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On the function of an enigmatic ornament: wattles increase the conspicuousness of visual displays in male fowl

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Males of many species perform elaborate displays in which multiple ornaments feature prominently. However, female preferences often depend upon both display movements and a subset of the ornaments. This response selectivity means that female choice cannot explain the function of nonpreferred ornaments. These structures may instead have an ancillary function (e.g. enhancing signal efficacy or modifying information content). Male junglefowl, *Gallus gallus*, possess multiple fleshy ornaments, which feature prominently during food-related displays (tidbitting). There is strong evidence for female choice based on display frequency and comb characteristics, but little evidence for choice based on wattles. Wattles are thin, elastic structures that hang loosely from a male's lower mandibles and vary in size over a male's lifetime. These structures swing rapidly during tidbitting, potentially increasing the area around the head and increasing image motion. Males also tidbit more vigorously with highly preferred food, increasing wattle displacement and thereby potentially affecting information content. We tested the prediction that wattles enhance signal efficacy and information content by conducting high-definition playbacks, using three-dimensional animations of tidbitting males with differing wattle properties. Results revealed that the food-searching response of receivers was robust to changes in wattle size and motion. Increased wattle displacement did not decrease orienting latency or increase food-searching duration, which suggests that wattles do not contribute significantly to information content. However, apparent wattle size significantly decreased orienting latency, demonstrating that wattles increase the conspicuousness of the tidbitting signal. These results suggest that wattles are maintained because they enhance signal efficacy.

Many animals perform complex visual signals in which elaborate ornaments are displayed prominently (e.g. peacock train fanning: Petrie et al. 1991; frigatebird gular sac inflation: Madsen et al. 2004; wolf spider courtship: Uetz & Roberts 2002). These visual displays and the structural design of the ornaments interact with the receiver's sensory and perceptual abilities and the signalling environment to determine signal efficacy (e.g. conspicuousness and discriminability from other similar behaviours; Guilford & Dawkins 1991, 1993; Endler 1992; Rowe 1999). In addition, the properties of display (e.g. speed, duration, orientation) and the characteristics of the ornaments (e.g. size, colour, movement) can contribute to the signal information content (Zahavi 1979; Hasson 1989; Candolin 2003; Galván 2008). The elongate tail of the male red-collared widowbird, *Euplectes ardens*, demonstrates how display behaviour increases signal detectability and facilitates assessment of the signal content. Female red-collared widowbirds prefer males with long tails. Males perform courtship flights across open savannah during which the tail is spread laterally and ventrally. Longer tails increase the display conspicuousness (Pryke et al. 2001), and the position of the tail during flight may facilitate female assessment of length (Pryke & Andersson 2005).

However, many species possess more than one prominent ornament. In particular, leking and polygynous birds often have both colourful feathers and fleshy structures, which are presented synchronously during visual displays. There are many examples in which female preference depends upon display properties, together with a subset of these ornaments (e.g. peacock: Loyau et al. 2005; frigatebirds: Madsen et al. 2004; fowl: Zuk et al. 1995). This response selectivity means that female choice cannot be invoked to directly explain the function of the other ornaments. One possible explanation is that the nonpreferred ornaments do not currently signal male condition (i.e. that these are unreliable signals; sensu Møller & Pomiankowski 1993). These structures may instead have an ancillary function such as enhancing or increasing

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signal efficacy or modifying the information content (e.g. by revealing signaller motivation; Morton 1977).

Male junglefowl, *Gallus gallus*, possess multiple fleshy ornaments on the head (Darwin 1871), which feature prominently during food-related displays (Stokes 1971). The comb is a single, medially located, turgid, red structure on top of the head. In contrast, the wattles are thin, paired, fleshy red protuberances that hang loosely from the lower the mandibles (Fig. 1a). Previous research has demonstrated female choice based on display performance (Pizzari 2003) and a subset of these ornaments (reviewed in Parker & Ligon 2003). Female preference depends upon comb characteristics (e.g. size, colour, hue; Parker & Ligon 2003), but despite a close correlation between comb and wattle properties, there is little evidence that wattles play any role in female mate choice (Zuk et al. 1990; Ligon et al. 1998; but see Zuk et al. 1992). The function of the wattles hence remains enigmatic.

Pizzari (2003) demonstrated female preference for males based on frequency of food-related displays, known as tidbitting (Davis & Domm 1943). This is a multimodal signal, typically composed of pulsatile vocalizations (food calls) and rhythmically repeated movements of the head and neck, including picking up and dropping of a food item (Davis & Domm 1943; Stokes & Williams 1972; Evans & Marler 1994). During the tidbitting display, the wattles (Fig. 1b–d) swing rapidly with each movement of the head. Females respond to tidbitting by approaching and searching for food near the male (Stokes & Williams 1972; Marler et al. 1986a, b; Gyger & Marler 1988). Previous research (Graves et al. 1985) revealed that female proximity to a male is correlated with the male's mating success and that females remain close to tidbitting males longer than they do nonsignalling males (Smith & Evans 2009). In this hierarchical social system (Collias & Joos 1953), 30% of subordinate displays involve suppression of the call and are composed of the movements alone (C. L. Smith, unpublished data). Playback experiments revealed that the sensory modalities are redundant (sensu Partan & Marler 2005); these purely visual displays are as effective as the vocalization alone or the multimodal display in evoking food searching by the hens (Smith & Evans 2008).

