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Referential signalling in birds: the past, present and future

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Many species produce specific signals in response to environmental events. The specificity of these signals allows receivers to react appropriately to an event in the absence of other contextual cues. These functionally referential signals can be auditory, visual or multimodal and occur in antipredator, food and social cohesion contexts. In birds, acoustic signals used in antipredator defence are the most often studied. However, several species of birds produce functionally referential signals in other modalities, including gestures, and in other contexts, including food and social contact. The prevalence of functionally referential visual or multimodal signals may be underestimated. More research using innovative techniques is needed to test these signals. Food calls, particularly those produced during food provisioning, also require further study and may shed light on the ontogeny of food signals. Comparative studies across closely related species of birds may also reveal differences in the development of functionally referential versus motivational signals. Taken together, the type of research into functionally referential signals suggested herein will likely further our understanding of the ecological, social and physiological pressures that have shaped communication in birds.

The meaning of animal signals is an enduring question in the field of animal communication. Animal signals were traditionally thought to indicate the internal motivational state of the animal (Rowell & Hinde, 1962). This motivational or affective model of animal signals posits that the structure of signals should vary along a gradient that reflects the signaller's internal response to the eliciting stimuli. However, if multiple stimuli elicit the same type of signal, then a receiver may not be able to link the signal directly to a specific external event (Premack, 1975). The discovery in the 1960s that some signals are apparently produced specifically in response to external stimuli generated significant research interest (e.g. reviewed in: Gill & Bierema, 2013; Suzuki, 2016; Smith & Evans, 2014; Townsend & Manser, 2013). The ability to refer to external events was believed to be unique to humans, and therefore these signals potentially afforded a means of identifying the evolutionary precursors of human language (Evans & Marler, 1995; Snowdon, 1993) and provided insight into the cognitive processes of nonhuman animals (e.g. Cheney & Seyfarth, 1990; Griffin, 2013). The term ‘functionally referential’ was coined to designate these apparently referential signals (Evans, Evans, & Marler, 1993; Macedonia & Evans, 1993). The term ‘functional’ acknowledges that the behaviours are interpreted in light of their usage by the signaller and the receivers' responses without knowledge of the underlying cognitive processes (Marler, Evans, & Hauser, 1992). The term is also a recognition of the possibility that signals could function as if they were referential without having the same meaning for either the signaller or the receiver as words do in human language (Marler et al., 1992).

The first two examples of functionally referential signals were the honeybee waggle dance documented by von Frisch (1974) and the vervet monkey, *Cercopithecus aethiops*, alarm call system that was first identified by Struhsaker (1967) and later expanded upon by Seyfarth, Cheney, and Marler (1980a, 1980b). The first example is a food-related signal. A worker bee performs the waggle dance when she returns to the hive after a successful foraging trip. The display produces both visual and vibrational signals, which reveal the direction of the foraging patch, relative to the sun, and the distance to the foraging patch (von Frisch, 1974). The display alone is sufficient for other workers to locate the same patch (Riley, Greggers, Smith, Reynolds, & Menzel, 2005). The second is a complex example of alarm signalling. Vervet monkeys produce three distinct alarm calls. Each call is elicited by a specific predator and produces a predator-appropriate response from other members of the troop (Seyfarth et al., 1980a). Furthermore, troop members respond with the correct antipredator behaviour to playbacks of the acoustic signal, which suggests that the calls could be correctly interpreted independently of the context in which they were

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produced (Seyfarth et al., 1980b). Since those first two examples, functionally referential signals have been investigated and identified in many mammals, including primates (e.g. rhesus monkeys, *Macaca mulatta*: Gifford, Hauser, & Cohen, 2003), prosimians (e.g. ringtailed lemurs, *Lemur catta*) and suricates (e.g. meerkats, *Suricata suricatta*: Manser, Seyfarth, & Cheney, 2002). Functionally referential signals have been identified in antipredator, feeding and social contexts (Townsend & Manser, 2013; Zuberbühler, 2009).

Many species of birds, such as Japanese great tits, *Parus major minor* (Suzuki, 2011, 2012a), smooth-billed anis, *Crotophaga ani* (Grieves, Logue, & Quinn, 2014), and Siberian jays, *Perisoreus infaustus* (Griesser, 2008, 2009), also produce functionally referential signals. The signals are used in contexts similar to those used by mammals. There have been several recent reviews of the research on functionally referential signals in birds. These reviews have focused on signals in the acoustic modality that function as alarm or food-related signals (e.g. Gill, & Bierema, 2013; Suzuki, 2016). However, recent research has revealed that birds produce functionally referential signals in additional modalities and contexts (e.g. Kaplan, 2011; Pika & Bugynar, 2011). In this review, I provide an overview of functionally referential signals in birds, with a particular focus on understudied areas of functionally referential signals, and suggest future research directions.

