The primary aims of this study were to tease apart the effects of eavesdropping and social experience on the dynamics of aggressive contests in male green swordtail fish (*Xiphophorus helleri*) and to assess the nature of the behavioural changes that accompany eavesdropping. *X. helleri* is an excellent model system for investigations of eavesdropping on visually based cues as male agonistic behaviour is conspicuous, stereotypical (e.g. Ribowski & Franck 1993a), and has been studied quite extensively (e.g. Franck & Ribowski 1987, 1989; Beaugrand *et al.* 1991; Ribowski & Franck 1993b). In addition, swordtails form strict linear dominance hierarchies both in the laboratory and in the field, a social environment that should be conducive to networking effects (Beaugrand *et al.* 1984; Franck & Ribowski 1993; Franck *et al.* 1998; Earley & Dugatkin 2002).

## 2. METHODS

### (a) Maintenance and experimental protocol

Heterosexual groups of *X. helleri* were obtained from Sunshine Aquatic Farms (Tampa, FL, USA) and were transferred to laboratory aquaria ranging in size from 189 l to 429 l. Each holding tank was equipped with chemical and biological filtration, substantial aeration, a gravel substrate at a depth of 6 cm, and plants and clay pots as refuge. The temperature was maintained between 25 and 27 °C and the pH at 7.6 with a 12 L : 12 D cycle. Aquarium salt and 'Stress Coat' were added as needed to reduce osmotic stress, condition the water, and replenish the fish's natural slime coat (e.g. following a water change). The fishes were fed 'TetraMin' flake food daily with occasional supplements of brine shrimp.

Males were removed from the holding tanks and measurements of body length, sword length, and body width were carried out. Lateral surface area ((body length × body width) + sword length) was then calculated (Beaugrand *et al.* 1996). Three fishes were matched for size (less than 0.2 lateral surface units difference) and placed in individual isolation tanks (8 l) for 48 h. Two of these fishes were designated as the initial contestants (F1 and F2) and the third as the bystander (B). Following isolation, the fishes were transferred to experimental tanks (38 l) that were partitioned into three compartments of equal size. Each fish was placed into one of the compartments and was visually isolated from all other fishes by an opaque, T-shaped partition. In addition, the bystander was separated from the initial contestants by one of three partitions: opaque plastic (opaque treatment), one-way mirror (mirror treatment), or clear glass (clear treatment) (figure 1). We minimized transfer of chemical cues between fishes by fitting the partitions against the sides of the aquaria as tightly as possible without compromising easy removal. If chemical cues cross the partitions, our experi-

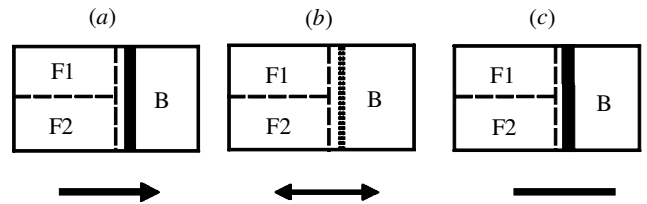


Figure 1. Apparatus used in experiment 1 with treatments: (a) one-way mirror, (b) clear glass, and (c) opaque plastic. F1 and F2 are the initial contestants while B is the bystander. The T-shaped dashed line is a partition that eliminates visual contact between F1, F2, and B. The arrows indicate the direction of potential information transfer after the T-partition is lifted.

mental design ensures that they would do so equivalently across treatments (i.e. each partition was fitted to the aquarium in the same manner) and thus should not bear on the interpretation of our results.

The fishes were given 16 h to acclimatize to the experimental aquaria before any behavioural observations commenced. The isolation period, together with the acclimatization time, aims at minimizing the influence of prior social experience obtained within the communal holding tanks; the behavioural effects of winning and losing persist for at least 24 h in *X. helleri* (Franck & Ribowski 1987). At the start of the trial, the T-shaped partition was lifted to facilitate an encounter between F1 and F2 and to reveal (or not reveal) these contestants to the bystander. In the opaque treatment, the bystander could not witness the fight between the initial contestants, nor were the contestants aware of the bystander's presence. The bystander was able to observe the encounter between F1 and F2 in the mirror treatment but the contestants remained naive to its presence. Tint was placed over the mirror side of the one-way glass to minimize reflection and thus to eliminate the possibility that the initial contestants could see (or respond to) their mirror image. In the clear treatment, both the bystander and the initial contestants were aware of one another's presence. The contestants could therefore interact with the bystander across the clear glass.

The aggressive (approach, threat display, attack, bite) and submissive (avoid, retreat) behaviour of F1 and F2 were recorded during one initial 45 min focal period and two subsequent 15 min observation sessions; the total allotted interaction time was 6 h. In addition, the initiator of each aggressive behaviour and the number of reciprocal acts (e.g. mutual threat displays, circling, mouth-wrestling) were recorded; for a detailed description of the reciprocal acts, see Franck & Ribowski (1989). The fish that aggressed towards its opponent at least 10 times without reciprocation was designated the dominant individual (Francis 1983). Following the initial bout, either the winner (W) or loser (L) was removed from the apparatus. The partition separating the bystander (B) from the remaining individual was then removed to facilitate either B versus W or B versus L contests. The same behavioural data were recorded for these bystander contests as in the initial bout and a winner and loser were determined following 75 min of observation time. A total of 103 bystander–winner contests (mirror,  $n = 34$ ; clear,  $n = 35$ ; opaque,  $n = 34$ ) and 75 bystander–loser contests ( $n = 25$  for each treatment) were conducted. The trials were observed from behind a mesh window to minimize distraction of the fishes by the observer. The data were logged manually; the contests were not recorded on video.

