

## Signalling in Territorial Systems: A Context for Individual Identification, Ranging and Eavesdropping

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# Signalling in territorial systems: a context for individual identification, ranging and eavesdropping

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## SUMMARY

Territorial systems are characterized by the relative longevity and stability of interactions between neighbouring individuals. Two abilities of signal receivers that can be seen as adaptations increasing the efficiency of territory defence will be discussed: identifying neighbouring individuals and ranging (i.e. determining the distance to) signallers. The costs involved in such discriminations will also be outlined. Although signalling has been traditionally considered as occurring between two individuals (signaller and receiver), long-range signals will be received by many individuals. In territorial systems a group of neighbours could be considered as a communication network: consisting at its simplest of a signaller and a number of receivers. The scope for low cost, low-risk information gathering in such networks by eavesdropping will be discussed with particular reference to territorial songbirds and electric fish.

## 1. INTRODUCTION

Considerations of the evolution of communication have dealt most commonly with the selection pressures affecting signalling behaviour and signal structure (e.g. Dawkins & Krebs (1978); Wiley & Richards (1978)). In extreme cases communication is considered to function solely in obtaining adaptive advantages for the signaller with benefits to the receiver being merely incidental to the process (e.g. Myrberg 1981). However, increasing attention is being focused on the selection pressures affecting animals as receivers and interpreters of signals (see Krebs & Dawkins 1984; McGregor 1991; Guilford & Dawkins 1991, 1992; Wiley 1993). The selection pressures affecting the evolution of perceptual abilities are particularly clear in the context of animals defending territories. In this context signal content and signalling system structure differ from other sorts of communication; these differences are germane to considerations of the evolution of signalling systems and attempts to model them, yet they have been largely ignored to date.

Territories can be broadly defined as defended areas (Davies 1978); generally territories have fixed locations and are defended by the same individuals for a significant portion of their lives. The result is a series of long-lasting stable associations between individuals (neighbours), characterized by repeated, commonly low-level, aggressive encounters. Changes in habitat quality, breeding status of mate and fitness of neighbours are likely over the extended time periods involved and continual information gathering is necessary to assess the value of defended resources and therefore to set the appropriate level of defence. Two pieces of information are pivotal to efficient territory

defence; the distance of a signalling individual and its identity. Territorial receivers are surrounded by signalling individuals, by far the most common being their territorial neighbours, however neighbours do not constitute a serious threat to territory tenure unless they have crossed territorial boundaries. An ability to individually identify a neighbour and to estimate its position relative to a shared boundary will minimize the number of 'false' responses, that is, approaches to neighbours signalling some distance outside the receiver's boundaries. Information on both identity and distance will be difficult for signallers to withhold: individually characteristic signals will inevitably result from individual variation in signal acquisition, development, production and perception mechanisms, and information on distance is an inevitable consequence of signal transmission through the environment (see below).

This paper emphasizes the selection pressures favouring the perception and interpretation of information by signal receivers in the context of territory defence. Most of the examples will be drawn from studies of territorial songbirds and weakly electric fish, however, the arguments should apply equally well to any animal employing long-range signals.

### (a) *The territorial context*

Territorial systems differ from other communication situations in the nature and extent of the signalling interactions between individuals. The difference in nature arises because the bulk of signalling in territory defence occurs between neighbouring territory holders; these are repeated interactions with the same individuals over extended periods of time, and are

therefore quite different from the single interactions between unknown individuals normally considered by communication theorists. The differences in extent of signalling interactions in territorial systems arise because any territorial individual is equidistant from half a dozen or so immediate territory neighbours and usually capable of receiving signals from more distant individuals too. Groups of territory holders can therefore be considered as an interacting network of signallers and receivers, where many combinations of signaller and receiver are possible. This is in stark contrast to the communicating dyad of signaller and receiver normally considered in discussions of the evolution of signalling.

## 2. SIGNAL CONTENT

### (a) *Distance information*

Territorial animals with an ability to decide whether a signaller was within their territorial boundaries would gain two benefits. First, they would reduce the energy expended in approaching to determine the position of the signaller. Second, they would minimize the risks of injury inherent in closely approaching another individual, especially another territory holder.