CRITERIA FOR DETERMINING FUNCTIONAL REFERENCE

Several criteria have been developed to allow researchers to determine whether signals should be considered functionally referential (Evans, 1997; Macedonia & Evans, 1993; Marler et al., 1992). The first criterion relates to the signal production. Referential signals should be structurally discrete and produced only in response to a specific class of stimuli. The stimulus class may be very narrow, such as a specific type of predator, or it may be quite broad, depending on the selective pressures under which the signal evolved, but all stimuli must form part of the same category. The second criterion relates to signal perception. Signals should elicit an appropriate response without the need for other cues, such as the sound or sight of a predator. The perception criterion suggests a methodology of presenting signals without other cues. This allows researchers to determine whether the putative reference indicated by the signal is indeed the category perceived by the receiver. The term 'contextual independence' was coined to describe this property of referential signals (Evans et al., 1993). The criterion of 'contextual independence' represents the strictest interpretation for functional reference (Marler et al., 1992). Although context may provide additional information for a specific instance of the signal (e.g. Cheney & Seyfarth, 1990), the receivers' responses should be appropriate to the category of the putative reference in the absence of additional context.

Although signals that meet the production and perception criteria would be classified as functionally referential, there is clear evidence that referential signals also contain motivational information (Manser et al., 2002; Marler et al., 1992; Seyfarth & Cheney, 2003). For example, male chickens, *Gallus gallus,* produce functionally referential alarm signals to aerial predators (Evans et al., 1993). The overall characteristics of the signal are significantly different from all other vocalizations, but fine-scale variation in the signal is correlated with the signaller's level of vigilance prior to the appearance of the predator (Kokolakis, Smith, & Evans, 2010). Receivers' responses are sensitive to both the referential category of the signal and the motivational component (Wilson & Evans, 2012).

Using these production and perception criteria, researchers could then systematically map a category of events that elicited a signal onto the characteristics of the signal produced by the signaller (signal production) and then determine how variation in the signal's characteristics affected the receivers' responses (signal perception). When examined in light of the species' physiological, environmental and social conditions, the information generated from these tests of production and perception specificity could reveal the evolutionary pressures that may have shaped the signal's form and function as well as providing insight into the animals' cognitive capabilities.

Examples of Avian Referential Signals

To date, referential signals have been identified in more than a dozen bird species, from three orders and five families, the majority of which are passerines. Birds produce functionally referential alarm calls (aerial and terrestrial) and food calls as well as referential gestures (Table 1). The most common type of referential signal is an aerial alarm, followed by terrestrial alarm calls and food calls. Although acoustic signals are the most widely identified in birds (reviewed in: Gill & Bierema, 2013; Suzuki, 2016), referential signals are not confined to the auditory modality. Research has demonstrated that visual signals, including gestures (e.g. ravens, *Corvus corvax*: Pika & Bugynar, 2011; Australian magpie, *Gymnorhina tibicen*: Kaplan, 2006) and multimodal signals (visual and vocal signals of the tidbitting signal in chickens: Smith & Evans, 2008, 2009), can also be functionally referential.

To date, only two bird species (chickens and white-tailed ptarmigan, *Lagopus leucurus*) have been found to produce three different types of functionally referential signals (food, aerial alarm and terrestrial alarms), with chickens being the first and one of the best-studied with regard to referential signalling behaviour in birds (Evans et al., 1993; Evans & Evans, 1999; Gyger & Marler, 1988; Gyger, Marler, & Prickert, 1987; Smith & Evans, 2008, 2009), and as such provide a good example of the connections between eliciting events, signal production and signal perception (Fig. 1).

Referential Alarm Calls in Birds

Several bird species produce the same alarm call for both aerial and terrestrial predators, whereas others produce signals that distinguish between aerial and terrestrial predators.

Chickens are an example of a species that produces both aerial predator alarm calls and terrestrial predator alarm calls. Chicken aerial alarm calls are brief, tonal sounds (Bayly & Evans, 2003). Both males and females with chicks produce alarm calls in response to objects within a specific size and shape range that are moving at a particular speed overhead (Evans et al., 1993). The criteria for eliciting a response are broad enough that predatory and nonthreatening objects may generate a call. However, there is a qualitative difference in the sounds produced in response to predatory and nonpredatory objects (Gyger et al., 1987). There may be several reasons that the category of eliciting stimuli is broad. Since chickens are prey for multiple aerial species, too much specificity would increase the likelihood of not calling when a dangerous predator appears. Their habitat often affords only brief glimpses of the sky, which allows them little time to assess a threat. Aerial predators are fast moving and thus represent a high risk of capture. Taken together, type II errors (e.g. calling to innocuous stimuli) may be less costly than type I errors (e.g. not calling to dangerous stimuli). However, calling by males is not reflexive but is subject to audience effects, whereby the likelihood of calling is affected by the presence of conspecifics (Evans & Marler, 1991). Aerial alarm calling also appears to be a form of mate investment since recently mated males are more likely to call (Wilson & Evans, 2008). The structural characteristics of male aerial alarm calls vary based on the threat posed by the predator and the vulnerability of the caller; thus, these calls are functionally referential and urgency-

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