### (b) Predictions

The presence of winner and loser effects was determined by analysing the outcome of the bystander contests (B versus W and B versus L) in the opaque treatment only. If the winner of the initial bout defeats the bystander in significantly more than 67% of the contests, then a winner effect exists. Similarly, if the loser of the initial bout submits to the bystander in significantly more than 67% of the contests, then a loser effect exists. This rigorous null hypothesis stems from the use of a 'self-selection' procedure for determining winners and losers as opposed to a 'random selection' procedure. In the random selection procedure, winning and losing experiences are imposed upon individuals in an independent fashion (e.g. by pitting them against considerably smaller or larger individuals; see Hsu & Wolf 1999) while in the self-selection procedure, the winner and loser are determined from a contest between two well-matched opponents. In the self-selection procedure, prior experience effects may be confounded by intrinsic differences in the contestants' fighting abilities; self-selected winners (losers) will win (lose) again in 67% of subsequent contests based on individual differences alone (Chase *et al.* 1994).

For example, imagine three individuals, A, B, and C with fighting abilities of 10, 20, and 30, respectively. If A and C interact first, then B is left as the bystander. Similarly, if B and C interact first, then A stands by. In these cases, C should win both the initial fight and the bystander contest based on its superior fighting ability relative to A and B. However, if A and B are the initial contestants and C is the bystander, then B would win the initial fight but would lose the bystander contest to C. Thus, considering all possible triadic arrangements, the initial winner should defeat the bystander in two-thirds of the trials. However, any probability significantly greater than 67% indicates the presence of prior experience effects (Begin *et al.* 1996).

The primary difference between the mirror and opaque treatments was the ability of the bystander to observe the initial interaction. In both of these treatments, the contestants were naive to the bystander's presence, while eavesdropping could occur only in the mirror treatment. Thus, differences between the mirror and opaque treatments in the dynamics (e.g. probability of escalation, probability of bystander initiation) or outcome of the bystander contests indicate the presence of an eavesdropping effect. If eavesdroppers increase their estimate of the winner's fighting ability after witnessing its victory, then the bystander should be less likely to initiate aggression, escalate, and thus win the bystander–winner contests than an individual that did not eavesdrop. Similarly, if eavesdroppers decrease their estimate of the loser's fighting ability after watching its defeat, then the bystander should be more likely to initiate aggression and win the bystander–loser contests than individuals that did not eavesdrop. As a consequence, we expect lower degrees of bystander contest escalation in the mirror than the opaque treatment (table 1).

In the clear treatment, the bystander and the initial contestants can interact and possibly mutually assess one another across the glass partition; this is not possible in the mirror treatment. Thus, any significant differences in bystander contest dynamics or outcome between the mirror and clear treatments indicate an influence of prior assessment—that is, assessment that occurs between the bystander and either contestant across the clear partition during the initial contest phase. Assessment across the clear glass may provide additional information to the bystander about the relative fighting ability of the initial contestants. If this

assessment reinforces the information gathered via eavesdropping, the bystander may even further increment or decrement its estimate of the fighting ability of the winner and loser, respectively. Under these circumstances, we predict that the bystander should be significantly less (more) apt to initiate and win the contests against the winner (loser) in the clear treatment than in the mirror treatment. Prior assessment should also reduce the probability of escalation in clear treatment contests relative to those in the mirror treatment, as encounters between familiar individuals are often settled by less expensive means than those between unfamiliar individuals (Johnsson & Akerman 1998) (table 1).

## 3. RESULTS

### (a) Initial contest dynamics

The dynamics of the initial contests could potentially influence the aggressive state of the winners and losers prior to their interaction with the bystander. Similarly, the eavesdropper's response to the winner and loser could depend upon the characteristics of the contest it had witnessed. Thus, an important question to address is whether the initial contestants behaved differently when exposed to the eavesdropper (clear) versus when they were naive to its presence (mirror, opaque)—that is, whether an audience effect existed. We confine the audience effect to situations in which behavioural modifications occurred during the contest phase of the initial interaction, i.e. between contest initiation and contest resolution in the presence of a bystander.

Log-linear analyses were conducted to ascertain whether the probability of initial contest escalation or patterns of initiation behaviour differed across treatments. Contests 'escalated' if the combatants engaged in circling or mouth-wrestling behaviour (e.g. Franck & Ribowski 1989). Fights involving prolonged bouts of mutual threat displays (more than 15 reciprocal displays) were also considered to have escalated because they were clearly more intense than interactions involving only a brief round of displays followed by attack–retreat sequences. The proportion of escalated contests was homogeneous across treatments ( $G = 0.83$ ,  $p = 0.66$ , d.f. = 2); overall, contests were significantly more likely not to escalate than to escalate (pooled:  $G = 15.86$ ,  $p < 0.0001$ , d.f. = 1). The probability that the initiator of approach, threat display, attack or bite would win the initial contest did not differ across treatments (all values:  $G < 4.23$ ,  $p > 0.12$ , d.f. = 2). The pooled data demonstrate that the initiator of threat display, attack or bite was significantly more likely to win the initial contest than the individual that did not initiate (all values:  $G > 19.4$ ,  $p < 0.0001$ , d.f. = 1). However, initiators of approach were equally likely to win or lose the contest ( $G = 1.1$ ,  $p = 0.29$ , d.f. = 1).

We recorded 25 parameters related to initial contest dynamics (e.g. total aggression and submission exhibited by the winner and loser, number of mouth-wrestles, circling bouts, etc.). However, all of the variables were highly significantly inter-correlated ( $p < 0.0001$ ). Thus, we focused on a parameter that encompassed the aggressive behaviour of both the subsequent winner and loser: total number of aggressive acts exhibited throughout the contest. A one-way analysis of variance was conducted to assess treatment differences in initial contest dynamics;

Table 1. Summary of cross-treatment comparisons and predictions.

(The > and < symbols indicate 'significantly' greater than or less than, respectively; BW, bystander-winner contests; BL, bystander-loser contests; M, mirror treatment; O, opaque treatment; C, clear treatment.)