The term range is used to refer to the distance between the signal receiver and the signaller (Morton 1982, 1986). The effects of range on animal sounds, particularly bird and insect songs, have been widely reviewed (e.g. Richards & Wiley 1980; Wiley & Richards 1982; Morton 1982; Römer 1992; Michelsen 1992; McGregor 1993); briefly, increasing range decreases the overall signal amplitude and increases the signal degradation (distortion). Degradation is caused by reverberations – echoes from the ground and objects such as tree trunks and vegetation – and irregular fluctuations in amplitude, often caused by variation in the wind speed (see Morton 1970, 1975, 1986; Richards & Wiley 1980; Wiley & Richards 1982; McGregor 1991). In principal either decrease in amplitude or increase in degradation could be used as cues to range, however, it has been argued that degradation is the more reliable cue to range. This is partly because degradation is largely unaffected by signaller behaviour, whereas amplitude can be altered by the singer (for more extensive discussion of this point see: Richards 1981; Morton 1982; Wiley & Richards 1982; McGregor 1991, 1993).

Playback experiments have shown an ability to estimate range (termed ranging by Morton (1982, 1986)) in a number of species. For example, Carolina wrens *Thryothorus ludovicianus*, respond to playback of less degraded songs by silently approaching the loudspeaker, whereas they respond to playback of more degraded songs from the same location by singing from a distance. The same difference in response is elicited in natural contexts by a male singing from inside versus outside of the territory boundary (Richards 1981). A similar result was found for the field cricket *Gryllus bimaculatus* (Simmons 1988). Further experiments have only found such a difference in response to more degraded and less degraded songs

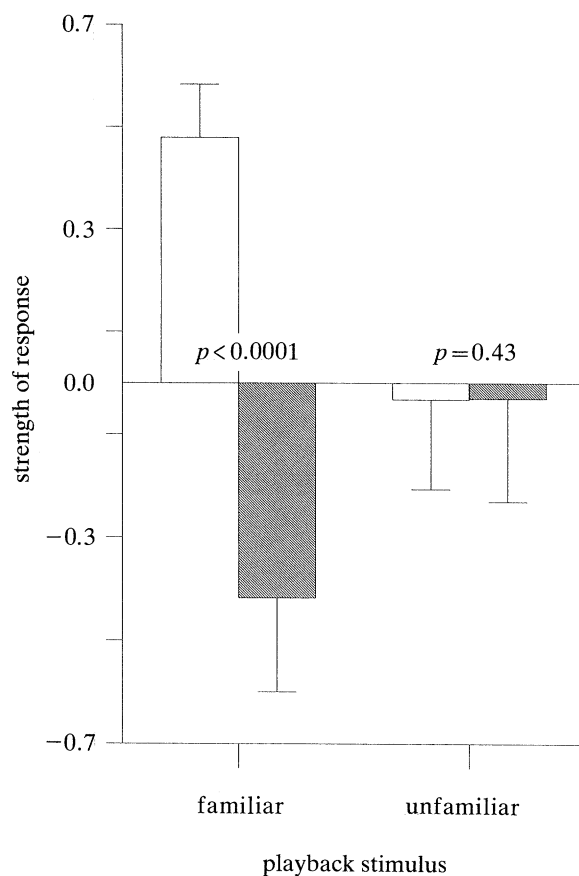


Figure 1. The effect of the extent of degradation (open column, less degraded; shaded column, more degraded) on the mean response ( $\pm 1$  s.e.) to playback of familiar and unfamiliar song types by 32 males great tits. Familiar song types are sung by the test male, a neighbour or both; unfamiliar are not sung within hearing of the test male. The strength of response is a single variable derived from eight original variables by principal component analysis; a large positive value indicates a strong aggressive response (see McGregor (1992) for details using the same data set). Probabilities refer to two-tailed paired *t*-tests.

when the songs are familiar to the test subject in great tits *Parus major* (McGregor *et al.* 1983; McGregor & Krebs 1984), Western meadowlarks *Sturnella neglecta* (McGregor & Falls 1984), humans (McGregor *et al.* 1985) and Kentucky warblers *Oporornis formosus* (Wiley & Godard 1992). In these experiments two kinds of sound were played back in more and in less degraded versions. An example of the response is shown in figure 1. Such results effectively rule out an unlikely alternative explanation of this pattern of response based on a lack of species specific releasing stimuli (for a fuller discussion of this topic see McGregor & Krebs (1984); McGregor (1991, 1993)).

