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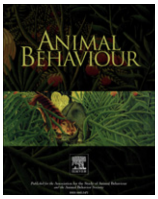

Tactical multimodal signalling in birds: facultative variation in signal modality reveals sensitivity to social costs

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The presence of eavesdroppers within a communication network can increase the costs associated with signalling. Hence, selection should favour the ability to vary signal structure with social context. One possible mechanism is the flexible combination of the components that form a multimodal signal. This phenomenon clearly occurs in social mammals, particularly primates, and has been identified as one of the foundation elements for the evolution of complex communication. However, this flexibility in signal component composition in relation to social context has not previously been demonstrated in other taxa. Here we show that subordinate male fowl, *Gallus gallus*, show facultative variation in the structure of their multimodal signals. Intriguingly, signallers were not sensitive to the behaviour of the intended receivers (hens) but rather to the attentional state of eavesdropping rival males. Subordinates switched from multimodal displays (movements and calls) to unimodal (silent) displays when the alpha male was attentive. Unimodal and multimodal displays had equivalent efficacy in attracting hens, but multimodal signals were associated with more rapid approach by the alpha male and increased probability of severe attack. Variation in signal type is hence driven by social costs. This is the first demonstration of facultative multimodal signalling in birds.

Many animals produce signals that simultaneously engage more than one of the receiver's sensory channels ('multimodal signals'; Guilford & Dawkins 1991; Partan & Marler 1999, 2005; Rowe 1999). Each modality may function either as a 'backup', thereby enhancing signal transmission ('redundant signal'; Partan & Marler 1999; Candolin 2003; Hebets & Papaj 2005), or serve to alter the information content ('nonredundant', 'multiple message hypothesis'; Møller & Pomiankowski 1993; Johnstone 1996; Partan & Marler 1999). Putative benefits of these multimodal signals are enhanced signal detectability, discriminability and memorability (Guilford & Dawkins 1991, 1993; Rowe 1999). However, these same characteristics may increase the costs of signalling (e.g. increased energetic expenditure, competition or predation risk; Partan & Marler 2005). Selection should therefore favour adaptations that enable the signaller to balance these opposing forces (Johnstone 1998).

Two potential mechanisms for balancing benefits and costs are variation in signal structure (Johnstone 1998) and behavioural flexibility (Jones 2005; Gerhardt 2009). Because redundant multimodal signals encode the same information through each sensory channel, the recipient need only perceive one channel to receive the message (Partan & Marler 1999, 2005; Rowe 1999). This would be beneficial in cluttered environments (i.e. where noise occurs in the same channel as the signal; Rowe 1999). In some systems, modalities can be flexibly combined ('fluid' or 'free'; Smith 1977; Wickler 1978) and this may be particularly advantageous when signals are produced within a matrix of intended and unintended receivers. Under these conditions, several individuals may gain information about the signaller either directly, through dyadic interactions, or indirectly, through eavesdropping (McGregor & Dabelsteen 1996; McGregor & Peake 2000; Peake 2006). It is now clear that future responses to the signaller can be affected by both direct and indirect experience (Oliveira et al. 1998; Bshary 2002; Mennill et al. 2003). The increased detectability, discriminability and memorability of a multimodal signal can potentially amplify both its costs and benefits within a communication network. For example, signallers that defeat conspecifics in an aggressive interaction or that attract females can more efficiently enhance their 'reputation', but the same logic applies to costs: losers or unsuccessful males should suffer a greater loss than would have been incurred if they had relied upon unimodal signals. This argument generates the prediction that animals should show flexibility in

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signal structure in response to social context (Peake 2006; McGregor 2009). There is good evidence for the former phenomenon in a wide variety of taxa, but the latter phenomenon has been much less studied and is only clearly apparent in a few mammalian species.

Compelling examples of tactical use of signal modality have been documented in California ground squirrels, *Spermophilus beecheyi*, and chimpanzees, *Pan troglodytes*. During encounters with pit vipers (but not infrared-insensitive nonvenomous snakes), California ground squirrels facultatively add thermal radiance to their visual tail-flagging display to engage the receiver's infrared sensory sensitivity (Rundus et al. 2007). This selective combination of signalling modalities probably controls energy expenditure, while also producing a more effective signal for those potential predators that can perceive it. Studies of chimpanzees reveal even more subtle flexibility in modality usage. Here, the combination of signal components depends not on the class of receiver, but rather on its attentional state (Leavens et al. 2004). For example, visual signals are preferentially directed towards receivers that are facing the signaller, whereas acoustic and tactile signalling are used when the receivers are looking away. Although there is extensive evidence that primates engage in such modality switching in response to the attentional state of receivers (Whiten & Byrne 1988; Hare et al. 2000; Povinelli et al. 2003; Poss et al. 2006; Leavens 2007), there has been no comparable demonstration for any other taxonomic group.