## (a) winner and loser effects

treatment	bystander wins
opaque—BW	< 33% = winner effect
opaque—BL	> 67% = loser effect

## (b) eavesdropping

comparison	bystander wins	bystander initiates	contest escalates
M versus O—BW	M < O	M < O	M < O
M versus O—BL	M > O	M > O	M < O

## (c) prior assessment + eavesdropping

comparison	bystander wins	bystander initiates	contest escalates
M versus C—BW	M > C	M > C	M > C
M versus C—BL	M < C	M < C	M > C

total aggression was transformed ( $y^{1/3}$ ) to achieve normality. The ANOVA revealed significant differences in total aggression among treatments ( $F_{2,176} = 5.93$ ,  $p = 0.0032$ ). Student–Newman–Keuls (SNK) multiple comparisons indicated no significant differences between the mirror and opaque treatments. However, the clear treatment was characterized by significantly lower levels of total aggression than the remaining two treatments ( $p < 0.05$ ).

A second one-way ANOVA partitioned total aggression into two categories: number of aggressive acts before and after contest settlement; each of these parameters was transformed to achieve normality ( $\log [y + 1]$  and  $y^{1/3}$ , respectively). Thus, we could assess whether modifications in fighting behaviour occurred during or after contest resolution in the presence of a bystander (clear). There were no differences among treatments in the number of aggressive acts exhibited prior to contest settlement ( $F_{2,175} = 0.14$ ,  $p = 0.87$ ). However, the amount of total aggression following contest resolution differed among treatments ( $F_{2,175} = 7.54$ ,  $p = 0.0007$ ). Significantly fewer aggressive acts were performed after contest settlement in the clear than in either the mirror or opaque treatments (SNK,  $p < 0.05$ ); the latter two treatments did not differ significantly. These data suggest that the presence of an audience did not affect the course of initial contest resolution but, rather, reduced the time the winner spent reinforcing its dominance status (figure 2).

(b) *Bystander contest dynamics*

We examined whether prior assessment (mirror versus clear) or eavesdropping (mirror versus opaque) had a significant influence on the probability that: (i) the bystander would initiate aggression, (ii) the bystander contests would escalate, and (iii) the bystander would win the contest. In keeping with our predictions, the observed proportions (e.g. of escalated versus non-escalated bouts) in the mirror test were independently compared with those of the opaque and clear treatments using either the  $G$ -statistic (likelihood ratio) or, if the criteria for this test were not met, Fisher's Exact statistic. All tests of pro-

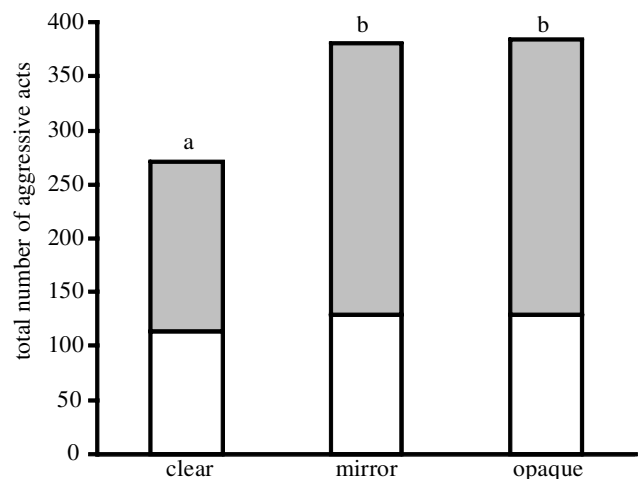


Figure 2. The total number of aggressive acts exhibited, summed for winners and losers, both before (white) and after (shaded) initial contest settlement. Columns marked with the same letters did not differ significantly in the amount of post-resolution aggression; columns with different letters are significantly different from one another.

portions have one degree of freedom unless otherwise specified.

(i) *Bystander-loser contests**Initiation*

The proportion of contests in which the bystander initiated approach (Fisher's,  $p > 0.99$ ), threat display ( $G = 0.16$ ,  $p = 0.69$ ), attack ( $G = 0.16$ ,  $p = 0.69$ ) or bite (Fisher's,  $p = 0.76$ ) did not differ significantly between the mirror and clear treatments. Similarly, no differences emerged in the mirror–opaque comparison (approach: Fisher's,  $p = 0.05$ ; threat display: Fisher's,  $p = 0.74$ ; attack:  $G = 0.88$ ,  $p = 0.35$ ; bite: Fisher's,  $p = 0.76$ ). The homogeneous data were pooled (all values:  $G < 4.98$ ,  $p > 0.083$ , d.f. = 2) and, in all cases, the bystander was significantly more likely to initiate than was the loser of the initial contest ( $G > 9.5$ ,  $p < 0.002$ ).

We also examined the relationship between initiation

behaviour and winning in the bystander–loser contests. The likelihood that initiators of approach, threat display, attack or bite would win the contest was not significantly different across treatments (all values:  $G < 5.6$ ,  $p > 0.061$ , d.f. = 1). The pooled data indicate that the initiators of any type of aggressive behaviour were significantly more likely to win the contest than individuals who did not initiate (all values:  $G > 7.94$ ,  $p < 0.005$ ). Overall, bystanders initiated more often and initiators were more likely to win the bystander contests. However, this is not evidence for an eavesdropping effect as such an effect can be assessed only by examining differences across treatments.

#### Escalation

There were no significant differences among treatments in the probability of bystander–loser contest escalation (mirror versus clear: Fisher's,  $p > 0.99$ ; mirror versus opaque: Fisher's,  $p = 0.70$ ). A significant majority of the contests did not escalate (heterogeneity among treatments:  $G = 0.6$ ,  $p = 0.74$ , d.f. = 2; pooled:  $G = 27.7$ ,  $p < 0.0001$ ).

#### Contest outcome

The bystander was equally likely to win the bystander–loser contests irrespective of treatment (mirror versus clear,  $G = 0.095$ ,  $p = 0.76$ ; mirror versus opaque,  $G = 0.398$ ,  $p = 0.53$ ). Overall, the bystander was significantly more likely than the previous loser to win these contests (heterogeneity among treatments:  $G = 0.4$ ,  $p = 0.82$ , d.f. = 2; pooled:  $G = 13.49$ ,  $p = 0.0002$ ). Additionally, the proportion of contests won by the bystander in the opaque treatment was not significantly different from 67% ( $G = 0.53$ ,  $p = 0.53$ ), indicating that the loser effect did not influence bystander–loser contest dynamics and that the contests were settled on the basis of some individual difference. Though the fishes were matched for size, we tested whether the minute existing size differences influenced contest outcome but found negligible effects ( $G = 0.5$ ,  $p = 0.48$ ).

