



Original Article

Color pattern facilitates species recognition but not signal detection: a field test using robots

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There are many factors that affect signal design, including the need for rapid signal detection and the ability to identify the signal as conspecific. Understanding these different sources of selection on signal design is essential to explain the evolution of both signal complexity and signal diversity. We assessed the relative importance of detection and recognition for signal design in the black-bearded gliding lizard, *Draco melanopogon*, which uses the extension and retraction of a large, black-and-white dewlap (or throat fan) in territorial communication. We presented free-living lizards with robots displaying dewlaps of different designs that varied in the proportion of the black and white components. We found no effect of dewlap brightness or design on the time it took for a lizard to detect the robot, consistent with the view that initial detection is likely to be primarily elicited by movement rather than specific color or pattern. However, males (but not females) responded with a greater intensity to the dewlap treatment that most resembled the natural dewlap color and design of the species. Furthermore, males were more likely to display to any dewlap color in the presence of a neighbor. These results suggest that dewlap pattern may play an important role in species recognition but has minimal influence on the initial detection of the signal. Importantly, our results also highlight that factors unrelated to discrimination, such as social cues and individual motivational state, may affect responses to species identity cues.

Key words: playback experiment, sensory drive, social signaling, sympatric congeners, visual ecology.

INTRODUCTION

Visual signals used in intraspecific social displays are often complex, comprising multiple components, such as the size of a morphological structure, its color and pattern, and accompanying behavioral displays (Hebets and Papaj 2005). Each component may be under selection for both the efficacy with which it is detected by the intended receiver and the information it conveys (Endler 1992; Andersson 2000; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). An effective visual signal must first be easily detected by the receiver's visual system in the environment in which the display is typically given. Once the signal is detected, the receiver must recognize the signal as conspecific (Cronin 1993; Andersson 1994) and may assess additional information encoded in the signal such as signaler quality (Ryan and Rand 1993; Hebets

and Papaj 2005). Understanding the relative contribution of selection for efficient detection and selection for information content on various signal components is critical to explain the evolution of both signal complexity and signal diversity (Espmark *et al.* 2000; Fleishman 2000; Fleishman *et al.* 2015).

Detectable visual signals are those with colors, patterns, or movements that are perceptually salient to receivers in the habitat in which the signal is typically given (Dawkins and Guilford 1997). In the specific case of color, the conspicuousness of a visual signal can be dependent on its contrast against the environmental background, where greater contrast (chromatic or achromatic) results in greater conspicuousness (Fleishman 1992; Fleishman and Persons 2001; Stuart-Fox *et al.* 2003; Hebets and Papaj 2005). Contrast can be further enhanced in multicomponent color signals through increased internal contrast between color patches within the signal (Marshall 2000; Bohlin *et al.* 2008). This additionally ensures that the signal is conspicuous against variable backgrounds (Renoult *et al.* 2015). However, the appearance of the signal will depend on the size and configuration of individual color patches, in

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relation to the distance of the receiver, as the receiver's visual acuity determines whether adjacent color patches can be distinguished (Endler 1987; Cronin *et al.* 2014). Many species also combine conspicuously colored ornaments with display motion, which helps capture the attention of conspecifics in complex visual environments by triggering the “visual grasp reflex”—an automatic orientation toward movement in the periphery of the visual field (Fleishman 1992; Peters and Evans 2003b; Steinberg and Leal 2013). However, the extent to which conspicuous coloration enhances signal detection (i.e., probability of triggering the “visual grasp reflex”) is unclear (Persons *et al.* 1999; Fleishman and Persons 2001).

Once the receiver detects and orients toward a signaler, the signal must be recognized as “conspecific.” For example, females will assess a signal for conspecific cues in order to avoid wasteful heterospecific matings (Servedio and Noor 2003). Territorial males may also evaluate these cues to avoid aggressive interaction and minimize energy expended on defending a territory or other resource against heterospecific males with which they are not in direct competition for reproduction (Servedio and Noor 2003; Grönig and Hochkirch 2008; but see Ord King and Young 2011, Drury *et al.* 2015). Signals important for species recognition are not only expected to differ from those of closely related sympatric species, but they are also expected to be under stabilizing selection whereby signals that deviate from the species typical signal are less likely to elicit responses from conspecifics and are therefore selected against (Pryke and Andersson 2008).

