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## Performing in front of an audience: signallers and the social environment

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### Introduction

Several signallers and receivers sharing the same active signalling space constitute a communication network. This type of environment imposes additional selection pressures on both signallers and receivers other than those classically considered in signaller–receiver dyads. In this chapter, we shall discuss how communication networks influence the behaviour of a signaller and, more specifically, the effect of an audience (defined below) on signalling behaviour.

An individual signaller has to cope with two main issues when signalling in a network: (a) it has to compete or cooperate with other signallers, and (b) it has to deal with the presence of several receivers. Signalling at the same time as other individuals poses a problem for the signaller: how does it ensure that its specific signal is detected by a receiver when other conspecifics are signalling? Signallers solve or minimize this problem by either cooperating or competing for the signal broadcast space. For example, in frog and insect choruses, individuals time their signals to avoid acoustic interference (e.g. alternating their calls) or compete for call order in the chorus (Gerhardt & Huber, 2002; Ch. 13). At the community level, different species with similar signals may broadcast their signals at different times of the day (Endler, 1992).

The presence of several receivers presents two additional problems for the signaller. The first is how to direct the signal to a specific receiver. For example, bird song often has a range that encompasses several neighbouring territories. When a bird sings, the song could potentially reach all the neighbours in surrounding territories. During interactions with neighbours, individuals may need to direct the

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signal to a specific individual, for example because that neighbour starts to sing close to the territory boundary. McGregor & Peake (2000) discussed several ways in which songbirds can direct the signal to a specific rival neighbour or intruder. For example, matched counter-singing (Stoddard *et al.*, 1992; Beecher *et al.*, 1996) is a good candidate for directing the signal to a specific individual bird.

The second issue that arises from the presence of several receivers, and one that this chapter covers in more detail, is how signallers communicate in the presence of additional receivers other than the primary target receiver. We will concentrate on conspecific receivers because heterospecific receivers, especially predators and parasites, have received considerable attention and are known to be important in shaping signals and signalling interactions (Bradbury & Vehrencamp, 1998; Chs. 2 and 8). The term audience has been used to describe conspecific receivers in the context of a communication network (McGregor & Peake, 2000; Doutrelant *et al.*, 2001). In this chapter, we shall begin by discussing this term and its use in the context of communication networks. We shall then discuss how the presence of several receivers may affect signalling behaviour and the choice and evolution of signalling strategies.

### Definitions of audience and audience effects

#### *Audiences*

We define audiences as individuals that are present during, but do not take part in, signalling interactions between others. We distinguish two types of audience: evolutionary audiences and apparent audiences.

#### Evolutionary audiences

By evolutionary audiences we mean individuals that were historically common in the environment of the signaller and that may have generated selection on the form and content of signalling behaviour. For example, it is widely accepted that bird song has a dual function, both as a signal to attract females and as a signal used in male–male competition (Berglund *et al.*, 1996; Searcy & Nowicki, 2000). The evolution of this dual function has been widely discussed in the literature (e.g. Searcy & Nowicki, 2000). One hypothesis suggests that song first evolved as a male–female signal with males acting as eavesdroppers (see Ch. 12 for similar discussion on fiddler crabs). This eavesdropping pressure caused by male audiences may have induced new selective forces on the form and content of the signal, resulting in the appearance of a dual function signal. If this hypothesis is correct, then males have acted as an evolutionary audience in bird song evolution. An evolutionary audience does not need to be present or apparent to affect

signalling behaviour at any instant in time, because selection has acted in the past (and presumably continues to act) on the signal (e.g. introducing or emphasizing features in the design of songs that males use in male–male competition). For more information on the effects and importance of evolutionary audiences, we refer the reader to Chs. 2 and 14.

#### Apparent audiences

Apparent audiences are individuals that affect the behaviour of the signaller only when they are present and detected. For example, in the presence of females, interacting male Siamese fighting fishes *Betta splendens* decrease highly aggressive behaviours (attempted bites) and increase the intensity of conspicuous displays (tail beats and gill cover display) (Doutrelant *et al.*, 2001). Unlike evolutionary audiences, the effects produced by this type of audience are triggered when the audience is present; males show no such effects on the different displays when the female is absent.

In this chapter, we are mainly concerned with the study of apparent audiences, as their effects can be studied experimentally and, unlike studies of evolutionary audiences, they do not rely on historical inference.

#### *Audience effects*

We define an *audience effect* as changes in the signalling behaviour during an interaction between individuals caused by the mere presence of an audience. Matos & McGregor (2002) found that male fighting fish engaged in visual signalling interactions changed their signalling (i.e. the visual displays directed towards the rival male) when a male audience was present. It is important to emphasize that the change in signalling behaviour occurred between the two individuals involved in the signalling interaction and not directly towards the audience. Whether the information content of signalling changes will depend on the balance of cost and benefit to the signallers (see below). This type of effect is specific to a communication network as it can only occur in situations where a minimum of three individuals is present: two individuals engaged in a signalling interaction and one individual making up the audience.