These data clearly illustrate homogeneity among treatments for all bystander–loser contest parameters. Given that no differences arose between the mirror and clear treatments, we can reject the hypothesis that prior assessment influences bystander–loser contest dynamics. Though no detectable differences arose between the mirror and opaque treatments with respect to contest initiation, escalation, or outcome, there was some evidence that the bystanders gathered information about the losers of the initial bouts. The degree of escalation in the initial contest had a significant effect on the bystander's response to the loser. Specifically, the eavesdropper was significantly less prone to initiate bites (logistic regression: Wald  $\chi^2 = 4.4$ ,  $p = 0.036$ , d.f. = 1) and to win (Wald  $\chi^2 = 4.5$ ,  $p = 0.034$ , d.f. = 1) after having witnessed contests in which the loser escalated. The bystanders also tended to initiate attack less often against losers that had escalated in the initial contest (Wald  $\chi^2 = 3.7$ ,  $p = 0.054$ , d.f. = 1). Thus, eavesdroppers appear to respond more cautiously, and often defer to losers that were more willing to escalate against their previous opponent. No such relationships arose in the clear or opaque treatments, sug-

gesting that the bystanders' response was a consequence of eavesdropping alone.

#### (ii) Bystander–winner contests

##### Initiation

Bystanders were significantly less likely to initiate attacks ( $G = 5.71$ ,  $p = 0.017$ ) and bites ( $G = 6.91$ ,  $p = 0.009$ ) in the mirror than in the clear treatment. No such differences arose with respect to initiation of approach ( $G = 1.89$ ,  $p = 0.17$ ) or threat display ( $G = 3.65$ ,  $p = 0.06$ ). The bystander's probability of initiating approach ( $G = 4.86$ ,  $p = 0.028$ , d.f. = 1), threat display ( $G = 4.97$ ,  $p = 0.026$ ) and attack ( $G = 3.98$ ,  $p = 0.047$ ) against the previous winner was significantly reduced in the mirror treatment relative to the opaque treatment. However, the bystander was equally likely to initiate bites in both treatments ( $G = 0.77$ ,  $p = 0.38$ ). These analyses suggest that eavesdropping influences the bystander's tendency to initiate aggression against a seen winner. Specifically, the bystander avoids confrontation with the winner after having witnessed it defeat another. Prior assessment, however, did not intensify the eavesdropping effect. Rather, the opportunity to assess the seen winner across the clear partition increased the bystander's tendency to initiate more escalated forms of aggression (attacks, bites) relative to situations when information about the initial contestants was available only through eavesdropping (Figure 3a,b).

The relationship between contest initiation and victory in the bystander–winner fights showed a similar pattern to the bystander–loser contests. The likelihood of winning after having initiated approach, attack or bite was homogeneous across treatments ( $G < 3.36$ ,  $p > 0.19$ , d.f. = 2); individuals that initiated had a significantly higher probability of winning the contests than individuals who did not (all initiation behaviours, pooled:  $G > 11.4$ ,  $p < 0.0007$ ). However, initiators of threat display were significantly more likely to win in the mirror ( $G = 4.97$ ,  $p = 0.026$ ) and opaque ( $G = 8.75$ ,  $p = 0.003$ ) treatments but not in the clear treatment ( $G = 0.08$ ,  $p = 0.77$ ).

##### Escalation

The bystander–winner contests were significantly less likely to escalate in the clear than in the mirror treatment ( $G = 4.94$ ,  $p = 0.026$ ) and were significantly more likely to escalate in the opaque than in the mirror treatment ( $G = 6.06$ ,  $p = 0.014$ ) (figure 4). Thus, eavesdropping decreased the bystander's willingness to escalate in contests against seen winners. In addition, prior assessment reduces the probability of escalation even further, which should be expected if the bystander and winner gain accurate information about one another across the clear partition, i.e. escalation may not be necessary if the dominance relationships are established prior to removal of the clear partition.

##### Contest outcome

Eavesdropping significantly reduced the bystander's probability of winning contests against a seen winner (mirror versus opaque:  $G = 4.63$ ,  $p = 0.031$ ; figure 5). This is probably due to the fact that bystanders were far less inclined to initiate or escalate contests against previous winners and thus should be more apt to submit to the

