Animal Behaviour 127 (2017) 197–203

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Flamboyant sexual signals: multiple messages for multiple receivers

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ARTICLE INFO

Article history:
Received 28 December 2016
Initial acceptance 9 February 2017
Final acceptance 2 March 2017
Available online 14 April 2017
MS. number: 17-00011

Keywords:
agamid
colour
dewlap
lizard
movement
multicomponent
sex differences
sexual selection

Animals are often faced with the challenge of signalling to multiple receivers that might differ in their detection abilities and preferences. Such conditions are expected to favour the evolution of complex signals. The superb fan-throated lizard, *Sarada superba*, possesses one of the most complex sexual trait of any lizard: an enlarged dewlap with blue, black and orange patches that is flapped rapidly during both courtship and aggressive displays. We examined the use of the tricoloured dewlap in social signalling to determine whether (1) movement enhances signal detection, and whether (2) males and females differ in their preference for colours. Using robotic lizard stimuli, we measured receiver responses to movement and colour individually, and found that movement attracted both sexes, but the latency to respond was faster when dewlaps had all three colours compared to none (white). Furthermore, the sexes did not differ in the ability to detect colours, as more than 80% of lizards preferred coloured to white dewlaps. Most strikingly, however, the sexes showed strong preferences for different colours. Females preferentially responded to orange colour on dewlaps, and males responded to blue and black, indicating that different colours are targeted at different receivers. These results highlight that complex signals can evolve due to simultaneous inter- and intrasexual selection.

Signals used by animals can be highly complex, comprising multiple components across different sensory modalities (Hebets & Papaj, 2004; Partan & Marler, 2005). Because of the costs associated with signal production (Roberts, Taylor, & Uetz, 2007; Stoddard & Salazar, 2011; de Crespigny & Hosken, 2007), signals are under strong selection to ensure transfer of information to appropriate receivers (Higham & Hebets, 2013; Partan & Marler, 2005; Roberts et al., 2007; Stoddard & Salazar, 2011; de Crespigny & Hosken, 2007). Successful transmission of information is affected by many factors, from environmental conditions to the psychology and preferences of receivers (Endler, 1992; Hebets & Papaj, 2004; Jørgensen, 2010; Partan & Marler, 2005).

Much of our understanding of multicomponent signal evolution has resulted from the rich body of research on communication in a single social context. For example, in some species, females vary in their preferences for male traits, and thus multicomponent signals enable male mating success (e.g. Balakrishnan, von Helversen, & von Helversen, 2001; Coleman, Patricelli, & Borgia, 2004). In other species, different components convey information about quality to receivers in multiple contexts (see Candolin, 2003 and Hebets & Papaj, 2004 for reviews). In the scarlet-tufted malachite sunbird, *Nectarinia johnstoni*, pectoral tufts signal territorial dominance to other males, whereas females choose mates based on tail length (Evans & Hatchwell, 1992 a, b). Similarly, body size in the eastern tiger salamander, *Ambystoma tigrinum*, benefits male–male competition, but tail length is under intersexual selection (Howard, Moorman, & Whiteman, 1997). Successful signalling of information to multiple receivers of the same or opposite sex can be challenging and, therefore, is expected to favour the evolution of complex signals that transfer information using different components (Hebets & Papaj, 2004).

Males of *Sarada superba* possess one of the most exaggerated and flamboyant sexual traits of any lizard (Fig. 1a; Deepak et al., 2016; Ord, Klomp, Garcia-Porta, & Hagman, 2015). The sexual signals of males comprise an enlarged tricoloured dewlap that is rapidly extended and retracted during both inter- and intrasexual interactions (Pal, Swain, & Rath, 2011; Patankar, Desai, Trivedi, & Balakrishnan, 2013). By contrast, females have a rudimentary white dewlap that does not seem to be essential for social communication. We hypothesized that the evolution of the moving tricoloured dewlap in males of *S. superba* is driven by the need to effectively communicate to multiple receivers. We used robotic lizard models to experimentally examine the role of movement and colour in signal detection and preference by both male and female conspecifics. The use of robotic stimuli allowed us to standardize and control the signal, which would not be possible with natural