#### *Why audience?*

Different authors have used different terms to designate extra potential receivers in a communication network, such as bystanders (Dugatkin, 2001), unintended receivers (Endler, 1993) or illegitimate receivers (Otte, 1974). Most of these terms, however, have been used in an interspecific context (with the exception of bystander) to describe predator detection of prey signalling behaviour (Otte, 1974; Endler, 1993; Bradbury & Vehrencamp, 1998; Ch. 2). Because we restrict our

definition of an audience to conspecifics, we exclude predators or parasites responding to the signal (Ch. 2). We chose the term audience because it is more descriptive of the role of the individual during the signalling interaction in two ways. First, it implies that individuals are present but do not take part in the interaction, although they are clearly able to. Second, it implies that the individuals may pay attention to the signalling interaction and thus potentially extract information.

We think that it is important to link the term audience to other network behaviours such as eavesdropping in this way because the presence of eavesdroppers can impose costs and benefits on signallers and to link these costs–benefits to the information content of the interaction. For example, the finding that eavesdroppers behave more aggressively to individuals that behave as losers in an aggressive signalling interaction (e.g. Chs. 2 and 14) identifies an immediate cost of an audience on the losers. It is worth noting though that we do not have to show that individuals are able to extract information to cause an audience effect. For example, audiences may be costly just because there is a high risk of the audience disrupting the signalling interaction (e.g. intervention behaviour of semi-captive zebras *Equus quagga*; Schilder, 1990). By comparison, non-apparent eavesdroppers do not promote an audience effect because signallers are unaware of their presence.

*Other uses of audience and audience effect in the literature*

The terms audience and audience effects have been used in the communication network literature to describe the effects on signalling interactions of the presence of additional potential receivers that do not take part in the interaction (Doutrelant *et al.*, 2001; Matos & McGregor, 2002). However, these terms have also been used in other studies in animal communication. In the following paragraphs we shall talk about these studies and underline the differences between the two uses of the term audience.

The first studies to use the terms audience and audience effects looked at the effect of the presence of a conspecific on the incidence of alarm and food calls in birds (Gyger *et al.*, 1986; Marler *et al.*, 1986; Gyger, 1990; Evans & Marler, 1994). These authors were interested in whether these calls were elicited by and directed to a specific class of individuals or audiences, namely conspecifics (e.g. conspecific versus predator; male versus female). In these studies, an audience is defined as any individual that is present in the same location as the subject (an apparent audience), and the audience effect is the change in signalling behaviour (e.g. increase in food call rate: Marler *et al.*, 1986) caused by the presence of the audience. In both cases, the signal was assumed to be directed towards the audience; for example, Gyger *et al.* (1986) performed two experiments to investigate whether

male cockerels *Gallus domesticus* modulated their alarm calls in the presence of an audience when a model of a predator was presented. The protocol of both experiments was the same; the birds were placed in a cage above which a model of a predator was 'flown'. The audience was housed in another cage next to the male's cage; both individuals could see the predator. In the first experiment, the audience was either their own mate or a female that was mated to another male, with an empty cage as a control. The second experiment was similar to the first one with the difference that instead of another male's female the authors used an unfamiliar male. The authors found that in both experiments males increased the rate of alarm calls when a conspecific was present compared with when alone. No significant difference was found between the presence of the male's mate compared with another male's mate, or between the male's mate compared with an unfamiliar male. The authors concluded from these results that the presence of a conspecific audience has an effect on alarm calling and that these calls may be primarily directed towards conspecifics and not towards the predator. Because there was no significant effect of the type of conspecific (own mate, other's mate, unfamiliar male), one can rule out the hypothesis that the observed increase in call rate is a result of sharing the risk with the other prey (Gyger *et al.*, 1986).

There are two main differences between the use of the terms audience and audience effects in these studies and our own use. First, we restrict audience effects to the signalling interaction between the two individuals; the audience is not the primary receiver of the signals but acts as a potential non-targeted receiver. In the predator/food call studies, the distinction between the audience and a primary receiver of the signal is blurred as the target receiver is the audience (Fig. 4.1). The second difference is that our definition is specific to communication networks. In the predator/food call studies, this was not necessarily true; only two conspecifics were necessary to produce the audience effect: the signaller and the audience. For example, in a similar study to the one described above, Marler *et al.* (1986) showed that male cockerels increased their food calls in response to the presence of one hen; such a situation is a signaller–receiver dyad.

We point out these differences in use of the terms to ensure that different phenomena are not confused by the use of a common term and suggest that the terms should be clearly defined when used.