Taken together, both detection and species recognition are important aspects of the signaling process (in addition to subsequent mate or rival assessment), and different components of multicomponent signals may function to enhance detection, species recognition, or both. In this study, we tested how the design of a multicomponent ornament functions in signal detection and recognition in a lizard. The black-bearded gliding lizard, *Draco melanopogon*, from Southeast Asia is a good model for addressing questions on signal detectability and species recognition because they possess a large

extendable throat fan or dewlap that is species typical in color and pattern. The species also occurs syntopically with as many as four other congeners at many locations (*Draco formosus*, *Draco quinquefasciatus*, *Draco sumatranus* and *Draco maximus*; Das 2010; Grismer 2011). Male *Draco* lizards defend territories from other conspecific males to maintain exclusive access to females (Hairston 1957; Alcalá 1967; Mori and Hikida 1993, 1994), and the extension of the dewlap is central to communicating aggression in territory defense (indeed, it appears to be the only social signal used in *D. melanopogon*, whereas in other species a push-up or head-bob display is also performed; Klomp DA, Ord TJ, personal observation). *Draco melanopogon* males have long black dewlaps with a bright white base, which provides a strong achromatic contrast both internally and against the background (Figure 1a and c). The high achromatic contrast of the dewlap may be important in initial signal detection (initiation of the visual grasp reflex) because the achromatic visual channel is associated with the perception of movement (Kelber *et al.* 2003; Osorio and Vorobyev 2005). Like other diurnal lizards, including agamids, gliding lizards are likely to be tetrachromatic (Yewers *et al.* 2015), with double cones used for luminance perception (Osorio and Vorobyev 2005). Lastly, the dewlap of *D. melanopogon* differs by a lesser or a greater degree from those of the 4 sympatric species at our field site—*D. formosus*: off-white and red dewlap; *D. quinquefasciatus*: a pale yellow dewlap; *D. sumatranus*: a bright yellow and white dewlap; *D. maximus*: a black dewlap with white rim—which implies dewlap color design could also be influential in species recognition and that deviating away from the population average design could begin to overlap with one or more congeners.

We used robotic playback of realistic *D. melanopogon* display, with different dewlap pattern treatments, to investigate the function of dewlap coloration and infer its potential adaptive significance. For this purpose, our robots included only the moving dewlap to circumvent any species identity cues that might be associated with morphology (e.g., body size or shape; Hankison and Morris 2003;

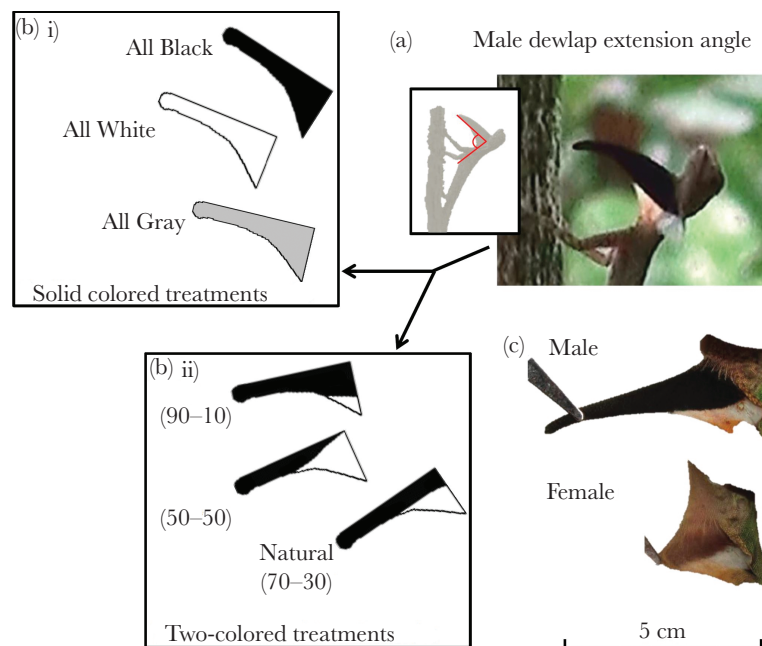


Figure 1

(a) Male *Draco melanopogon*, dewlap naturally extended (image a still from behavioral trials) and the angle of dewlap extension as measured from still; (b) robot, dewlap treatments ((i) solid color and (ii) 2-colored); and (c) artificially extended dewlaps of a male and female *D. melanopogon*.