### (b) *Individual identification*

The ability of territory holders to identify individual neighbours is crucial both to the contention that signalling in a territorial context merits special consideration and also to the structural effects discussed below. Fortunately for both these arguments

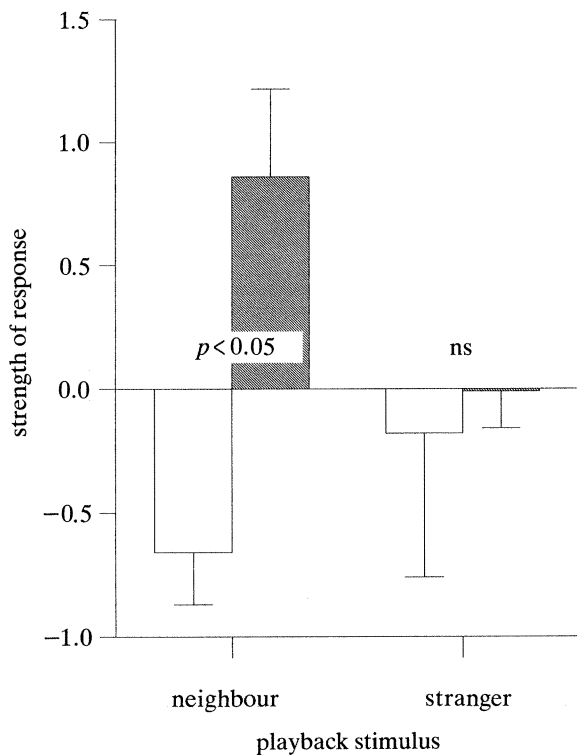


Figure 2. The mean response ( $\pm 1$  s.e.) to playback of EODs to 6 *G. carapo* from a territorial neighbour and a fish from another tank (stranger). The open columns indicate playback from the usual boundary between the test fish and the neighbour; shaded columns, the opposite boundary. Strength of response is explained in figure 1 caption. Probabilities refer to Wilcoxon matched-pairs signed ranks test.

there is extensive evidence of such an ability in a variety of animal groups, as reviews by Falls (1982) and Ydenberg *et al.* (1988) make apparent. However, since this ability is so important to future arguments in this paper, I will present evidence from two species from different animal groups to illustrate the nature of the evidence.

(i) *Neighbour–stranger discrimination in a weakly electric fish*

Two groups of freshwater fish, South American gymnotoids and African mormyriforms, communicate using electric signals (electric organ discharges or EODs) (for recent review see Kramer (1990b)) *Gymnotus carapo* is a South American weakly electric fish. In the field it is solitary, usually spaced 2–3 m apart with individuals keeping the same daytime position for several days (Lissman 1961; Hopkins & Heiligenberg 1978; Westby 1988), it also vigorously defends territories in the laboratory (Black-Cleworth 1970). Visual inspection of the EOD waveform shows that individuals are qualitatively individually distinctive and this is confirmed quantitatively by a series of measurements of the waveform (see Fig. 3, Tables I & II in McGregor & Westby (1992)). The ability of *G. carapo* to use this variation in electric signals to discriminate between individuals was investigated with playback. The technique, commonly used in studies of neigh-

