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Gliding lizards use the position of the sun to enhance social display

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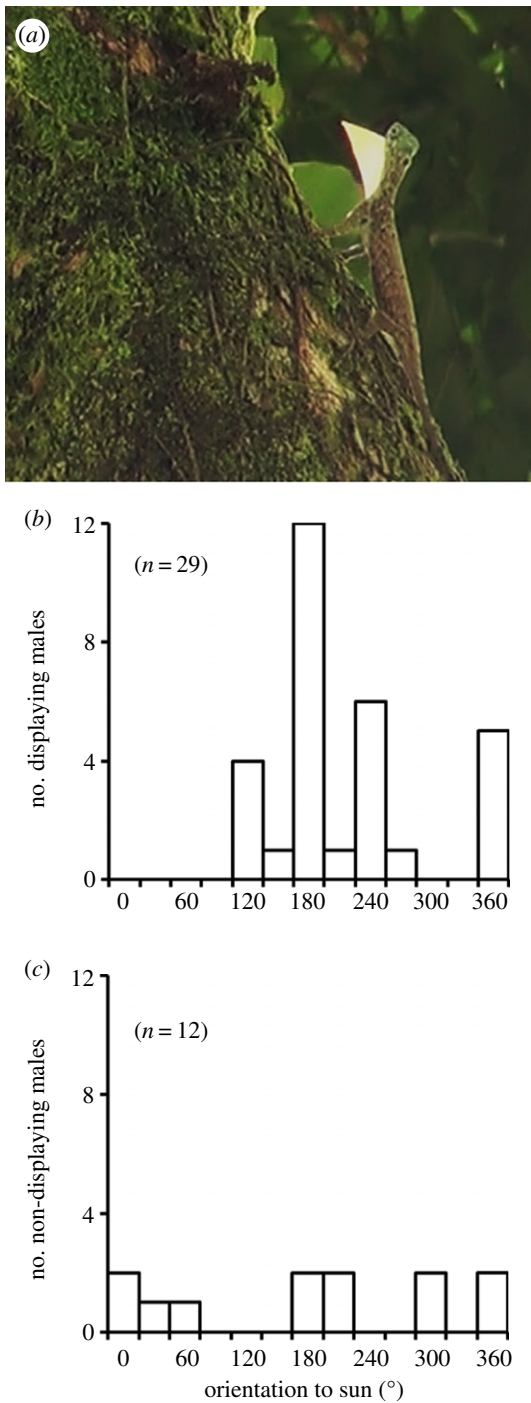
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Effective communication requires animal signals to be readily detected by receivers in the environments in which they are typically given. Certain light conditions enhance the visibility of colour signals and these conditions can vary depending on the orientation of the sun and the position of the signaller. We tested whether *Draco sumatranus* gliding lizards modified their position relative to the sun to enhance the conspicuousness of their throat-fan (dewlap) during social display to conspecifics. The dewlap was translucent, and we found that lizards were significantly more likely to orient themselves perpendicular to the sun when displaying. This increases the dewlap's radiance, and likely, its conspicuousness, by increasing the amount of light transmitted through the ornament. This is a rare example of a behavioural adaptation for enhancing the visibility of an ornament to distant receivers.

1. Introduction

The detectability of visual signals is partly determined by the environment in which the signal is given [1,2], and may be enhanced (or reduced) by different environmental conditions, such as light intensity or visual noise (e.g. windblown vegetation) [2–4]. Animals may employ behavioural strategies that take advantage of optimal conditions to increase signal detectability; for example, by choosing certain locations or times of day to display [5–7]. Many studies have shown that animals can adjust aspects of acoustic communication (e.g. call frequency, amplitude and duration) to compensate for background noise [8,9]. Examples of adaptations for visual signals are relatively rare, but some bird species have been shown to orient or selectively display in sunlight to increase the conspicuousness of iridescent or short-wavelength-rich plumage [10–12]. However, the extent to which other animals strategically adjust the presentation of their visual displays, and how they do so, remains unclear.