Ord and Stamps 2009). We tested 2 nonmutually exclusive hypotheses: 1) that achromatic contrast (both internal achromatic contrast and contrast with the background) enhances signal detection and 2) that the specific pattern of the *D. melanopogon* dewlap facilitates species recognition. We presented territorial males in the wild with 6 different treatments in which we varied the proportion of black and white on the dewlap (including a solid gray treatment) and estimated achromatic contrast using models of *Draco* vision, taking into account the distance of the receiver. The first hypothesis predicts that treatments with higher achromatic contrast should be detected sooner by conspecific male and female lizards (i.e., receivers orient toward the robot more quickly). If achromatic contrast is unimportant for detection, then we expect no difference in detection time between treatments. The second hypothesis predicts that lizards will be more likely to respond (i.e., display to the robot), respond sooner or with greater intensity to the most population typical (or “natural”) dewlap design, but responding least to the treatments that deviate away from the population-typical dewlap design. Specifically, presenting dewlaps that varied along a gradient from more to less similar to the population-typical design allowed us to assess possible stabilizing selection on dewlap pattern, as predicted by the species recognition hypothesis. We also assessed sex differences in detection and responses to the dewlap treatments as different receivers may exert variable selection on multicomponent signals (e.g., males and females may attend to different cues within multicomponent signals; Hebets and Papaj 2005; Searcy and Nowicki 2005).

METHODS

Quantifying the color and behavior of free-ranging lizards

We studied a wild population of *D. melanopogon* at Ulu Gombak forest reserve, north of Kuala Lumpur (Peninsula Malaysia) between 14 May 2011 and 22 May 2011, to collect baseline habitat color and behavior data for visual modeling of dewlap conspicuousness, programming of the robot, and creating its dewlap treatments. The dewlap colors of 5 free-living adult male lizards were measured with a JAZ EL-200 spectrometer with inbuilt JAZ-PX pulsed xenon light source, calibrated using a diffuse white reflectance standard (Ocean Optics) and taken at a 45° angle relative to the surface. Background color can be classified into 4 groups (green, brown, dark brown/black and white/pale green), covering the predominant background colors of leaves, bark and lichen. A minimum of 10 measurements for each color group were also taken with the spectrometer and averaged for use in visual modeling (see Appendix S1, Visual modeling methodology). In order to quantify the proportions in which these colors are present in the background to the lizard’s dewlap display, we took digital photographs framing the lizard’s perch to the side, capturing representative background vegetation color and density. The proportions of each color in these photographs were estimated using a 1 cm² grid overlaid on the background photographs (see Klomp et al. 2014).

Side-welling absolute irradiance (90° from the ground) was measured with a JAZ-ULM-200 spectrometer and cosine-corrected irradiance probe (Ocean Optics) from the position of capture facing away from the sun to not saturate the sensor, as described in Klomp et al. (2014). We used side-welling irradiance rather than down-welling irradiance, as this better represents illumination of the dewlap. Details of visual modeling to estimate the achromatic contrast of natural dewlaps and dewlap treatments are given in Appendix S1.

In order to mimic the movement of the dewlap during its display sequence, we collected data on display bout duration, interval length and dewlap extension frequency, angle, and speed. These data were collected from videos of 18 free-living lizards displaying recorded using a Sony Handycam HDR-XR550VE digital camcorder mounted on a tripod. Following video recording, we calibrated the image by placing a ping-pong ball of known size attached to an extendable pole at the same perch site from which the lizard was recorded to have displayed (see Ord et al. 2007). We were then able to use stills from the size-calibrated footage to measure dewlap length, area, natural extension angle and the proportions of each color in the dewlap, using ImageJ (Abramoff et al. 2004). We obtained information on the speed and temporal pattern of the dewlap extension using the MATLAB-based program “Analysis of Image Motion” v 1.2 (Peters et al. 2002; Peters 2006) and frame-by-frame analysis using video time codes from QuickTime clips of video recordings (see Ord et al. 2010).