### Audience effects

Relatively few studies have addressed directly the question of whether audience effects occur. In this section, we summarize these studies and discuss other systems in which audience effects appear to have an important influence on signalling behaviour.

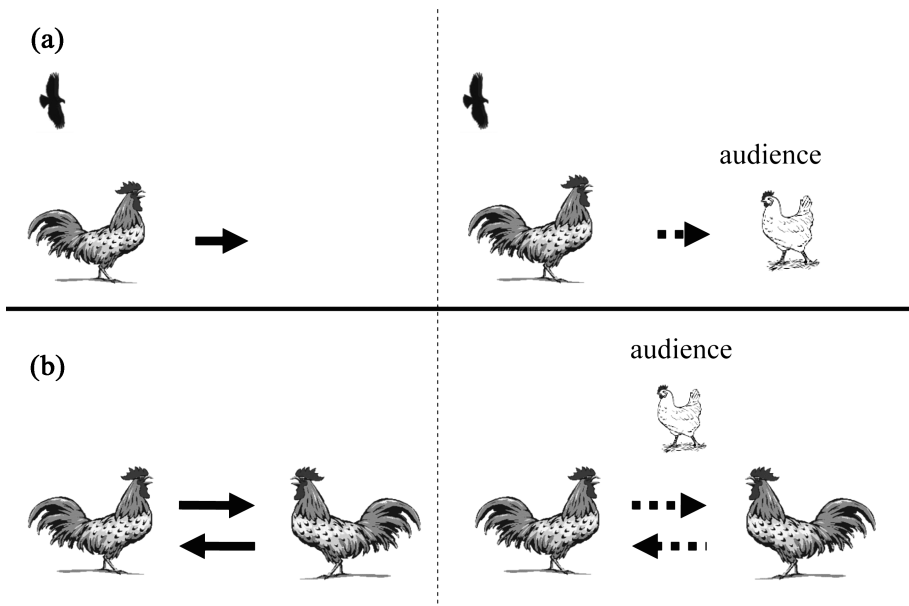


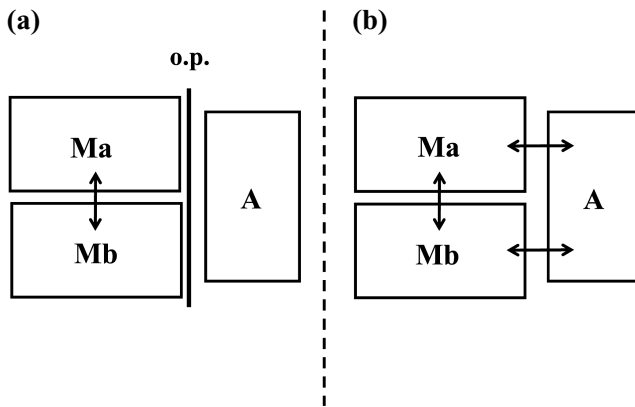
Fig. 4.1. The audience effect in different types of study. (a) In predator/food call studies (Cyger, *et al.*, 1986), the change in behaviour (dotted arrows) is triggered by the presence of the audience (the hen) and directed towards the audience. (b) In the audience effects described in this chapter, the change in behaviour (dotted arrows) is triggered by the presence of the audience (non-target receiver, the hen) and directed towards the target receiver (the other male).

*Male–male aggressive signalling interactions*

Individuals often use signals to compete for resources such as territories, food or mates. These displays are used to assess the opponents’ fighting ability and motivation (Huntingford & Turner, 1987; Bradbury & Vehrencamp, 1998). In a communication network, this information is available not only to the opponent but also to other individuals that are within signal range. This audience of non-targeted receivers may introduce extra costs or benefits to signallers; as explained above, some studies show that eavesdropping fish are more likely to initiate aggressive interactions with a loser than with a winner (Oliveira *et al.*, 1998; Earley & Dugatkin, 2002; Chs. 2 and 5). If an audience has high costs or benefits to signallers, then signallers should adjust their behaviour towards the opponent in order to conceal or enhance information, respectively (McGregor & Peake, 2000).

Siamese fighting fish

Siamese fighting fish often use signals to mediate competition over resources such as territories, food or mates, and such visual displays have been



**Fig. 4.2.** Representation of the experimental design used in Matos (2002) to study the effect of a male audience on male-male interactions in *Betta splendens*. (a) In the first 10 minutes, both males were allowed to interact in the absence of an audience. (b) In the second 10 minute period, either an audience or an empty tank was revealed (removal of the opaque partition) to the males. Ma and Mb are the interacting males; A is the audience tank; o.p. is an opaque partition; arrows represent the direction in which visual contact was possible.