The radiance of translucent ornaments can be enhanced by direct sun exposure when light is transmitted through the ornament as well as reflected by it (radiance is the sum of both transmitted and reflected light) [13,14]. Given this, animals with translucent visual signals could enhance signal conspicuousness by orienting the ornament perpendicular to the position of the sun. We tested whether individuals of the gliding lizard, *Draco sumatranus*, orient perpendicular to the sun when displaying (figure 1a). *Draco sumatranus* live in open areas with full sun exposure [15,16]. Both males and females possess throat-fans (or dewlaps) that are extended and retracted in territorial or courtship broadcast displays [17,18]. The male dewlap is relatively large, yellow and appears translucent; whereas the female dewlap is smaller, grey/blue and appears more opaque [16] (figure 2a,b). As transmission through the female dewlap is minimal, whether they should orient
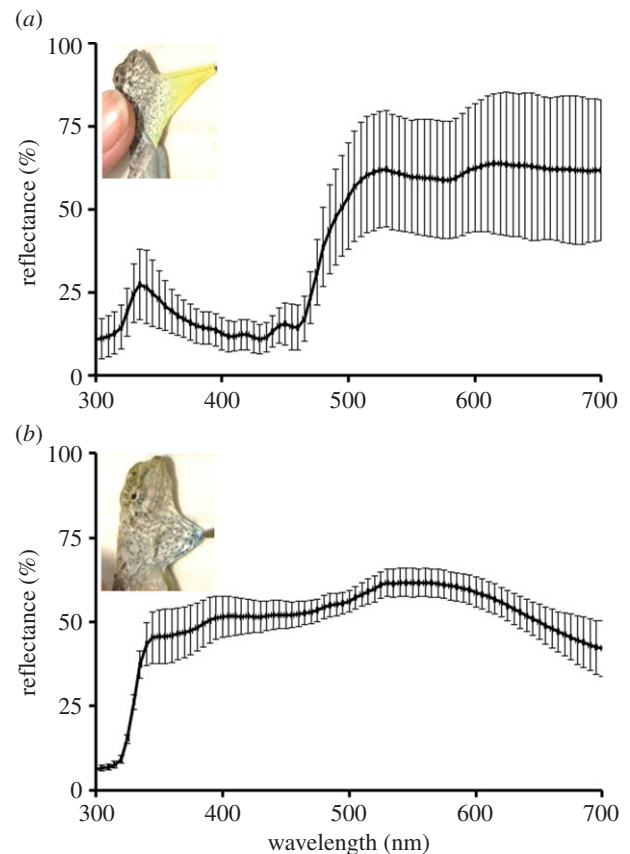
Figure 1. (a) *Draco sumatranus* male displaying, showing the transmission of sunlight through the dewlap (photo: T. J. Ord). (b) Perch angle for displaying males, and (c) perch angle for non-displaying males, measured in relation to the sun. Both perpendicular angles (90° and 270°) have been transformed to equal 180°.

displays perpendicular to the sun depends on how reflection of direct sunlight affects signal conspicuousness.

2. Material and methods

We observed free-living *D. sumatranus* lizards on the Universiti Malaysia Sarawak, Kota Samarahan campus (01.4681° N, 110.4433° E; 10 m elev., WGS 84) near the city of Kuching, Sarawak, East Malaysia (northern Borneo) between June and July 2015. The lizards live on rows of trees lining both sides of roads throughout the campus, and were sighted by walking up and down the roads between 07.30 and 13.30 h daily (when broadcast signals are most often produced [17]). We recorded the lizard's sex,

Figure 2. (a) *Draco sumatranus* male yellow dewlap colour reflectance; (b) *Draco sumatranus* female blue dewlap colour reflectance.

whether it was performing dewlap displays, and its position on the tree trunk relative to the sun. Sex was determined by body morphology, which differs between the sexes [15], and by dewlap colour and size. Broadcast displays are predominantly used by males to advertise territory ownership to male neighbours and potential mates in all directions, at a range of distances [3,19]. Female dewlap displays are less frequent (proportion of lizards observed displaying in this study: males: 0.71; females: 0.28), but also appear to be used as an aggressive display (although this has yet to be confirmed empirically).

In recording the position of the lizard, we took the centre of the trunk surface directly facing the sun to be 0° and estimated the angle between that point and the position of the lizard on the trunk (see the electronic supplementary material, figure S1). This meant that a lizard positioned at 0° had its back to the sun, while at 90° the sun shone directly on the flank of the lizard and a single side of the extended dewlap. Angles around the trunk were estimated in 15° bins. *Draco* lizards are predominantly positioned vertically on the tree trunk, and broadcast displays are performed with their heads in line with the body. *Draco* lizards are territorial and can be observed on the same two to three adjacent trees on consecutive days [18]. To avoid re-sampling, we systematically surveyed lizards such that we did not return to the same group of trees twice. Though lizards live on trees arranged in linear rows, the habitat is still three-dimensional, with lizards interacting with each other over roads and in some instances with lizards in forest further back from the roads. Additionally, we sampled several roads with different linear directions (two running north–south, one east–west and one undulating northwest–southeast, covering 6 km).