Robot construction

We constructed three programmable robots, each consisting of a plain plywood box from which a dewlap extended and retracted on a simple wire mechanism controlled by a stepper motor powered by several batteries (Supplementary Figure S1). The robots had Arduino Pro Mini microcontrollers that we programmed with the population typical speed, dewlap extension angle, and temporal movement patterns of *D. melanopogon* (Supplementary Figure S2), such that only the color and pattern of the dewlap varied among our treatments (Supplementary Tables S1 and S2). The robot boxes were mounted on poles with quick-release pads that connected to a tripod below to enable the robot to be presented at a similar height to the natural perch height of the lizards (robot: 3.2 m; mean natural perch height: 4.0 ± 2.1 m, Supplementary Table S1). The color of the plywood box was designed to blend in with the background, by closely matching the average spectra of the habitat (Supplementary Figure S3).

Experimental dewlap treatments

We varied the achromatic component of the signal by altering the proportion of black and white across five dewlap types, with a sixth treatment included of solid gray. Specifically, 3 treatments were solid colors—black, white, and gray (20% reflectance)—and therefore lacked internal contrast, while the remaining 3 were two-colored treatments—70% black and 30% white (the population typical), 50% black and 50% white, and 90% black and 10% white (Figure 1)—that varied in internal contrast. The black and white colors for all treatments matched the natural black and white colours of the *D. melanopogon* dewlap (Supplementary Figure S3). These 6 treatments were chosen to provide variation in achromatic contrast (internal contrast and contrast with the background) and gradual variations along a scale from population-typical, or “natural,” to unnatural.

Appearance of dewlap treatments to receivers

Of the solid colored dewlap treatments, both white and black produce high achromatic contrast against the background, whereas the gray achromatically matches the background (Table 1). For the two-colored treatments, black and white together in the dewlap produces a high achromatic internal contrast (Table 1), which increases the conspicuousness of the signal, so long as the receiver is close enough to distinguish the two colors (Marshall 2000;

Table 1**Achromatic contrast against the background and internal contrast of the black and white colour patches, for natural dewlaps and dewlap treatments**

	Mean JND (range) ^a
Viewed close enough for colour patches to be resolved:	
i. Natural dewlap, contrast against the background	
Black	33.25 (25.36–42.67)
White	24.28 (21.84–27.51)
Overall, weighted	30.56 (24.30–37.60)
ii. Dewlap treatments, weighted contrast against the background	
Solid black	39.02
Solid white	36.00
Solid gray	3.21
70% Black 30% white (natural)	38.11
50% Black 50% white	38.65
90% Black 10% white	38.72
iii. Achromatic contrast between internal color patches (black and white)	
Natural dewlap	60.76
Two-colored dewlap treatments	75.02
Viewed from a distance, color patches blend together:	
iv. Natural dewlap, contrast against the background	5.16 (2.98–7.33)
v. Dewlap treatments, contrast against the background	
70% Black 30% white (natural)	13.40
50% Black 50% white	22.61
90% Black 10% white	7.05

^aJND values are only indicative of relative differences in achromatic contrast - see Appendix S1 for extended discussion.

**Weighted contrasts against the background for dewlap treatments are all approximately the same except for solid gray because the contrast of the solid white and solid black components are very similar. However, contrasts of 2-colored treatments are expected to be higher than solid colors when the 2 color patches can be resolved because of high internal contrast.

Bohlin *et al.* 2008; McLean *et al.* 2014). The larger the relative size of the color patches (i.e., the closer the color proportions are to equal in the dewlap) the greater the internal contrast. Whether the black and white components can be distinguished depends on the size of the color patches and the distance and visual acuity of the receiver (Endler 1987; Fleishman 1992). When color patches are indistinguishable from one another, either because the receiver's visual acuity is too low to resolve small color patches or the receiver is at too great a distance from the signaler, color patches appear as a "blended" average weighted by the relative proportions of the constituent colors. This is important because where the color patches are distinguishable, the treatment is more conspicuous than when are not distinguishable—both because of the internal contrast and because both black and white are individually more conspicuous than an average gray (see Dewlap treatments, weighted contrast against the background, Table 1).

Dewlap treatments—predictions

Assuming that the black and white components of the signal can be resolved, in terms of signal detectability, we predict that the 50% black 50% white treatment should be detected most readily as it features the greatest level of internal contrast. This is followed by the natural and the 90% black 10% white treatments (featuring less internal contrast), followed by the solid black and solid white treatments (no internal contrast, but high contrast against the background), and that the solid gray treatment would be the least readily detected.