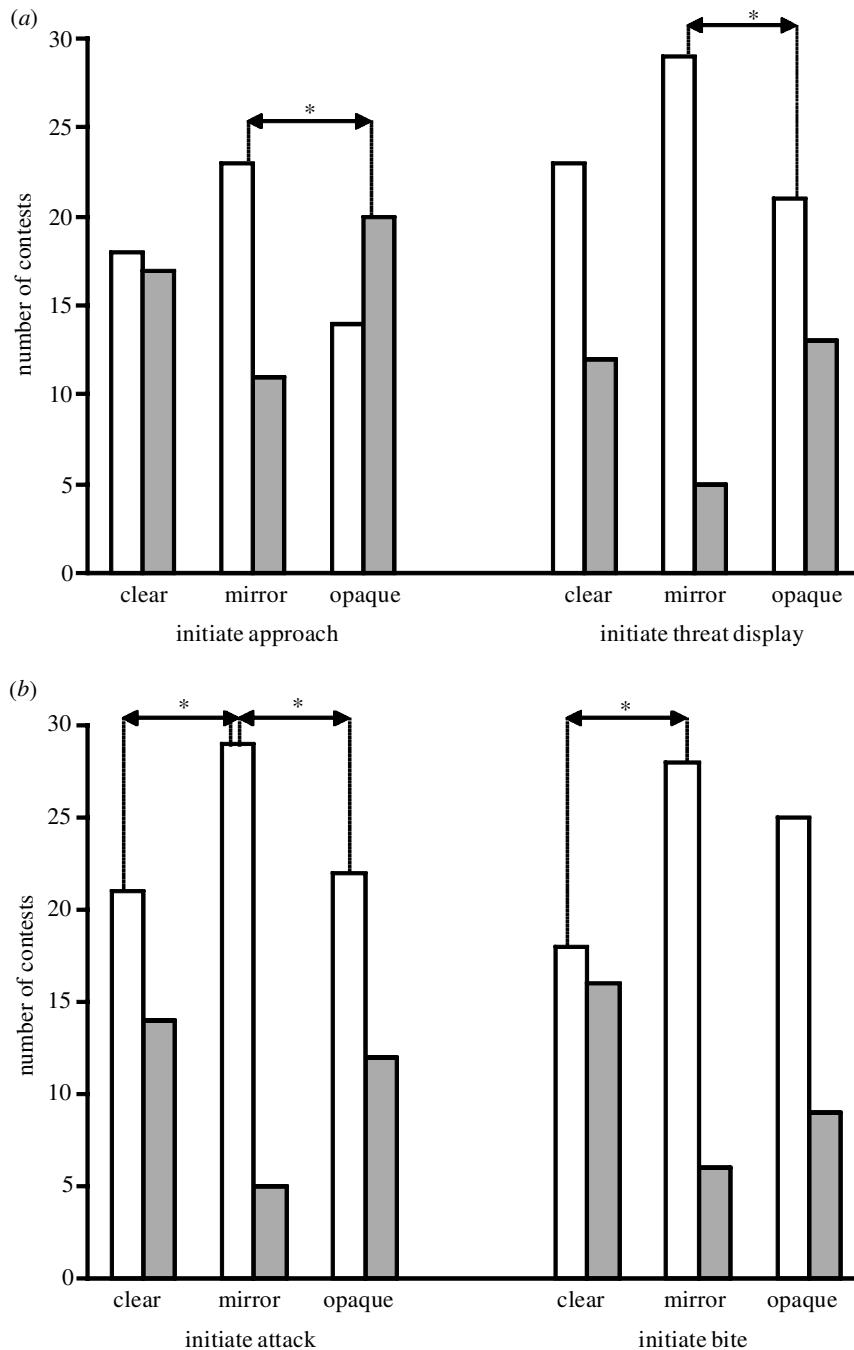


Figure 3. Treatment differences in the probability that the bystander will: (a) initiate approach or threat display, and (b) initiate attack or bite in the bystander–winner contests. An asterisk indicates a significant difference between treatments; white bars indicate that the winner initiates; shaded bars indicate that the bystander initiates.

seen winner. Interestingly, logistic regression analyses revealed that the degree of escalation in the bystander–winner contests had a significant impact on the bystander’s likelihood of victory in the mirror treatment and had marginal effects in the opaque treatment. In both, the bystander’s probability of winning increased (and the previous winner’s decreased) as the contests escalated to higher degrees (mirror: Wald  $\chi^2 = 4.26$ ,  $p = 0.039$ , d.f. = 1; opaque: Wald  $\chi^2 = 3.84$ ,  $p = 0.05$ , d.f. = 1). No such relationship existed in the clear treatment (Wald  $\chi^2 = 1.94$ ,  $p = 0.16$ , d.f. = 1).

When eavesdropping was coupled with the capacity to assess the winner more directly, the bystander’s prob-

ability of victory increased significantly (mirror versus clear:  $G = 5.31$ ,  $p = 0.021$ ; figure 5). Thus, with regard to contest outcome, prior assessment appears to negate rather than intensify the eavesdropping effect. In addition, the winner effect did not influence bystander–winner contest dynamics as the proportion of fights won by the bystander in the opaque treatment was not significantly different from 67% ( $G = 0.57$ ,  $p = 0.45$ ; figure 5). Size differences among the contestants did not significantly influence fight outcomes ( $G = 0.24$ ,  $p = 0.63$ ). Unlike the bystander–loser contests, interactions between the winner and bystander in the mirror treatment were not influenced by the intensity of the initial contest, suggesting that the

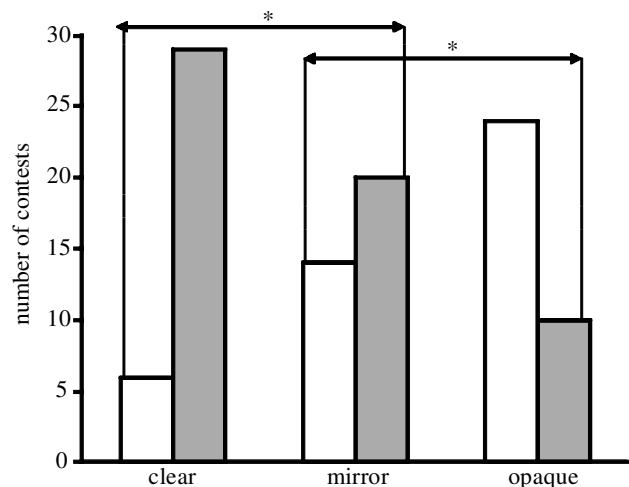


Figure 4. Treatment differences in the probability that the bystander–winner contests will escalate. An asterisk indicates a significant difference between treatments; white bars indicate that the contests escalated; shaded bars indicate non-escalated contests.

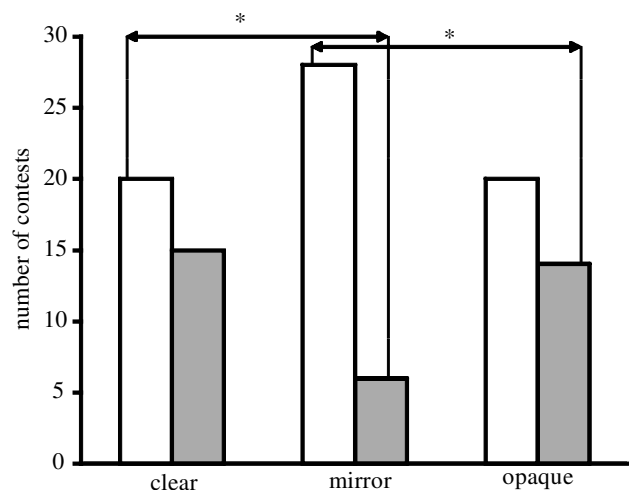


Figure 5. Treatment differences in the probability of bystander victory; an asterisk indicates a significant difference between treatments; white bars indicate that the previous winner has won; shaded bars indicate that the bystander has won.

eavesdroppers perceived winners to be equally strong regardless of whether they defeated the loser via escalated or non-escalated means.