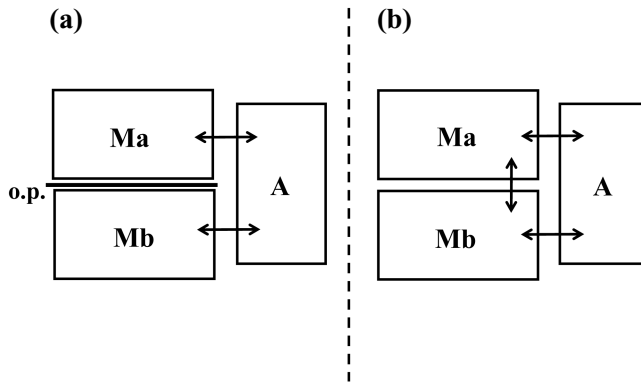
used as a model system to address different questions related to communication networks (e.g. eavesdropping: Oliveira *et al.*, 1998; McGregor *et al.*, 2001). One of the first experiments to address specifically whether male Siamese fighting fish were affected by the presence of an audience during an aggressive interaction was performed by Matos (2002). Two males were allowed to interact through a clear partition (tank walls), and a third male (the audience) was placed at a small distance from these males (Fig. 4.2). This small distance prevented the audience from taking part in the interaction yet, at the same time, allowed both males to see the audience. Each trial of the experiment was divided into two 10 minute periods: in the first period the two individuals were allowed to interact without the audience being present; the second period started when an opaque partition that separated the audience from the two males was removed, allowing the males to see the audience while interacting. Previous studies have shown that one can predict the winner of a fight between two male fighting fish from display difference at the beginning of the interaction (Simpson, 1968). In this experiment, the winner of the signalling interaction was defined as the individual that displayed most during the first 10 minutes of the interaction (the other male was the loser). It is important to note that the barriers between males prevented actual fighting and none of the interactions reached an outcome (e.g. displaying submissive colouration). No displays directed towards the audience were observed. Matos (2002) found that 'winners' did not change their signalling behaviour in the presence of an audience. In

contrast, when an audience was present 'losers' reduced the time they spent in gill cover display (a purely visual display) and the time spent near the opponent compared with when there was no audience. However, there was no significant change in the more aggressive displays that had both tactile and visual components (i.e. attempted bites and tail beats). This change in behaviour may be viewed as an attempt by the loser to restrict the information available to the eavesdropper while at the same time providing adequate information for assessment by the opponent. Another hypothesis is that by reducing the less-aggressive displays whilst maintaining the more aggressive forms, 'losers' may seem more aggressive to the audience. Thus even though the audience may have seen that individual lose, it would be more reluctant to interact with it because of its aggressiveness ('good loser' hypothesis: Peake & McGregor, 2004).

This study (Matos, 2002) suggests that there is an audience effect when a male audience is present during male–male interactions and that the presence of the audience can be more costly for the individual that is losing the interaction than for the winner. The finding that the audience effects in this situation involved a change of signalling behaviour by the loser fits both observations that losers are more rapidly approached by males that saw them lose (Siamese fighting fish: Oliveira *et al.*, 1998; McGregor *et al.*, 2001; swordtail fish *Xiphophorus helleri*: Earley & Dugatkin, 2002) and that this effect disappears in combats where both individuals escalated (Earley & Dugatkin, 2002).

In an earlier study, Doutrelant *et al.* (2001) also found that female audiences affected male–male *B. splendens* aggressive displays. In this experiment, a female audience was presented to a pair of males that interacted through a clear partition. The effect of the presence of an audience was then compared with a treatment where males were allowed to interact with no audience present. Males increased the amount of conspicuous displays (e.g. tail beats and time with gill cover erect) and decreased the more aggressive displays (e.g. attempted bites) towards opponents when a female was present. The authors interpreted this result as males trying to compromise between having to interact with an opponent and at the same time provide information to the audience by using more conspicuous displays, which are more often used in both aggressive and courtship contexts. Doutrelant *et al.* (2001) also performed a second experiment to examine whether male audiences affected signalling interactions but did not find an audience effect (except for a tendency for males to spend less time near the opponent). However, the result of these two experiments cannot be compared directly because of differences in the experimental design and procedure (i.e. the audience was closer to the males and the males were pre-exposed to the audience in the female experiment, while in the male experiment the audiences were further away and there was no





**Fig. 4.3.** Schematic representation of the experimental design used in both Matos & McGregor (2002) and Matos *et al.* (2003). (a) In a five minute pre-exposure period, both males could see the audience tank. (b) In the 10 minute interaction period, the opaque partition was removed and both males were allowed to interact with each other in front of or in the absence of the audience. Ma and Mb are the interacting males; A is the audience tank; o.p. is an opaque partition; arrows represent the direction in which visual contact was possible.

pre-exposure period). Both distance and pre-exposure to another individual have been shown to have a strong effect on male aggressive display (Bronstein, 1989; Halperin *et al.*, 1998; also see below).