In terms of species recognition, we predict that the natural treatment (70% black 30% white) will appear most similar to a *D. melanopogon* dewlap and thus will elicit the greatest response from conspecifics (e.g., the greatest number of dewlap displays or the shortest delay to display). The treatment predicted to elicit the next greatest response is the 50% black 50% white treatment, as it

still prominently includes both dewlap colors, though the proportions are unnatural. The solid black and the 90% black 10% white treatment resemble the primary black component of the *D. melanopogon* dewlap, but with no or minimal white, and thus we predict that they will elicit the next greatest response. Finally, we predict the least response to the solid white and gray dewlap treatments, which least resemble the natural dewlap. If there is strong stabilizing selection to only respond to conspecifics (i.e., heterospecific interaction is particularly costly) then we expect little to no response to the treatments which deviate from the population-typical dewlap (i.e., natural treatment).

In our experiments, robots were presented at a range of distances (1.9–9.5 m, Supplementary Table S1), and under some circumstances (e.g., at relatively great receiver distances), the constituent color patches may appear as a "blended" average. In this case, the natural treatment would appear similar to the solid gray treatment (see Supplementary Figure S3). Therefore, the natural dewlap treatment, together with the solid gray, would be least detectable (see Table 1) but should elicit a similarly strong response once detected.

Field robot playback experiments

We returned to the same field site at Ulu Gombak between 17 June 2013 and 31 July 31 and presented the robots with different dewlap treatments to free-living *D. melanopogon*. Robots were positioned at approximately 5 m from the focal lizard (Supplementary Figure S4) and away from nearby trees. This was done because previous studies have suggested that lizards may respond to any stimulus, irrespective of its conspecific or heterospecific cues, simply because it is positioned in an area of the environment that is typical for a conspecific male rival or mate (Ord and Stamps 2009).

The robots were programmed with an initial 7-min no-display period to allow the lizard to recover from any disturbance experienced during the setup of the robot in its immediate environment.

Focal lizards were video recorded at a distance of at least 6 m (and at least 5 m away from the robot). The position of the robot relative to the focal lizard was recorded and this allowed us to be confident about the direction in which the focal lizard would need to look in order to be orientating toward the robot. Video recording continued once the robot began to display for 5 min, after which the presentation was terminated. Playbacks were made to 218 lizards. The trees on which focal lizards were found were flagged to ensure that each new trail was out of visual range of all previous trials.

During filming, we noted the presence of any neighbors as well as species and sex, in a 10-m radius from the focal lizard. As ambient light level can influence detectability of visual signals (Mottram 1916; Endler 2000), immediately following each playback trial, we measured light level at the site of first display using an LI-250A light meter fitted with an LI-190SA Quantum Sensor (LI-COR, Inc.). The average of 2 light readings taken over a 15-s period with the sensor positioned perpendicular to the ground was used to approximate the amount of light that would enter a lizard's left and right eye. However, lighting conditions changed relatively little between trials as all were conducted in full shade forest, where the subject, the robot, and background are all entirely shaded from the sun. We then measured the distance between the robot and the lizard and the distance between the lizard and any neighbors that were seen, using a measuring tape.

Analysis and statistical methods

All footage were reviewed in real time using the event recorder “Jwatcher” (version 0.9—Blumstein and Daniel 2007). We recorded the time it took for the lizard to move its eye toward the robot (“latency to orientate”), per Fleishman (1992). We then recorded whether or not the lizard displayed once detection was assumed to have occurred (“display post orientation”) and, for those that did display, the time it took for the lizard to start to display (“latency to display”). Finally, we recorded the overall display level as the number of dewlap extensions in a 2.5-min period from the first display (“number of displays”), which represents the intensity of the response of individuals to the robot stimulus. Two lizards that took over 5 min to orientate to the robot were excluded from the analysis.

We tested the effect of dewlap treatment on each variable using generalized linear models in R version 3.0.3 (6 March 2014). The variables “latency to orientate” and “latency to display” were modeled with a Gamma error distribution and log link function because they are strictly positive and continuous, but left skewed. The variable “display post orientation” was scored as either “yes” or “no,” and thus modeled with a binomial distribution, and “number of displays” was modeled using a negative binomial distribution (as count data that was over-dispersed), following Zuur et al. (2013).