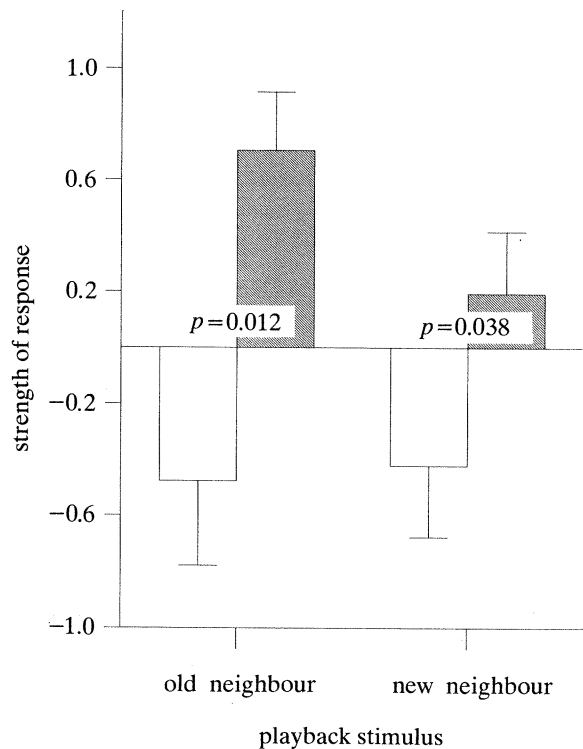


Figure 3. The mean response ( $\pm 1$  s.e.) to playback of two current neighbours to 13 male great tits aged 2 or more years. Old neighbours have shared a boundary with the test male from the test male's first year; new neighbours have shared a boundary only for the current year. Open columns, playback from the usual boundary between test male and neighbour; shaded columns, opposite boundary. Strength of response is explained in figure 1 caption. Probabilities refer to Wilcoxon matched-pairs signed ranks test.

bour discrimination in birds (for a review, see Falls (1982)), relies on differences in strength of response to the simulated presence of a signalling individual at, or just inside, the territory boundary. The strength of response elicited from the territory holder depends both on the location of playback simulating an intruder and on the identity of the intruder. Playback of a neighbour's signal from the usual (correct) territorial boundary elicits a weaker response than playback from the directly opposite (incorrect) boundary. There is no such difference when the signals of non-neighbours (strangers) are played from these same two positions. The explanation of such a pattern of response has a theoretical basis in the 'dear enemy effect' (Fisher 1954) and has been discussed by a number of authors (Ydenberg *et al.* 1988, 1989; Getty 1989; McGregor 1991). Briefly, the asymmetry in response to neighbours reflects the perceived threat to territory tenure: neighbours signalling from their usual location are the most common situation and represent little threat to tenure, however, a neighbour signalling from a new location (such as the incorrect boundary) is a threat to tenure because there is no agreed boundary at that location. A stranger represents a threat to territory tenure regardless of position because, by definition, there are no such agreed boundaries. The experiment produced a clear result (figure 2); there was a significant difference in res-

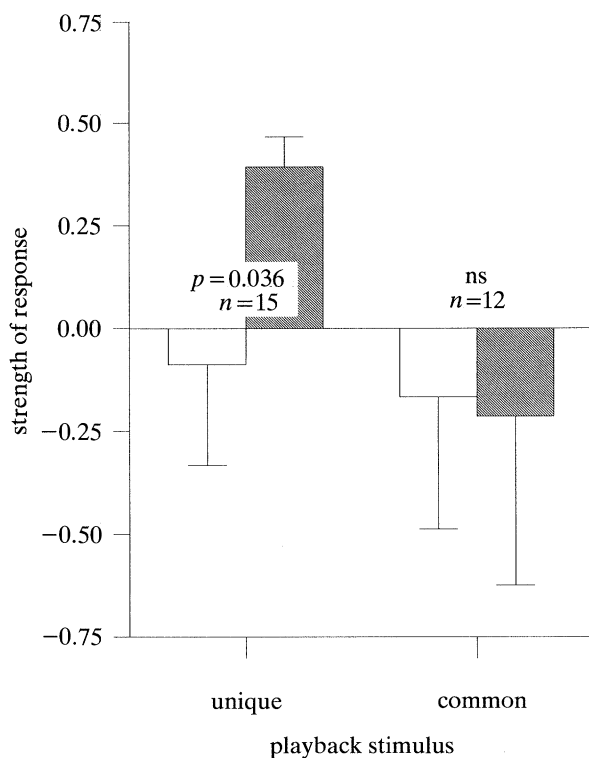


Figure 4. The mean response ( $\pm 1$  s.e.) of male great tits aged 2 or more years to playback of two song types from the same current new neighbour (defined in figure 3 caption). Unique, a song type that has only been sung by the neighbour; common, a song type sung by 2–5 other neighbours. Open columns, playback from the usual boundary between test male and neighbour; shaded columns, opposite boundary. Strength of response is explained in figure 1 caption. Probabilities refer to Wilcoxon matched-pairs signed ranks test.