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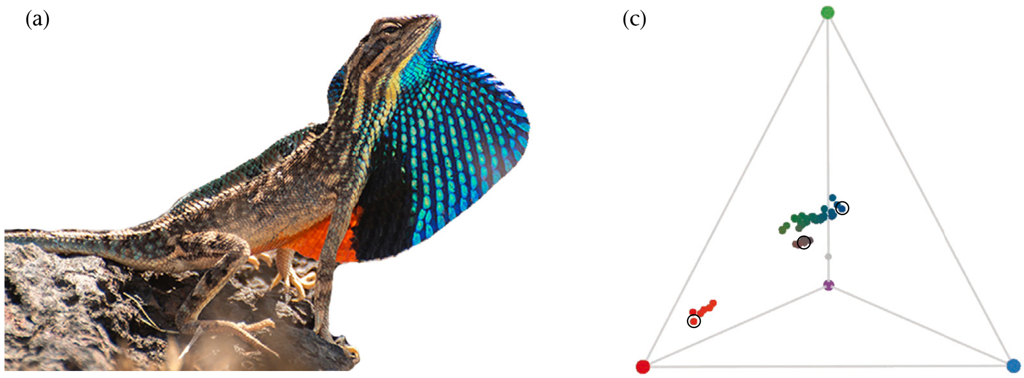
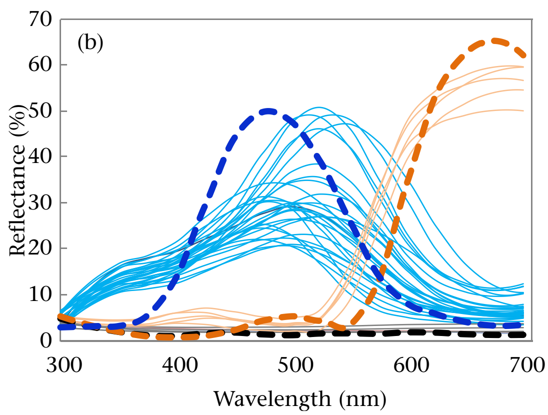
http://dx.doi.org/10.1016/j.anbehav.2017.03.021
0003-3472/





(d)

Contrast (Euclidean distance)

	Natural dewlap patch:		
	Blue	Black	Orange
Blue model	0.107	0.252	0.398
Black model	0.198	0.016	0.305
Orange model	0.309	0.291	0.058

Figure 1. (a) Male of the superb fan-throated lizard with his dewlap extended in display. (b) Reflectance spectra of natural colour patches (solid lines) and of robotic model stimuli (dashed lines). Reflectance of the blue patch is variable as it is iridescent and depends on the angle of measurement. (c) Tetrahedral colour space showing the chromatic components of natural patches and of robotic model stimuli (circled). (d) Euclidean distances with cone stimulation for average natural colours compared to robotic model colours. Values for colours compared to the same colour on the robotic model are shown in bold.

stimuli (Taylor, Klein, Stein, & Ryan, 2008). We discuss our results in the light of complex signal evolution for multiple receivers.

METHODS

The study population of *S. superba* is endemic to the Chalkewadi plateau, an isolated lateritic plateau in the northern Western Ghats of India. These plateaus are a unique feature of the northern Western Ghats and are characterized by a rocky lateritic substrate that is devoid of vegetation. These small (snout–vent length (SVL): males = 5.3–7.7 cm; females = 3.8–6.8 cm) diurnal lizards are most active during the dry season from March to June, during which they primarily engage in breeding activities. At the beginning of the breeding season, males develop blue, black and orange patches on their enlarged dewlap, which is used for intra- and intersexual communication. Males use small lateritic rocks as perches to display to conspecifics, during which the dewlap is rapidly extended and retracted. Abundant light and the absence of vegetation to obstruct their visual display allow males to communicate with conspecifics across relatively large distances (up to 20 m).

We first conducted systematic field observations, during which we recorded both the courtship ($N = 30$) and territorial displays ($N = 30$) of free-ranging and unmanipulated males of *S. superba*. Displays were recorded using a digital video camera and the recordings were then used to measure the average frequency of dewlap flapping to replicate for the robotic models (see below). We also measured the percentage reflectance of the three dewlap colours within 5 min of capture ($N = 6$ males) to replicate for the robotic models (see below). Spectral measurements were taken using a fibre-optic probe connected to a spectrometer (JAZA2474, Ocean Optics, Dunedin, FL, U.S.A.) and light source (PX lamp, Ocean Optics). The PX lamp triggering rate was set at 10 ms, boxcar at 5, and the probe was maintained at an angle of 45° against the surface, which measured an area of 3 × 3 mm on the skin. All measurements were first corrected against white and black reflectance standards (as per Whiting et al., 2006), and measurements for each skin surface were averaged from three spectra readings. Since the focus of this study was to quantify conspecific responses to blue, black and orange colours, and not to variation in hue and brightness within colours, we designed robots with dewlap colours that were similar to the average colour values of typical males.

Designing the Robotic Lizard Stimuli

Data from field measurements of male behaviour and spectrophotometry of colour were used to design and program the robotic models, such that the movement rate of the dewlap and the reflectance for each of the colours on the robotic dewlaps were similar to the natural range observed for this species. Robotic lizard models were made to the size of an average male (SVL = 6.5 cm) and had an extendable dewlap that was programmed to extend and retract at a frequency of 0.5 Hz, which was the mean frequency calculated from field recordings of male displays. Analysis of display repertoires of free-ranging *S. superba* revealed that mean frequencies of dewlap flapping were similar during courtship (mean ± SE = 0.52 ± 0.05 Hz, $N = 30$) and aggressive male–male interactions (0.5 ± 0.06 Hz, $N = 30$), with low variation in each