In a more recent experiment, Matos & McGregor (2002) looked directly at the effect of the sex of the audience. Three different types of audience were used: male, female *B. splendens* and female *Xiphophorus* spp. (to control for responses not specific to conspecifics). A control with no audience present was also used. The design and procedure of the experiment was similar to that in Matos (2002), except that the males were first pre-exposed to the audience and then were allowed to see and interact with the opponent (Fig. 4.3). The audience was visible for the entire trial. No distinction was made between winners and losers as data were only collected from one of the individuals involved in the interaction. No differences were observed between the female *Xiphophorus* spp. treatment and no audience; therefore the *Xiphophorus* spp. treatment was used as the control. Males behaved more aggressively (i.e. attempted more bites and spent less time near the opponent) when a male audience was present than with a female audience (Matos & McGregor, 2002). To explain this difference, the authors suggested that the presence of a female might confront the males with a trade-off between expelling their male opponent and not driving away a potential mate. Males of this species often bite when courting a female and highly aggressive males may cause females to flee because of the high risk of injury (Bronstein, 1984). The results of these

experiments suggest that the sex of the audience is important in determining how males should behave during aggressive signalling interactions.

#### Field crickets

Tachon *et al.* (1999) studied male–male competition for resources in the field cricket *Gryllus bimaculatus*. They tested whether the presence of a female influences the aggressive behaviour between males. In each test, a group of five males in an arena under three different treatments was observed. Besides the two obvious treatments, presence and absence of females, they used a third condition where a paper impregnated with female scent was introduced into the arena. Previous studies had shown that this scent elicited behavioural responses from males of this species (Otte & Cade, 1976; Hardy & Shaw, 1983).

Tachon *et al.* (1999) found that males increased their level of aggressive displays (e.g. aggressive stridulation and mandible flaring) towards other males in the treatment where the females were present. Interestingly, there was no evidence that the female scent produced the same effect as the actual presence of a female. Female scent alone in this system may be a poor predictor of female presence and the cost of escalating increases when there is a high probability that the female is not present. However, in this example, it is not clear what effect direct female–male interactions had on male–male competition, as opposed to the effect of the mere presence of the female. Further studies are needed to attempt to distinguish these effects and thus to confirm whether this is an example of an audience effect.

#### Parental behaviour

Male parental care is common in many species. If there is a direct link between the care provided to the young and their survival until reproductive age, it might be of advantage for the females to choose a good father as a potential mate. One way of assessing paternal care is to observe male interactions with young (e.g. affiliate signalling behaviour). If females do choose a good father for their future mate, then it should be to the advantage of the male to try to perform as a better ‘parent’ when a female is present.

#### Vervet monkeys

Vervet monkeys *Cercopithecus aethiops* have a complex social system where individuals influence their own or other group members’ dominance rank by socializing with individuals of different rank. In such a system, female mate choice or preference to associate with a male can influence the male’s future position in the hierarchy (Ch. 25). Interactions between males and infant are quite common and males often form strong protective relationships with the females and their young. These relationships may reduce the harassment that females and infants

receive from other group members. Therefore, females may prefer to associate with males that perform more affiliatively towards their infant.

Hector *et al.* (1989) investigated whether male vervet monkeys changed their interaction with an infant in the presence versus 'absence' of the mother. In this experiment, the females were placed (a) behind a one-way mirror, where they could see both male and infant but not vice versa; (b) behind a Plexiglas partition, where male, female and infant could see each other; and (c) behind a metal partition, where the female could not see the dyad and the male and infant could not see the female. The results of this experiment showed that males are sensitive to the presence of the mother and engaged in more affiliative and less-antagonistic behaviour toward the infant when the male was able to see the mother. However, it is not clear whether the effect is simply caused by the presence of the female or occurs because the females could still potentially signal to the dyad through the Plexiglas, affecting the behaviour of both infant and male. A further treatment would be needed to address this question, where the female is placed behind a one-way mirror and the dyad can see the female but not vice versa.

The authors further studied if females varied their behaviour towards males that they saw performing more affiliative behaviours towards their infants and found that females tolerated the males more and also performed more affiliative behaviours towards them. In spite of the lack of an appropriate control, this study showed that potentially individuals may adjust their behaviour when an audience is present and that there are direct consequences to the individual.

#### Budgerigars

Female birds may assess male parental care behaviour by the male's extra-pair behaviour during the period prior to egg laying. In species with obligate biparental care, males that provide more care to the young should be preferred as a mate, as less-committed males increase the female's costs of feeding and spending more time with the young. Extra-pair activity by the male (e.g. displaying to another female) may provide information to the female on the male's attentiveness towards the female and the nest.