#### 4. DISCUSSION

Our experimental design allowed us to partition the independent influences of three phenomena on aggressive contest dynamics in *X. helleri*: eavesdropping, social experience (winner and loser effects) and the audience effect. Our data support the proposition that male green swordtails extract information from aggressive interactions between others. However, eavesdropping affected primarily the bystander's response towards the winner of the witnessed bout. Eavesdropping significantly reduced the bystander's willingness to initiate contests with seen winners, as in the study by Oliveira *et al.* (1998) on Siamese fighting fish.

In swordtails, eavesdroppers were also less prone to escalate than those that had not observed the contest. Oliveira *et al.* (1998), however, found that *B. splendens* escalate (e.g. frequency of display) to similar degrees towards seen and unseen winners. They attribute the bystander's willingness to escalate to its recognition of the seen winner as a formidable intruder; the winner was introduced into the bystander's (resident) area of the aquarium. From the perspective of territorial defence, it may pay an owner to react more strongly (but perhaps more cautiously at the outset) towards an individual that poses a greater threat of usurpation. In fact, territorial songbirds respond more vigorously to simulated intrusions by perceived winners than by perceived losers of computer-generated acoustic interactions (e.g. Naguib & Todt 1997; Naguib *et al.* 1999; Peake *et al.* 2001). In our study, however, neither the previous winner nor the bystander could be considered the resident. Thus the bystander contests can be seen as fights for ownership of the space rather than resident–intruder battles. Though subtle, this different dynamic may be quite important.

Johnstone's (2001) recent modification of the hawk–dove game defined eavesdroppers as individuals who always submit to previous winners and defeat previous losers. This strict form of eavesdropping was favoured when the value of the contested resource was considerably less than the cost of losing an escalated battle ( $V/C$  approximately 0.25), i.e. under these conditions eavesdroppers should avoid both initiating and escalating against seen winners. Because the bystanders in our experiment were not territory owners *per se*, the value of the contested resource (space) was probably less than that for resident fighting fish or territorial songbirds. As  $V/C$  increases, individuals should be more prone to escalate in order to maintain possession of the resource and this may be independent of whether the intruder is a seen winner (e.g. Oliveira *et al.* 1998). Differences in potential  $V/C$  ratios may explain why swordtail eavesdroppers exhibited a more pronounced aversion to seen winners than did the fighting fish or songbirds. This proposition could be experimentally addressed by manipulating, from the eavesdropper's perspective, the value of the resource or the costs of fighting (e.g. increasing size asymmetries between the eavesdropper and the watched contestants, manipulating the social experience of the bystander, or altering the quality of the contested resource).

Eavesdropping provides only indirect information to the bystander about the winner's fighting ability. When given the opportunity to gather more accurate information about the winner's physical prowess relative to itself, does the bystander utilize this information in lieu of that obtained through eavesdropping? Two aspects of our data suggest that this may be the case. First, the clear treatment afforded bystanders the opportunity to interact with winners across the glass partition and, indeed, this occurred in most all of the trials. Our data indicated that prior assessment negates the eavesdropping effect. In fact, the bystander's probability of winning was almost identical to that found in the opaque treatment, where the bystander contests were probably settled on the basis of some individual difference. This suggests that assessment across the clear partition provided accurate information about fighting ability that was used by both the winner and the

bystander to settle the ensuing contest. The fact that the bystander contests in the clear treatment rarely escalated also supports this interpretation. However, the triadic interactions that occurred in the clear treatment are improbable in natural situations. As such, the bystander may not be able to gain information about the winner's fighting ability *relative to itself* prior to an ensuing contest and thus information obtained through eavesdropping should be more influential. Interestingly, Peake *et al.* (2002) revealed that great tits (*Parus major*) integrate information obtained through prior assessment and eavesdropping, in gauging the fighting ability of unfamiliar individuals. The birds responded more intensely towards unfamiliar opponents that had defeated a perceived winner than those that had lost to a perceived loser. In this sense, the eavesdropper utilizes both direct and indirect information to make more informed decisions about the physical prowess of others in the communication network.

Second, the bystanders most often avoided escalated confrontations with seen winners in the mirror treatment but, in instances where escalation did occur, the bystander's probability of winning increased dramatically. This clearly indicates that the information obtained through eavesdropping (i.e. increased perception of winner's fighting ability) becomes irrelevant when the bystander assesses the previous winner in a more direct fashion. Hsu & Wolf (2001) documented a similar finding in the cyprinodont fish *Rivulus marmoratus*. They found that prior fighting experience influenced the outcome of non-escalated contests but not escalated contests. This result was consistent with the hypothesis that winning and losing experiences change an individual's perception of its own fighting ability rather than its actual fighting ability. Similarly, our results demonstrate that eavesdropping alters an individual's perceived, rather than its actual, probability of winning against seen winners.

Though eavesdropping clearly influenced the bystander's response to a seen winner, it had relatively little impact on the dynamics of bystander–loser contests. Bystanders were significantly less apt to initiate high-intensity aggression (e.g. bite) and win against losers they had seen engage in an escalated fight. Selection should favour individuals who retain information about potentially dangerous contestants. In non-escalated fights, which predominated in the bystander–loser trials, the bystander may only retain information about the winner or may have too little information to gauge the fighting ability of the loser. In such cases, the bystanders may respond similarly to seen versus unseen losers, as we have documented. However, the bystander may view both the winner and loser of an escalated bout as potentially dangerous opponents and thus may retain information about each contestant. This may explain why eavesdroppers differentially respond to losers only if the losers persisted in the initial contest. As initial contest escalation did not influence the dynamics of the bystander–loser contests in the opaque or clear treatments, it is clear that escalation does not change the loser's motivational state, but rather the way the eavesdropper perceives the loser.