ponse to neighbour playback from correct versus incorrect boundaries, with the strongest response to playback from the incorrect boundary. However, playback of EODs from strangers (territorial fish from another tank) elicited a similar strength of response at the two boundary locations. Therefore, this example clearly shows that features of *G. carapo* EOD waveforms are individually distinctive and that fish defending territories can discriminate between their neighbours and other fish using such characteristics.

#### (ii) *Individual identification by songbirds*

Playback experiments to territorial male songbirds using the correct–incorrect boundary paradigm explained above for electric fish have shown that individuals are able to discriminate between two current neighbours (e.g. great tits, figure 3; McGregor & Avery 1986; McGregor 1989; hooded warblers, *Wilsonia citrina*, Godard 1991, 1992). These experiments also produced direct (Godard 1991) and indirect (McGregor & Avery 1986; McGregor 1989) evidence that songs learned for neighbour discrimination are retained for considerable periods, for example, from one breeding season to the next

(Godard 1991). Indeed, although great tits retained the ability to learn songs for neighbour discrimination throughout life, learning in later life was impaired by previously learned songs; a form of proactive memory interference operating through similarity and capacity constraints (illustrated in figure 4; McGregor & Avery 1986; McGregor 1989). A laboratory operant conditioning paradigm has also been used to study individual identification abilities; after being trained to respond to the songs of one particular individual, male great tits responded to novel (previously unheard) songs of the particular individual with the conditioned response (Weary 1988, 1992; Weary & Krebs 1992). That is, the males were apparently detecting individual characteristics of voice. Such characteristics can be demonstrated quantitatively in various aspects of great tit song (Weary 1988; Weary *et al.* 1990).

#### (c) *Costs of discrimination ability*

An ability to discriminate requires the appropriate perception and interpretation machinery and these in turn will have associated developmental and maintenance costs. Weakly electric fish have considerably larger brains than non-electric teleosts of a similar size (Bullock & Heiligenberg 1986) and therefore incur such development and maintenance costs. This difference is commonly held to reflect the processing requirements of electrolocation, but extracting information on species, sex and individual identity of an electric signaller will also add significantly to the processing and hence brain size needed (Kramer 1990a; McGregor & Westby 1992). Although there is no direct evidence linking ranging and individual identification abilities with larger than average brains in songbirds, there is good evidence that learning many songs to sing results in a larger brain (Nottebohm 1981; Kroodsma & Canady 1985; T. DeVogd, personal communication). It seems reasonable to extend these results to songs learned for discrimination tasks and therefore songbirds will be paying comparable brain tissue development and maintenance costs to electric fish.

Discrimination ability also has the potential for a second type of cost, that is, the memory interference effects identified in great tits (McGregor & Avery 1986; McGregor 1989). Electric fish may incur a similar cost in identifying individuals, indeed memory interference is likely to be more severe than in songbirds because electric signals are far less variable than song and therefore similarity constraints are relatively more important. The impairment of future discrimination learning seems to result from the storage of songs learned in previous years for discrimination interfering with learning songs of newly arrived neighbours, it could be avoided by re-learning neighbours' identities each year. However, a cost of forgetting the identity of last year's neighbours is that information on interactions with previous neighbours and agreed boundary locations will not be available at the crucial initial stages of territory establishment at the beginning of the breeding season. Presumably the value of such information outweighs the benefits

associated with the avoidance of memory interference. Ranging ability probably suffers the same proactive memory interference effects as individual identification ability, because the most likely mechanism for the perception of degradation (and hence range) is comparison to an internal standard, such as songs learned by the bird to be sung or to identify its neighbours (Morton 1982, 1986; McGregor & Krebs 1984).