The tidbitting display is composed of three distinct head and neck movements: 'twitch': a rapid horizontal side-to-side motion with the neck held fully upright; 'short bob': an abrupt vertical plunge from the upright position to a point halfway above the ground, returning to the upright position; and 'long bob': vertical movement of the head, plunging through the full arc towards the ground and ending in the upright pose (see Fig. 1 in Smith & Evans 2009). Each of these motor patterns imparts momentum into the wattle, causing it to swing (Fig. 1a). During a twitch, the wattle lags behind the head at the start of the movement and then continues further in the direction of the movement after the head has reached its furthest lateral displacement (Fig. 1b). During shorter vertical movements, the wattles swing forward and together (Fig. 1c). However, during longer vertical movements, they separate and swing outwards and upwards during the downward phase of the motion, occasionally swinging far enough to slap the side of the male's head (Fig. 1d), and then swing back together during the upward phase. Wattle size is testosterone dependent (Domm 1939; Ligon et al. 1990), and loss of social status results in a reduction in wattle size (Ligon et al. 1990).

Males perform these movements at a significantly higher rate during tidbitting than during self-feeding (C. L. Smith & C. S. Evans, unpublished data), suggesting that this increased frequency of motion reflects selection for signal function. Males show a higher rate of food calling (Marler et al. 1986a) and movements (Stokes 1971) when presented with a highly preferred food item. Faster head and neck movements increase the amplitude of wattle motion, suggesting that these elastic structures may facilitate detection of the male display by females, as well as providing an indication of the quality of the food item.

The physical characteristics of the wattle, its pronounced movement during tidbitting and the likelihood that hens will experience the unimodal form of the display at a reasonable frequency, when considered together, generate the prediction that these structures have a hitherto unsuspected function, which is to enhance efficacy and/or increase the information content of the tidbitting signal. Here we report an experimental test of the wattles' effect on signal efficacy and information content of the tidbitting display. We created high-resolution three-dimensional animations that precisely reproduced the movement of live males performing the tidbitting display and manipulated the properties of the wattles to create four treatments: 'wattleless' (structure absent), 'blade' (structure rigid), 'normal' (displacement matched to donor male) and 'extrafloppy' (displacement exaggerated). We then conducted playback experiments using high-definition plasma screens, a method that is well established in this system (Evans & Marler 1991; Evans et al. 1993a, b; McQuoid & Galef 1993; Clark & Jones 2001; Smith & Evans 2008, 2009) to test female responses. We tested for differences in the latency to orient, the latency to food-search after orienting to the signal and the overall food-search duration based variation in the presence, speed and movement of the wattles. The efficacy hypothesis predicts reduced latency to orient in treatments containing wattles and/or wattle movements, and the information content hypothesis predicts that hens will begin to food-search sooner and continue to food-search for longer based on the presence and movement of the wattles.

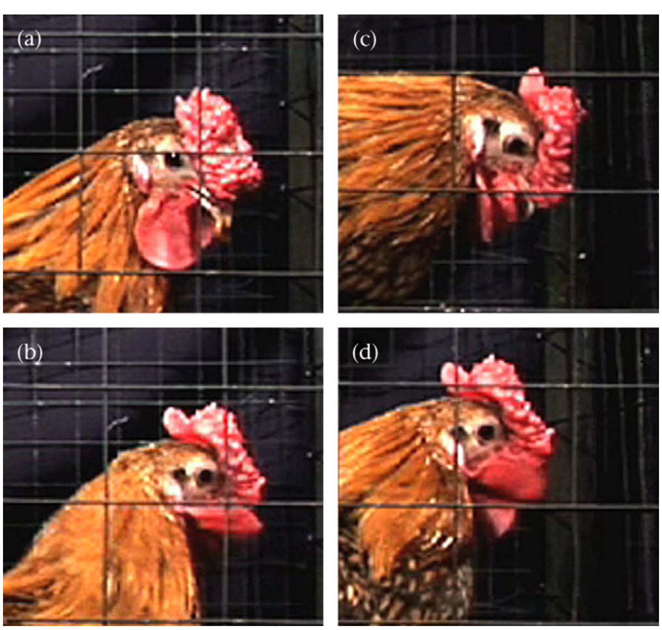

Figure 1. Wattle movement during the tidbitting display. Wattles (a) hang loosely from the male's mandibles when the head is stationary, (b) lag behind the horizontal movement of the head during the 'twitch' motor pattern, (c) tend to swing forward and together during shorter vertical 'short bob' movements, and (d) separate and swing outwards and upwards during the downward phase of the longer vertical 'long bob' motions, occasionally swinging far enough to slap the side of the male's head and then swing back together during the upward phase.

METHODS

Subjects

We used 26 golden Sebright bantam females for this study; 24 were used as test subjects and two as audience hens. All hens