The lack of winner and loser effects in this study runs contrary to several other examinations of social experience in green swordtails (see, for example, Thines & Heuts 1968; Beaugrand *et al.* 1991; Beaugrand 1997;

Beaugrand & Goulet 2000). However, in none of these earlier studies were the previous winner or loser pitted against a naive individual, as in our opaque treatment. Rather, an individual who had recently experienced victory was confronted with an opponent who had recently experienced defeat. Each of these studies came to a similar conclusion—previous winners were significantly more likely to win the contests than previous losers. This type of design amplifies the experience asymmetries between contestants and does not allow for independent tests of the influence of prior victory versus defeat. Although behavioural and physiological correlates of winning and losing have been uncovered in this species (Hannes *et al.* 1984; Franck & Ribowski 1987), our results demonstrate that when previous dominants or subordinates contest against individuals with no prior experience, winner and loser effects appear to play a negligible role in delegating outcome.

In addition to eavesdropping and experience effects, we were also able to assess the influence of an audience on initial contest dynamics. There was a significant decrease in aggression after contest settlement when the bystander was present (clear). Although we did not quantify interactions between the contestants and the bystander across the clear partition, it was evident that the winner directed its attention to the bystander after having defeated its opponent and thus, spent less time harassing the subordinate. This could account for the significant post-settlement reduction in total aggression in the clear treatment when compared with the two remaining treatments. We found no evidence for an audience effect on pre-settlement contest dynamics. That is, regardless of whether the initial combatants were being viewed by a bystander or not, the details of the initial fights remained essentially the same. Doutrelant *et al.* (2001) reported similar findings in *B. splendens* where male–male contests were unaffected by the presence of a third male. As in Doutrelant *et al.*'s (2001) experiment, it seems unlikely that the lack of an audience effect was due to the contestants being unaware of the bystander's presence. In fact, the initial contestants often aggressed towards the bystander across the clear partition, suggesting that they were cognizant of the audience throughout the contest phase.

According to current studies on communication networks, the audience effect requires that contestants modify their behaviour in the presence of a third party and that bystanders are unable to interfere with the focal exchange (R. J. Matos, personal communication). Our clear treatment aimed at elucidating the effects of prior assessment, so bystanders were allowed to interact with the contestants across the partition. Thus, the clear treatment may not be ideal for isolating the audience effect. To pinpoint the audience effect, the bystander could be placed at a distance from the contestants in order to minimize three-way interactions (Doutrelant *et al.* 2001). Alternatively, a one-way mirror could be positioned in a manner that allows the contestants to view the bystander but not vice versa (i.e. the reverse of our mirror treatment).

In conclusion, we have demonstrated that eavesdropping is an influential component of contest dynamics in *X. helleri*. Our results support the view that aggressive communication occurs in a networking environment, and



we also unveil some added complexities that merit attention in future studies on eavesdropping. This experiment has provided, to our knowledge, the most detailed examination to date of networking in visually based aggressive signalling systems and we hope that our results inspire further investigations of the potential interactions between audiences, eavesdropping, prior social experience, and contest dynamics. Our data also confirm that future studies addressing the influence of eavesdropping on higher-order social phenomena such as dominance hierarchy formation in *X. helleri* may, in fact, be fruitful.

We thank the Kentucky Academy of Science, American Livebearers Association, Sigma-Xi Grants-in-Aid, and the National Science Foundation for funding portions of this research. We are grateful to Meredith McGee, Matthew Druen, Gary Cobbs, Trish Sevene-Adams, Yuying Hsu, Larry Wolf, Matthew Grober and Peter McGregor for invaluable advice and discussion throughout the course of this study. We express our gratitude to Ricardo J. Matos and one anonymous referee for providing useful suggestions on an earlier version of this manuscript.