Budgerigars *Melopsittacus undulatus* are socially monogamous birds where both members of the pair provide parental care. The males of this species provide most of the food to the nest, both at the start of the nesting period and through brooding. As a consequence, male commitment to the female and brood is very important to the female and survival of the brood, and females may use cues of male commitment when they are choosing a potential mate. Baltz & Clark (1994) investigated whether male budgerigars were less likely to court another female when their own mate was present. In other words, they tested whether there is an effect of an audience (their mate) on the male's extra-pair behaviour. The study was conducted on

a captive population housed in an outdoor aviary. Nestboxes were provided, simulating the nests in natural cavities observed in the wild. The authors assumed that the females lost visual contact with the male when inside the nestbox. The behaviour of each male and its mate was recorded in the periods where the female was inside (no audience) and outside (audience) the nest. Males significantly increased extra-pair courtship behaviour when out of view of the female (i.e. when the female was inside the nestbox) relative to when the female was in view. However, the results of this experiment can also be explained by an alternative hypothesis. Males may reduce the time courting other females because with their mate outside the nest they are more vulnerable to extra-pair courtship and copulations by other males in the flock. Therefore, the reduction of courtship may be a result of mate guarding (Baltz & Clark, 1994). In another study, Baltz & Clark (1997) showed that the necessity for mate guarding did not change the males' response to the extra-pair female. The authors used the same experimental design as before but this time the mate was separated from the rest of the flock in both treatments. This procedure prevented other males from interacting with the female (subject's mate) and thus reduced the necessity for mate guarding. Once again, males reduced courtship behaviour towards extra-pair females when their mate was visible. Although this study suggests that there maybe an audience effect, we consider it poor evidence for audience effects as we define them in this chapter. The main problem with the experimental design of both studies is that the audience effect is not caused by the mere presence of the audience, the male–female pair are only separated visually by an opaque partition, and, as the authors state, both individuals could still contact each other through calls even when they could not see each other. We suggest that further studies would be required to confirm the presence of an audience effect in such system.

#### *Human behaviour*

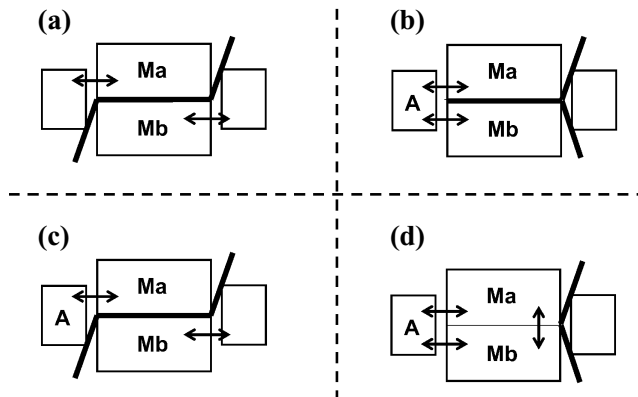
Social psychologists have long recognized that audiences have an important effect on human behaviour (e.g. Zajonc, 1965; Blumstein, 1973; Felson, 1982; Ch. 19). These effects extend from a change in the performance of simple motor tasks, when compared with apparently 'non-social' contexts (Zajonc, 1965), to changes in more complex forms of social behaviour such as interpersonal strategies used during social interactions (Blumstein, 1973). One interesting area of study with regard to audience effects in humans is impression management theory. This theory focuses on the principle that a person is aware of being characterized or typified by others when performing a behaviour and responds by trying to make these characterizations favourable. As a consequence, most human behaviour is designed to obtain 'favourable' reactions from an audience (Felson, 1978, 1982). For example, Felson (1982) found an effect of third-party

presence on aggressive interactions between humans. The study was based on interviews with patients with previous mental health problems, with ex-criminals and with a sample of the general population. All groups answered a questionnaire asking them to describe in detail four aggressive incidents. The replies showed that the outcome of an interaction between individuals of the same sex was more severe when an audience was present (when allowing for third-party instigation or mediation of the fight). There was a higher probability that individuals would escalate from verbal insults to actual physical contact. However, the authors also found that the same was not true in conflicts between the sexes; the cause of such a difference may be that the audience is more likely to disapprove of severe aggression in between-sex conflicts (Felson, 1982).

The general idea that individuals may try to manipulate their characterization by others has recently been used to explain altruistic behaviour in humans and non-human animals (Zahavi & Zahavi, 1997; Wedekind & Milinski, 2000; Milinski *et al.*, 2001; Bshary, 2002). This idea is discussed by Bshary & D'Souza in Ch. 22.