#### (d) Summary

Early neighbour-stranger discrimination playback experiments were largely serendipitous (Falls 1992), whereas investigations of ranging were directed by suggested advantages to individuals defending territories. However, both sets of experiments make it clear that ability to identify the signals of neighbouring individuals and ability to range are common in territorial species. The identification of costs associated with such discrimination abilities – growth and maintenance of brain tissue, memory interference – raises the interesting question of evolutionary trade-offs with the value of the information gained.

### 3. STRUCTURE OF SIGNALLING SYSTEMS

It is invariably the case that any signalling animal is within receiving range of a number of other potential signallers. Although this fact is tacitly acknowledged, it is almost universally ignored and signalling is considered to occur between a dyad of signaller and receiver; notable exceptions are studies of chorusing in insects and anuran amphibians (see Otte 1974; Wells 1988). Signalling behaviour and signal structure have evolved in a communication network of many signalling individuals. These are particularly apparent in territorial systems but certainly occur in other signalling situations (see below). Theoretical arguments and models dealing solely with dyads of signaller and receiver are not therefore an adequate representation of communication behaviour in most natural contexts of signalling.

In this section I shall follow the theme developed in the previous section on signal content and discuss the adaptations of receivers that have evolved to gather information in communication networks of signalling and receiving individuals.

#### (a) Eavesdropping

In a communication system employing long-range signals such as sound, individuals not directly involved in a signalling interaction can none the less gather information from it. I propose that the term eavesdropping best describes this behaviour. A comparable use of eavesdropping is to describe situations usually involving predators and prey (Barclay 1982; Harper 1991). For example, playback experiments have shown that Mediterranean house geckos *Hemidactylus tursicus* use the signals of calling male decorated crickets *Gryllodes supplicans* to intercept females approaching callers (Sakaluk & Belwood 1984).

Intraspecifically, Myrberg (1981) has used the term interception to describe comparable behaviour; drawing the distinction between a sound signal considered to have been heard by a receiver, and the same signal that may be overheard by other individuals. He argues that interception should not be considered as communication behaviour because interceptors are not the intended receivers of the signal. To some extent this distinction is driven by a definition of communication that only recognizes advantages to the signaller and considers any benefit to receivers to be incidental (Myrberg 1981, p.399). Communication is perhaps better thought of as mutual exploitation between signaller and receiver leading to a coevolutionary arms race (e.g. Krebs & Dawkins 1984, p. 390). As noted in the Introduction, the role of receivers in communication is now more widely considered, therefore eavesdroppers (or overhearers) form as much a part of the environment in which signals and signalling behaviour have evolved as the transmission constraints imposed by the physical environment. Indeed, it is difficult to see how long-range signalling could avoid eavesdropping, especially if the signals function in mate attraction where long range and wide spread are major components of effectiveness. These considerations suggest that eavesdropping is an important feature of communication systems employing long-range signals and that it has played a role in signal evolution. More particularly it is likely to have had important effects on the evolution of the perceptual abilities of receivers.

#### (b) Evidence for eavesdropping

To date there have been no direct investigations of eavesdropping within species. Perhaps this is not surprising given the paucity of studies of receivers in signalling systems and a general preoccupation with signalling dyads rather than communication networks. However, there are several observations that are consistent with eavesdropping. For example, Myrberg (1981, Table 2c.8) lists a series of cases where fish sounds (usually courtship sounds) from one male elicit similar sounds from other males even in the absence of females. Electric fish emit electric signals (EODs) almost continuously throughout life and aspects of the signal change in association with behaviours such as feeding, fighting and resting. They are therefore particularly likely to have evolved an ability to eavesdrop. An early study of electric eels (*Electrophorus electricus*) noted that captive eels would converge on a feeding site from many metres away, suggesting that they were cuing in to changes in EODs of feeding individuals. When the EODs of an electric eel feeding on a shrimp were relayed to a nearby, electrically isolated, tank containing many other motionless eels, they responded by showing considerable movement (Bullock 1969). In territorial songbirds, the activity of neighbours can potentially indicate the presence of an intruder. In fan-tailed warblers (*Cisticola juncidis*), there is a decrease in vocal activity during playback to immediate neighbours and an increase when playback ceases (Gray 1992). Such a pattern of response is

