Exaggeration of display characteristics enhances detection of visual signals

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(Accepted: 11 January 2011)

Summary
Many animal signals have been produced by selection operating upon behavioural precursors that lack signal function, a process known as 'ritualization'. When the precursor remains in the repertoire, comparisons of its structure with that of the derived signal permit inference of the forces responsible. Selection for signal efficacy and recognition produce characteristic changes (e.g., increases in intensity and duration, and repetition). The tidbitting display of male fowl, Gallus gallus, has long been considered an example of ritualization. However, the changes associated with this evolutionary process have never been characterized, nor has there been any test of whether the signal is perceived as distinct from its putative precursor (self-feeding). To address this, we first analysed video recordings of males feeding and tidbitting. We found a significant increase in the intensity, duration and repetition of specific movements during the tidbitting display compared to feeding. These results suggest that tidbitting is a ritualized form of self-feeding behaviour, but the critical test requires assessment of receiver response. If females recognized the tidbitting signal as distinct from male feeding behaviour, we predicted that females would food search significantly more in response to tidbitting. The results of high-definition video playbacks support this hypothesis. This is the first empirical demonstration of the perceptual and functional predictions made by a classic ethological hypothesis.

Keywords: visual signals, signal design, Gallus gallus, multimodal communication.

1. Introduction
The structure of a visual signal is shaped by the often opposing forces of female preference for exaggerated traits (e.g., large ornaments, bright col-

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oration and conspicuous displays) and the direct costs to the signaller (e.g., energetic, immunocompetence and increased predation risk; Bradbury & Vehrencamp, 1998). Measuring the difference between extant behavioural or morphological characteristics and the derived signal can reveal information about the forces that shaped the signal design. For example, the tail streamers of the barn swallow (Hirunda rustica) reveal female preference for elongate feathers, beyond the length at which these are aerodynamically efficient. This increment in tail length reveals the tradeoffs between natural and sexual selection (Rowe et al., 2001).

For the signal to be effective it must be detectable by the intended receiver and recognizable (i.e., distinguishable from other behavioural correlates and other signals in the repertoire). Characteristics of visual signals including coloration (Endler, 1992), velocity of movements (How et al., 2008), and duration of display (Peters & Evans, 2003) interact with the signalling environment and the receiver’s sensory systems to determine the likelihood of signal detection (Dawkins & Guilford, 1991; Endler, 1993; Candolin, 2003). Increases in display complexity, including repetition or the addition of new display elements (multicomponent) or of new modalities (multimodal), may further facilitate signal detection and recognition (Cullen, 1966; Bradbury & Vehrencamp, 1998; Ryan, 1998; Rowe, 1999).

Signals are often variants of functional behaviours that have changed through selection (e.g., for efficacy or female preference; Zahavi, 1980). If there is a strong linkage between the signal form and content (Bradbury & Vehrencamp, 1998), the signal often retains elements of the original functional behaviour. For example, in the ‘snap’ display of great blue herons, Ardea herodias, males perform mock nest building movements during courtship (Mock, 1976). In some cases, species retain the signal precursors in their behavioural repertoire, although the original function may have been modified (e.g., the presentation of empty nuptial gifts instead of wrapped prey items by some species of dance fly; Sadowski, 1999).

Courtship displays in galliforms are a classic example of a behaviour for which some species appear to have retained the functional precursor and others to have lost it (Schenkel, 1956; Stokes & Williams, 1971). Fowl, Gallus gallus, appear to be a case in which both behaviours are extant. Upon discovery of a palatable food item in the presence of a female, males begin a series of rhythmically repeated movements of the head and neck, including picking up and dropping of the food item (Davis & Domm, 1943;