Male junglefowl, *Gallus gallus*, respond to the discovery of food by tidbitting. This is a redundant multimodal signal (sensu Partan & Marler 2005) in which the signal elements can be flexibly combined (Davis & Domm 1943). Communication occurs within a network of intended receivers (females) and competitors (males). Social groups are highly stable (Collias 1987), and the costs and benefits of signalling are well documented (Stokes 1971; Marler et al. 1986a, b). These are just the conditions that have likely selected for facultative variation in signalling modality in primates (Humphrey 1976; Byrne & Whiten 1988).

The multimodal tidbitting signal combines a visual display with vocalizations, known as food calls (see Supplementary Video S1). The vocalizations are individually distinctive (C. S. Evans & C. L. Smith, unpublished data) and are composed of a repeated series of pulsatile sounds. The calls are audible up to 30 m away (Stokes 1971; Stokes & Williams 1971, 1972; C. S. Evans & C. L. Smith, unpublished data) and have characteristics suggesting that they should be easily localizable (Evans & Evans 1999; Wood et al. 2000). The vocalizations are always accompanied by the visual display, which is a continuous series of repeated movements of the head and neck (Davis & Domm 1943), including three distinct motor patterns (Smith & Evans 2009). Playback experiments demonstrate that the components in each modality are functionally referential (i.e. they evoke food-searching responses in the absence of contextual cues; calls: Evans & Evans 1999, 2007; visual displays: Smith & Evans 2008, 2009) and are redundant, providing the same information and evoking the same responses singly or when combined (Partan & Marler 1999; Hebets & Papaj 2005). The performance of the multimodal signal is highly variable, dependent upon the quality and quantity of food available as well as the responses of conspecifics (Stokes 1971; Marler et al. 1986a; Smith & Evans 2009). Males signal longer and show a higher rate of food calling (Marler et al. 1986a) and movements (Stokes 1971) when presented with a highly preferred food item. In addition, social context has a powerful modulating effect on signal production. Laboratory studies have shown that production of food calls is potentiated by hens and inhibited by rival males (Marler et al. 1986b; Evans & Marler 1994). When dominant males tidbit in the presence of hens, females typically respond by approaching and searching for food near the signalling male (Stokes & Williams 1972; Marler et al. 1986a, b; Gyger & Marler 1988).

In fowl, females prefer to mate with males that provide more food to any female in the group, regardless of male rank (Pizzari 2003). Females subsequently remain closer to males that tidbit than to males that perform other behaviours (Smith & Evans 2009), and mating success is also linked to proximity to females (Graves et al. 1985). However, mating does not typically occur immediately after tidbitting (Stokes & Williams 1971); hence, females must retain some memory of the individual males' rate of performance. There is also competition between females because only the first hen to approach a tidbitting male receives food (Stokes & Williams 1971) and females subsequently alter their behaviour towards females that they have observed winning or losing previous aggressive female–female interactions (Hogue et al. 1996). Taken together, this suggests that there is 'interceptive' (sensu Myberg 1981; Searcy & Nowicki 2005) and 'social' (sensu McGregor & Dabelsteen 1996) eavesdropping as well as the use of 'reputation' (sensu Bshary 2002) by female fowl.

Male–male competition is also an important factor in tidbitting signal production, and a more subtle audience effect is apparent under naturalistic conditions. Subordinate males sometimes perform the visual display while omitting the more conspicuous vocalizations (C. L. Smith, unpublished data). This is likely a response to social cost, as the dominant male will often attack a lower-ranking male that tidbits multimodally (Stokes 1971). Facultative variation in signalling behaviour by subordinate males may hence reduce the likelihood or intensity of agonistic encounters with the dominant males, while still enabling them to perform behaviours known to influence female choice.

Our aim in the present study was to identify the factors affecting variation in multimodal signalling behaviour. We used high-definition video and audio monitoring of fowl living in naturalistic social groups to document the prevalence of unimodal (visual only) tidbitting by males of different ranks and examined the social context of these displays by measuring receiver distance. Video recordings also allowed us to establish the attentional states of the signals' intended receivers and potential eavesdroppers. In addition, we determined the relative efficacy of the combined and individual modalities by assessing the likelihood of the signalling male attracting hens. Lastly, we examined whether switching to unimodal signalling by subordinate males reduces the probability and severity of attack by the dominant male.

METHODS

Subjects

Subjects were 24 male and 48 female sexually mature (1–7 years old) fowl, *Gallus gallus*, from a population originally derived from golden Sebright bantams that had been allowed to breed freely for several generations. Although Sebrights are morphologically distinct from junglefowl, their behaviour closely resembles that of the ancestral form, the red junglefowl, *Gallus gallus* (Collias & Joos 1953; Collias 1987; Andersson et al. 2001; Schütz & Jensen 2001), from which all domesticated strains have been derived (Fumihito et al. 1994, 1996). In particular, Sebrights have not been subjected to artificial selection for rapid growth or increased egg production.

Materials and Procedures

We used 12 social groups, with a composition modelled on that described in wild junglefowl (Collias & Collias 1967). Each group was made up of six birds (two males, four females), assigned at random. By chance, the alpha and beta males were the same age in six of the 12 groups. Four of the remaining six groups had alpha