#### **Priming: a mechanism of audience effects or a functional alternative?**

In the experiments discussed above showing that male Siamese fighting fish behaved more aggressively towards an opponent when a male audience was present (Matos & McGregor, 2002), the trial procedure allowed males to see the audience before they started interacting. This procedure was used to ensure that the males were aware of the presence of the audience during the interaction. In a further series of experiments, Matos *et al.* (2003) found that the presence of an audience before an interaction affected how male *B. splendens* behaved during the interaction. Using a similar design to that described by Matos & McGregor (2002), the authors divided each trial into two continuous periods: a pre-exposure period (when males could either see an empty tank or a tank containing an audience) and an interaction period (when both males were allowed to interact with each other in the presence or absence of an audience). In the first experiment, four different treatments were used in which the audience was (1) present in the pre-exposure period, (2) present during the interaction period, (3) present in both periods or (4) absent in both periods. The authors then separated the behaviours overt aggression (i.e. attempted bites and latency to first bite) and a display score (combined measure of the other displays, i.e. time spent flaring the gill cover, number of tail beats and time spent near the opponent); for details on the method see Matos *et al.* (2003). Overall, males behaved more aggressively (i.e. shorter latency to attempt to bite the opponent) during the interaction in the treatments where the males were pre-exposed to the audience (treatments 1 and 3). This effect is similar to aggressive priming. The presence of the audience before the interaction may have increased



**Fig. 4.4.** Schematic representation of the second experimental design used in Matos *et al.* (2003). (a–c) The five minute pre-exposure period when both males were pre-exposed to an empty tank (no pre-exposure) (a); both males were pre-exposed to an audience (b); and only one of the males (Ma) was pre-exposed to the audience (c). (d) The 10 minute interaction period following all treatments, where both males were allowed to interact in front of an audience. Ma and Mb are the interacting males; A is the audience; thick lines between the tanks represent opaque partitions; arrows represent the direction in which visual contact was possible.

the motivation to behave aggressively. As a result, individuals escalated more rapidly into more aggressive forms of behaviour when they interacted with the opponent.

The authors also found that priming effects overrode any effect of presenting the audience only during the interaction. The levels of aggression between the two treatments where males were pre-exposed (treatments 1 and 3) were similar, independent of audience presence during the interaction period, while much lower levels of aggression were seen in treatments 2 and 4. In fact, there was no significant difference between the treatments with the audience absent in both periods (treatment 4) and with the audience present during the interaction (treatment 2). These results may suggest that audiences do not affect male–male fighting fish interactions, as the audience affected only treatments with pre-exposure. In this respect the results matched those of Doutrelant *et al.* (2001), in which male audiences did not have an effect on male–male signalling interactions (see above). However, we should also note that in both studies the authors did not look at losers and winners separately.

Matos *et al.* (2003) performed a second experiment to look at the interaction between audience effects and pre-exposure to the audiences; the design allowed independent pre-expose of the two opponent males (Fig. 4.4). As in the first

experiment, the trials were divided in two periods: five minutes of pre-exposure and a 10 minute period in which the two opponents were allowed to interact. There were three treatments in the pre-exposure period: both males pre-exposed to an empty tank (no pre-exposure; Fig. 4.4a), both males pre-exposed to the audience (symmetric pre-exposure; Fig. 4.4b), and one of the opponents pre-exposed to the audience while the other male was pre-exposed to an empty tank (asymmetric pre-exposure; Fig. 4.4c). The audience was always present in the interaction period (Fig. 4.4d). The results confirmed that pre-exposed males tend to behave more aggressively (higher display scores and overt aggression); both the no pre-exposure and the symmetric treatments showed the same tendencies. In the asymmetric treatment, pre-exposed males also tended to display more than the ones not pre-exposed with one exception: non-pre-exposed males matched the number of attempted bites of the pre-exposed males. A possible explanation is that it may be costly for individuals not to retaliate when its opponent escalates, because of the high risk of injury, especially in a confined space such as the experimental tanks (Maan *et al.*, 2001). However, this cost may be enhanced by the presence of the audience. By matching the opponent in more aggressive behaviour, males may be either decreasing the ability of an audience to discriminate loser from winner or manipulating the information to seem more aggressive. These results support the previously discussed idea that males, particularly losers, may gain by performing more aggressively during an interaction in the presence of an audience, as it may decrease the chances of future harassment by that individual (Earley & Dugatkin, 2002; Matos *et al.*, 2003).

These two studies taken together support the idea that previous studies on audience effects (i.e. Doutrelant *et al.*, 2001; Matos & McGregor, 2002) have underestimated the effect of pre-exposure on male aggression. Nevertheless, they also suggest that the social environment (i.e. audiences) is important in determining the dynamics of signalling interaction.