To evaluate the level of support for alternative models of the effect of dewlap treatments on detection and response, we used a model selection approach. We compared the computed values of Akaike's information criterion, corrected for small sample size (AICc; Akaike 1974; Burnham and Anderson 2002) for a set of models in which predictor variables differed. Models with the lowest AIC value were considered the best supported models, although any model within 2 units of these lowest models ($\Delta\text{AIC} \leq 2.0$) were also considered biologically viable (as described in Symonds and Moussalli 2011). We then computed their relative weights (AICw) to give a measure of the relative support for each model compared with all others considered. Effect sizes (F -values) are reported to indicate both the magnitude and the direction of effect.

To determine the best model to explain a lizard's detection time (latency to orientate), we assessed the relative support of models including dewlap treatment, robot distance from the focal lizard, and light level as well as null model (intercept only). As we expect that the detection of different colors and patterns to be worse at greater distances and with lower light levels, we also included models with the interaction of dewlap treatment with robot distance and dewlap treatment with light level in the candidate set. Additionally, recent work by Nava et al. (2009) found sex differences in motion detection in the Sagebrush lizard (*Sceloporus graciosus*), so for this set of models, we also included “sex” as a factor on its own as well as with the interactions between sex and treatment, robot distance, and light.

To determine the best supported model for the effect of dewlap treatment on each of the lizard “response” variables (i.e., “display post orientation,” “latency to display,” and “number of displays”), we compared AICc model values, weights, and effect sizes between a set of candidate models that included robot distance from the focal lizard, the presence (or absence) of neighbors, and a null model. Again, as responses to a stimulus can be affected by social factors such as the sex of the receiver, the distance to the stimulus and the presence of other observers, we also included the interaction of dewlap treatment with sex, robot distance, and the presence of a neighbor in this candidate set.

RESULTS

Latency to orientate

Male and female *D. melanopogon* lizards detected the robot stimulus with similar latency, with none of the models that included “sex” as a factor ranking highly (Table 2). The best supported models were those that include an interaction of dewlap treatment with robot distance and the dewlap treatment considered alone. However, both models had low effect sizes, and there were no obvious patterns for treatment across different distances in plots of the data (Figure 2). The “all-white” treatment seemed to have been detected with slightly longer latencies at a distance, which might account for the treatment by robot distance model ranking highly. Regardless, overall detection times were generally comparable across all treatments suggesting that all dewlap patterns were similarly detectable.

Display response following detection

In assessing the salience of the different dewlap treatments to *D. melanopogon* males and females, we first looked at the factors affecting whether or not an individual displayed to robot stimuli. Dewlap treatment had little effect and males were instead more likely to display to any treatment in the presence of a neighbor (Table 3 (i), Supplementary Figure S5). Second, latency to display was not well predicted by any of the candidate models and the intercept-only model ranked the highest for both males and females (Table 3 (ii)). Finally, there was a strong effect on the overall intensity of response (number of dewlap extensions performed by focal lizards). The model that included an interaction term between dewlap treatment and sex ranked the highest of all models considered and was supported by a large effect size (Table 3 (iii)). More specifically, males displayed the most to the population-typical dewlap pattern (Figure 3a), whereas the intensity of response in females was generally low and unrelated to dewlap pattern (Figure 3b).

Table 2
Candidate model set for detection of the robot (“latency to orientate”; $n = 218$)

Model	AIC _c	Δ AIC _c	AIC _w	F (effect size)
Intercept only	1830.27	2.94	0.08	
Sex	1830.40	3.06	0.08	1.23
Treatment	1827.74	0.40	0.30	1.84
Treatment \times Sex	1833.41	6.08	0.02	0.77
Robot distance	1832.21	4.87	0.03	0.07
Robot distance \times Sex	1831.02	3.69	0.06	1.99
Light	1832.28	4.94	0.03	0.02
Light \times Sex	1833.44	6.11	0.02	0.63
Treatment \times Robot distance	1827.33	0.00	0.36	1.76
Treatment \times Robot distance \times Sex	1834.15	6.82	0.01	0.86
Treatment \times Light	1834.83	7.50	0.009	0.69
Treatment \times Light \times Sex	1849.40	22.07	0.000006	0.34

Compelling models with Δ AIC_c ≤ 2.0 are highlighted in boldface.