We predicted lizards should orient perpendicular to the sun during dewlap displays in either direction (angles of 90° or 270° relative to the sun), making the data axially bimodal. For statistical analysis, we multiplied our data by two and subtracted 360° from resulting angles greater than 360°, as outlined by Batschelet

Table 1. V tests (V), effect size (u) and p-values for displaying and non-displaying males and females. Values of V converging on 1 indicate orientations cluster around the expected angle of 180°, while values converging on −1 indicate orientations do not cluster at the expected angle.

	V	u	p
males			
displaying ($n = 29$)	0.46	3.55	0.0001[a]
not displaying ($n = 12$)	−0.22	−1.075	0.86
females			
displaying ($n = 7$)	0.70	2.60	0.003[a]
not displaying ($n = 18$)	−0.74	−4.46	1

[a]P-values that remain statistically significant after considering false discovery rates for four comparisons [23].

[20]. This transformed the data such that all perpendicular orientations were represented by angles of 180°. To test whether orientations clustered on this perpendicular angle, we used the V test (a modified Rayleigh test) which tests circular uniformity against non-uniformity with a specified mean angle [21,22]. Analysis was performed in the program ORIANA v. 4.0 (Kovach Computing Services, Pentraeth, Isle of Anglesey, Wales, UK).

3. Results

Males were significantly more likely to orient themselves perpendicular to the sun when extending the dewlap in display (figure 1b), but not in the absence of giving a display (figure 1c and table 1). Despite the small sample of females observed displaying, those that did so also oriented perpendicular to the sun, but again only during display (table 1).

4. Discussion

The clear orientation of displaying male *D. sumatranus* perpendicular to the sun seems to represent a deliberate behavioural strategy for increasing signal conspicuousness. Recent studies in birds have indicated that orienting plumage ornaments to exploit direct sunlight may enhance conspicuousness [12,24]. Specifically, direct sunlight may increase reflectance if the surface of the ornament is specularly reflective—that is, when light is reflected by a surface at a specific angle [25]—or result in greater contrast against the background if the sunlight illuminates the ornament differently from the ornament's background. Here, we show lizards strategically orient themselves relative to the position of the sun, presumably to enhance luminance through transmission of sunlight through the translucent dewlap.

While it is intuitive that transmission should increase the radiance of the dewlap, the degree to which this increases conspicuousness to receivers remains to be tested. However, Fleishman *et al.* [14] examined the translucent dewlap of *Anolis lineatopus*, a New World ecological analogue of *Draco sumatranus*, and found transmission did not increase the luminance contrast of the dewlap against the background specifically, but did likely facilitate a receiver's ability to discriminate the colour of the dewlap from those of the background. This would presumably aid in the dewlap being detected and identified as conspecific [14].

In *D. sumatranus*, transmission in the female dewlap appears minimal compared with males, yet females also oriented the dewlap perpendicular to the sun. Indeed, the position of the sun has a strong effect on male orientation behaviour even though light transmission through the male dewlap only increases radiance for viewers with the sun at their back. This is probably because direct sunlight increases dewlap conspicuousness even when only reflected light reaches the receiver's eye. Direct sunlight is rich in short wavelengths, so ultraviolet and blue ornaments should be especially conspicuous in direct sunlight [26]. Both the female and male dewlaps reflect UV light but the female dewlap more so (figure 2, males are yellow with a UV peak, while females are UV–blue). Therefore, orienting to maximize direct sun exposure of the dewlap should increase the visibility of these wavelengths to receivers, particularly in the case of the female dewlap.

Many recent studies have shown animals are able to integrate information about their own appearance and their surroundings to modulate behaviour and reduce predation risk [27–31]. Studies addressing the interaction between colour and behaviour in signalling are rarer, but they too show that animals have the capacity to select display locations and orientations that improve signal effectiveness [5,10,12]. This study presents one of the few examples outside of birds and highlights the importance of light transmission for translucent ornaments. By explicitly considering the strategies signallers use to enhance conspicuousness, we can obtain a clearer understanding of the selection pressures that produce novel signalling behaviours and act on signal design.

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