Previous studies have shown that priming is an important mechanism mediating aggressive interactions (e.g. Potegal & Popken, 1984; Bronstein, 1989; Halperin *et al.*, 1992) as it affects the individual's aggressive motivation. For example, priming may decrease the time to initiate aggression or increase the attack behaviour of individuals (e.g. Potegal & ten Brink, 1984; Halperin *et al.*, 1998). However, the effect on the outcome of interactions is not always clear. It seems that priming may have a more pronounced effect during the initial stage of the fight, either causing the individual to display more actively at the beginning of the interaction or to escalate and initiate aggression more quickly (Potegal & Popken, 1984; Bronstein, 1989; Halperin *et al.*, 1998). In several species, individuals that display more intensively and escalate earlier during an interaction usually gain a

competitive advantage over their opponents (Huntingford & Turner, 1987). In such a case, priming may produce a positive effect as it increases the probability that the individual will win the fight. In some cases, however, priming can have a negative effect, male *B. splendens* that have been isolated and then primed with a conspecific image behaved more aggressively towards their opponents but lost most of the interactions (Halperin *et al.*, 1998). These individuals could have been manipulated by priming into aggressive levels that they were not able to sustain during the entire fight, causing them to tire faster than the opponents and subsequently lose the interaction. We conclude that priming may have an important impact on the outcome of the interaction, but whether this impact is positive or negative may depend on whether the initial stages of the interaction determine the outcome and on the length of the interaction.

One potential mechanism behind such aggressive priming is the production of hormones caused by the presentation of a social stimulus. In a recent study, Oliveira *et al.* (2000) showed that watching a fight raises the androgen levels of adult male cichlid fish *Oreochromis mossambicus*. Priming may involve a similar mechanism, and the facilitation of aggressive behaviour through pre-exposure may be caused by an increase in androgen levels initiated by the pre-exposure to the audience. Oliveira *et al.* (2000) suggested that these hormones mediate changes in the perceptual abilities and readiness to interact of males, which, in turn, would enhance their success in social interactions.

Further studies are needed to comprehend fully the relation between the adaptive value of priming and the presence of an audience. Advances in the understanding of the effects of the social environment on the neuroendocrinological system may be an important contribution in this area (Ch. 21).

### Summary and future directions

One important question in the general context of communication networks is how narrowly or broadly we wish to define the social context of signalling. Recent studies have shown that mate preferences can be altered by viewing sexual interactions (Westneat *et al.*, 2000). In several species, seeing a male mate enhances this male's attractiveness to females (Dugatkin, 1992; Ch. 5). Such choosing females would be eavesdropping on the signalling-mating interaction of two other individuals and responding accordingly. The same reasoning might apply for other interactions as well. It appears that most dyadic interactions are actually embedded in a social context or network. This raises the question of how common the well-studied dyadic interactions actually are, as these studies have only considered them in a social void. This situation might be more of an exception than the rule. In this context, more knowledge on sensory ecology and



especially the role of private channels would be very helpful. Communication via private channels uses sensory channels not available to the audience. This has been documented for swordtails (*Xiphophorus* spp.): males signal in the ultraviolet, a part of the spectrum that cannot be detected by a predator, the Mexican tetra *Astyanax mexicanus* (Cummings *et al.*, 2003). True dyadic interactions may be brief and limited to signals transmitted in close contact. A potential example might be nipping in poeciliid fishes; here, males nibble a female's genital region and chemical signals are transmitted (Parzefall, 1973). Such signals are not available to any other individual, although the male's response to the signal might be (Parzefall, 1973).

Another aspect to consider is that many social interactions relevant to several aspects of an individual's life may happen simultaneously and influence each other. Any given individual will have to include this into its signalling decisions. For instance, a singing bird may simultaneously be faced with the problems of attracting a female, discouraging a neighbour from entering its territory and avoiding predators. This leads to a more complicated network of social interactions, the components of which may influence each other to shape a 'social interaction network'. Our singing bird example also illustrates that each context alone would select for a different signal or signalling strategy. Signals have to be effective enough to transmit accurate information to target receivers but private enough to prevent this information from being detected by 'unwanted' untargeted receivers. Any signal that is under such conflicting demands will be a compromise, depending on the associated costs and benefits. Only recently has formal modelling been used to address this problem (Johnstone, 2001; Ch. 26).

We have attempted to show that the presence and type of audience can have important effects on the signalling strategies of individuals. The nature of information and the extent to which it is broadcast may depend on the type of audience and on the role of each signaller during an interaction. Audiences may also influence the evolution of new types of signal. During signal evolution, different pressures may arise in signal design depending on whether it is specialized to advertise or privatize information (e.g. 'normal' song versus quiet song; Dabelsteen *et al.*, 1998; Ch. 3). Audience effects may be closely linked with mechanisms such as priming effects, which may influence motivation of signallers and consequently their signalling strategy. In natural systems, the social environment affects how animals make behavioural decisions. Individuals can use signalling interactions between others as a source of information; this can in many ways have important consequences for the fitness of individuals. In order to improve our understanding of the evolution of signals and signalling strategies, we must take into account the individuals' social environment and the costs and benefits associated with the presence of audiences and eavesdroppers.

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