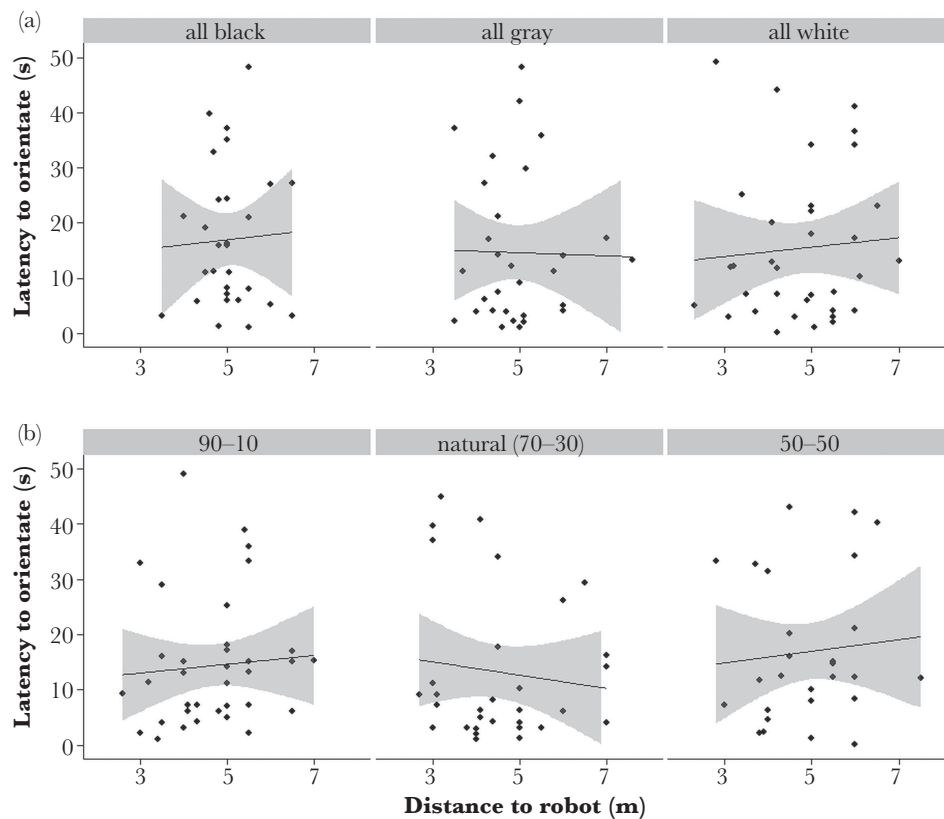


Figure 2

Latency to orientate to each treatment as a function of robot distance from the focal lizard (males and females combined): (a) solid colored treatments and (b) 2-colored treatments. Each dot represents the response of an individual lizard to the robot. Trend lines represent the mean orientation time as a function of robot distance, with gray bands representing 95% confidence intervals.

DISCUSSION

We examined the possible functions of the black and white components of a visual ornament, the dewlap, in *D. melanopogon* to shed light on the evolution of signal complexity and signal diversity in gliding lizards more broadly. There has been an extensive radiation of this single genus throughout Southeast Asia, resulting in over 40 recognized species (McGuire and Heang 2001), all of which differ in some aspect of the color and pattern of the dewlap. Given the range of habitats occupied by different species and the frequency of sympatric occurrence, differences in dewlap design could

reflect differences in signal detection requirements or the need for improved species recognition.

Despite differences in the computed conspicuousness of the achromatic contrast of our dewlap treatments, our experiment revealed that dewlap pattern had little impact on detection under the same environmental conditions that *D. melanopogon* communicate with one another. The achromatic visual channel is known to be associated with the perception of movement (Fleishman 2000; Kelber *et al.* 2003; Osorio and Vorobyev 2005), but the *D. melanopogon* visual grasp reflex appears to be activated by the motion of