## REFERENCES

- Bakker, T. C. M., Bruijn, E. F.-D. & Sevenster, P. 1989 Asymmetrical effects of prior winning and losing on dominance in sticklebacks (*Gasterosteus aculeatus*). *Ethology* **82**, 224–229.
- Beaugrand, J. & Goulet, C. 2000 Distinguishing kinds of prior dominance and subordination experiences in males of green swordtail fish (*Xiphophorus helleri*). *Behav. Proc.* **50**, 131–142.
- Beaugrand, J., Goulet, C. & Payette, D. 1991 Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: effects of body size and prior dominance. *Anim. Behav.* **41**, 417–424.
- Beaugrand, J. P. 1997 Erratum to 'Resolution of agonistic conflicts in dyads of acquainted green swordtails (*Xiphophorus helleri*): a game with perfect information'. *Behav. Proc.* **41**, 293–310.
- Beaugrand, J. P., Caron, J. & Comeau, L. 1984 Social organization of small heterosexual groups of green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under conditions of captivity. *Behaviour* **91**, 24–60.
- Beaugrand, J. P., Payette, D. & Goulet, C. 1996 Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience and prior residency. *Behaviour* **133**, 303–319.
- Begin, J., Beaugrand, J. P. & Zayan, R. 1996 Selecting dominants and subordinates at conflict outcome can confound the effects of prior dominance or subordination experience. *Behav. Proc.* **36**, 219–226.
- Breithaupt, T. & Atema, J. 2000 The timing of chemical signaling with urine in dominance fights of male lobsters (*Homarus americanus*). *Behav. Ecol. Sociobiol.* **49**, 67–78.
- Chase, I. D., Bartolomeo, C. & Dugatkin, L. A. 1994 Aggressive interactions and inter-contest interval: how long do winners keep winning? *Anim. Behav.* **48**, 393–400.
- Doutrelant, C., McGregor, P. K. & Oliveira, R. F. 2001 The effect of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens*. *Behav. Ecol.* **12**, 283–286.
- Earley, R. & Dugatkin, L. 2002 Group fusion and the dynamics of hierarchy formation in the green swordtail (*Xiphophorus helleri*). (In preparation.)
- Enquist, M. & Leimar, O. 1983 Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387–410.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990 A test of the sequential assessment game: fighting in the cichlid fish, *Nannacara anomala*. *Anim. Behav.* **40**, 1–14.
- Evans, C. S. & Marler, P. 1994 Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Anim. Behav.* **47**, 1159–1170.
- Francis, R. C. 1983 Experiential effects on agonistic behaviour in the paradise fish, *Macropodus opercularis*. *Behaviour* **85**, 292–313.
- Franck, D. & Ribowski, A. 1987 Influences of prior agonistic experiences on aggression measures in the male swordtail (*Xiphophorus helleri*). *Behaviour* **103**, 217–240.
- Franck, D. & Ribowski, A. 1989 Escalating fights for rank-order position between male swordtails (*Xiphophorus helleri*): effects of prior rank-order experience and information transfer. *Behav. Ecol. Sociobiol.* **24**, 133–143.
- Franck, D. & Ribowski, A. 1993 Dominance hierarchies of male green swordtails (*Xiphophorus helleri*) in nature. *J. Fish Biol.* **43**, 497–499.
- Franck, D., Klamroth, B., Taebel-Hellwig, A. & Schartl, M. 1998 Home ranges and satellite tactics of male green swordtails (*Xiphophorus helleri*) in nature. *Behav. Proc.* **43**, 115–123.
- Hannes, R.-P., Franck, D. & Liemann, F. 1984 Effects of rank-order fights on whole-body and blood concentrations of androgens and corticosteroids in the male swordtail (*Xiphophorus helleri*). *Ethology* **65**, 53–65.
- Hsu, Y. & Wolf, L. L. 1999 The winner and loser effect: integrating multiple experiences. *Anim. Behav.* **57**, 903–910.
- Hsu, Y. & Wolf, L. L. 2001 The winner and loser effect: what fighting behaviours are influenced? *Anim. Behav.* **61**, 777–786.
- Hughes, M. 1996 The function of concurrent signals: visual and chemical communication in snapping shrimp. *Anim. Behav.* **52**, 247–257.
- Johnsson, J. & Akerman, A. 1998 Watch and learn: preview of the fighting ability of opponents alters contest behaviour in rainbow trout. *Anim. Behav.* **56**, 771–776.
- Johnstone, R. A. 1997 The evolution of animal signals. In *Behavioural ecology: an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 155–178. Oxford, UK: Blackwell Science.
- Johnstone, R. A. 2001 Eavesdropping and animal conflict. *Proc. Natl Acad. Sci. USA* **98**, 9177–9180.
- McGregor, P. K. 1993 Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Phil. Trans. R. Soc. Lond. B* **340**, 237–244.
- McGregor, P. K. & Dabelsteen, T. 1996 Communication networks. In *Ecology and evolution of acoustic communication in birds* (ed. D. Kroodsma & E. Miller), pp. 409–425. Ithaca, NY: Cornell University Press.
- McGregor, P. K. & Peake, T. M. 2000 Communication networks: social environments for receiving and signalling behaviour. *Acta Ethol.* **2**, 71–81.
- McGregor, P. K., Dabelsteen, T., Shepherd, M. & Pedersen, S. B. 1992 The signal value of matched singing in great tits: evidence from interactive playback experiments. *Anim. Behav.* **43**, 987–998.
- McGregor, P. K., Dabelsteen, T. & Holland, J. 1997 Eavesdropping in a territorial songbird communication network: preliminary results. *Bioacoustics* **8**, 253–254.
- McGregor, P. K., Otter, K. A. & Peake, T. M. 2000 Communication networks: receiver and signaller perspectives. In *Animal signals: signalling and signal design in animal communi-*

- cation (ed. Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 329–340. Trondheim, Norway: Tapir Academic Press.
- McGregor, P. K., Peake, T. M. & Lampe, H. M. 2001 Fighting fish *Betta splendens* extract relative information from apparent interactions: what happens when what you see isn't what you get? *Anim. Behav.* **62**, 1059–1065.
- Marden, J. & Rollins, R. 1994 Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Anim. Behav.* **48**, 1023–1030.
- Mesterton-Gibbons, M. & Adams, E. 1998 Animal contests as evolutionary games. *Am. Sci.* **86**, 334–341.
- Mesterton-Gibbons, M., Marden, J. H. & Dugatkin, L. A. 1996 On wars of attrition without assessment. *J. Theor. Biol.* **181**, 65–83.
- Naguib, M. & Todt, D. 1997 Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Anim. Behav.* **54**, 1535–1543.
- Naguib, M., Fichtel, C. & Todt, D. 1999 Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc. R. Soc. Lond. B* **266**, 537–542.
- Oliveira, R. F., McGregor, P. K. & Latruffe, C. 1998 Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc. R. Soc. Lond. B* **265**, 1045–1049.
- Payne, R. 1998 Gradually escalating fights and displays: the cumulative assessment model. *Anim. Behav.* **56**, 651–662.
- Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2001 Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proc. R. Soc. Lond. B* **268**, 1183–1187.
- Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2002 Male great tits assess competitors by combining information from direct experience with that gathered by eavesdropping. (In preparation.)
- Ribowski, A. & Franck, D. 1993a Demonstration of strength and concealment of weakness in escalating fights of male swordtails (*Xiphophorus helleri*). *Ethology* **93**, 265–274.
- Ribowski, A. & Franck, D. 1993b Subordinate swordtail males escalate faster than dominants: a failure of the social conditioning principle. *Aggressive Behav.* **19**, 223–229.
- Schuett, G. W. 1997 Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim. Behav.* **54**, 213–224.
- Sparkes, T. C., Yan, H. Y., Prater, C. & Akamatsu, T. 2000 Condition-dependent acoustic signals and their importance for resolving aggressive conflicts in the skunk loach (*Botia morleti*): integrating sensory and behavioural approaches. *Am. Zool.* **40**, 1217.
- Thines, G. & Heuts, B. 1968 The effect of submissive experiences on dominance and aggressive behaviour of *Xiphophorus* (Pisces, Poeciliidae). *Z. Tierpsychol.* **25**, 139–154.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.