consistent with birds attending to the vocal interaction between a neighbour and an intruder and then increasing the level of territory defence when an intruder has apparently been evicted from a neighbour's territory and when its current position is unknown because it (i.e. playback) is silent. A study of red-capped cardinals (*Paroaria gularis*) clearly showed neighbours functioning as an early warning system of intruders. This species is a small, monogamous finch which defends linear territories based on lake and river edges in the Amazon basin; territorial intruders are escorted to territory boundaries. Territory holders detected an intruder immediately in ten out of 11 cases when the intruder had just been expelled from a neighbour's territory, whereas only two out of 14 intruders were immediately detected if they had remained undetected on the neighbour's territory (Eason 1992). The immediate detection rate for intruders coming from areas with no neighbours was 37 out of 67 cases; illustrating both the attention territory holders paid to neighbours and the tendency for intruders to avoid defended areas en route to an intrusion.

These examples show that eavesdropping could provide valuable information on the presence of potential mates, food availability and the presence of territorial intruders. The fact that all these examples were noted incidentally during the course of other studies suggests that eavesdropping is a noticeable and common behaviour.

#### (c) *Potential for eavesdropping in a territorial context*

There are *a priori* reasons for suggesting that there is another sort of information that eavesdroppers could acquire in territorial systems. Eavesdropping on the signals produced in a dispute between a territorial neighbour and another individual (neighbour or stranger) could allow a territory holder to assess the other individual by proxy with no risk to themselves. This is possible because a territory holder has an accurate idea of the fighting ability of a neighbour and can therefore assess the other individual relative to itself. In a situation where a neighbour is in dispute with a stranger, eavesdropping has the twin advantages of being a minimal risk, low-cost assessment mechanism and allowing information on a potential intruder to be gathered before any interaction involving the territory holder directly. The beneficial priming effect of early warning of a fight is well documented (e.g. Hollis 1984) and if the warning is combined with information on the relative fighting ability of the opponent the effect is likely to be that much greater. When the interaction occurs between two of its neighbours, an eavesdropping territory holder could gain information about short-term changes in fighting ability which could reflect influences of parasites and pathogens. It could also allow an assessment of the extent of involvement of the neighbours in the current dispute and therefore the risks inherent in trespass, perhaps to attempt an extra-pair copulation.

#### (d) *Potential for eavesdropping in other contexts*

Any long-range signals are susceptible to eavesdropping, the following example on mate choice illustrates the sort of information that eavesdroppers may gain in a non-territorial context. Mate attraction signals are likely to be particularly far travelling, and are therefore especially vulnerable to eavesdropping. For example, males displaying on leks will be transmitting signals that can be received by females other than the intended recipient of courtship and also by other lekking males. The female audience could gather information on male features pertinent to future choice by observing the display without the risks attendant on closely approaching the male such as forced copulations and interception by peripheral males. Other males on the lek could acquire information on such features as the presence of females and the performance of the male, both types of information will allow them to assess the potential gain and likelihood of success in usurping that position in the lek.

#### (e) *Summary*

Although there has yet to be an experimental investigation specifically directed at eavesdropping, a number of observations are consistent with the idea. Eavesdropping has the potential to allow low cost, no risk assessment of both neighbours and strangers in a territorial system. The advantages in other systems are likely to be different, but are likely to be of the same level and therefore eavesdropping is to be expected in any signalling system employing long-range signals.

I thank the conference organizers for the opportunity to express these ideas and co-workers Mark Avery, John Krebs and Max Westby for permission to use joint data. Discussions with Torben Dabelsteen developed many of these ideas and comments from Gillian Gilbert, Rachel Scudamore and Xanthe Whittaker improved the manuscript.

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