Table 3
Candidate model sets for response to the robot

Model	AIC _c	ΔAIC	AIC _w	F (effect size)
i. Display post orientation (yes/no, <i>n</i> = 218)				
Intercept only	298.44	6.96	0.02	
Sex	292.39	0.91	0.34	8.16
Treatment	302.86	11.38	0.002	1.14
Treatment × Sex	305.46	13.98	0.0005	0.40
Robot distance	300.55	9.07	0.006	0.00
Robot distance × sex	295.72	4.24	0.06	0.86
Neighbor present	297.50	6.02	0.03	3.06
Neighbor present × Sex	291.48	0.00	0.54	0.15
Treatment × Robot distance	309.30	17.82	0.00007	1.13
Treatment × Robot distance × Sex	312.49	21.01	0.00001	2.16
Treatment × Neighbor present	309.37	17.89	0.0007	0.59
Treatment × Neighbor present × Sex	320.90	29.42	0.0000002	0.20
ii. Latency to display (<i>n</i> = 93)				
Intercept only	964.12	0.00	0.46	
Sex	966.23	2.12	0.02	0.004
Treatment	970.77	6.66	0.02	0.82
Treatment × Sex	979.95	15.83	0.0002	0.63
Robot distance	966.12	2.01	0.17	0.14
Robot distance × sex	970.02	5.90	0.02	0.35
Neighbor present	966.22	2.11	0.16	0.01
Neighbor present × Sex	970.29	6.17	0.02	0.13
Treatment × Robot distance	981.34	17.22	0.00008	0.35
Treatment × Robot distance × Sex	989.65	25.53	0.000001	1.37
Treatment × Neighbor present	978.08	13.96	0.0004	1.07
Treatment × Neighbor present × Sex	985.58	21.46	0.00001	2.56
iii. Number of displays in 2.5 min post initial display (<i>n</i> = 64)				
Intercept only	414.31	15.53	0.0004	
Sex	406.15	7.37	0.02	11.10
Treatment	410.80	12.02	0.002	3.05
Treatment × Sex	398.78	0.00	0.86	2.77
Robot distance	414.96	16.18	0.0003	1.48
Robot distance × sex	403.81	5.03	0.07	3.30
Neighbor present	416.35	17.57	0.0001	0.07
Neighbor present × Sex	409.81	11.03	0.003	0.34
Treatment × Robot distance	417.86	19.08	0.00006	1.07
Treatment × Robot distance × Sex	405.15	6.37	0.04	2.27
Treatment × Neighbor present	419.16	20.38	0.00003	0.68
Treatment × Neighbor present × Sex	410.61	11.83	0.002	1.54

Compelling models with ΔAIC_c ≤ 2.0 are highlighted in boldface.

the dewlap and not enhanced by dewlap color. This is consistent with the argument that signal detection in visually communicating species relies more on conspicuous movement—the way in which the visual signal is presented to social partners—rather than coloration per se (Fleishman 1992). In our system of lizards, the dewlap is rapidly extended and retracted in repeated bouts of display. This dynamic aspect of the dewlap display was consistent across all of our treatments. Our results therefore suggest that selection for efficient detection has not played a large role in the evolution of color signals, and signal detection is probably dependent on the speed and repetition of movement associated with the dewlap display. Similar findings have been found for other lizards that use large conspicuously colored dewlaps for territorial communication (Caribbean *Anolis* lizards; Ord and Stamps 2008).

Species recognition, however, does appear to play a role in color signal evolution in *Draco*. Species recognition is important for reducing costly heterospecific aggression in many animals (Lorenz 1962; Losos 1985; Alatalo *et al.* 1994). We found that males responded with the greatest intensity to the population-typical dewlap design, suggesting that male lizards identified the stimulus as a dewlap belonging to an individual with whom they are in competition for resources (i.e., most likely a conspecific male). Additionally, focal

lizards responded to the gray dewlap treatment with a similar intensity to the natural dewlap treatment, which appear similar when the 2 colors cannot be resolved and instead appear as a “blended average.” This suggests that lizards may not be able to resolve the 2 colours of the *D. melanopogon* dewlap in natural conditions for distances at which broadcast displays are typically given. Instead, the 2 colours may be more important in close-range interactions (during which the black and white components may be resolved), such as aggressive competition and courtship. Given that dewlap stimuli deviating away from the species norm (apart from gray) were clearly less evocative to males and would presumably be signals less effective at maintaining territory boundaries, our data also suggest that dewlap design is probably subject to stabilizing selection. Nevertheless, males did respond to nonspecies typical dewlap designs, albeit at lower response intensities. Whether or not this reflects some level of selection resulting from interspecific territoriality among sympatric congeners that overlap in resource use (e.g., Orians and Willson 1964; Cody 1969; Grether *et al.* 2009; Peiman and Robinson 2010) is unclear and requires further investigation.

We also found no effect of treatment on whether or not focal lizards responded to the robot stimulus in the first place nor on the time it took for lizards to respond. That is, dewlap design only

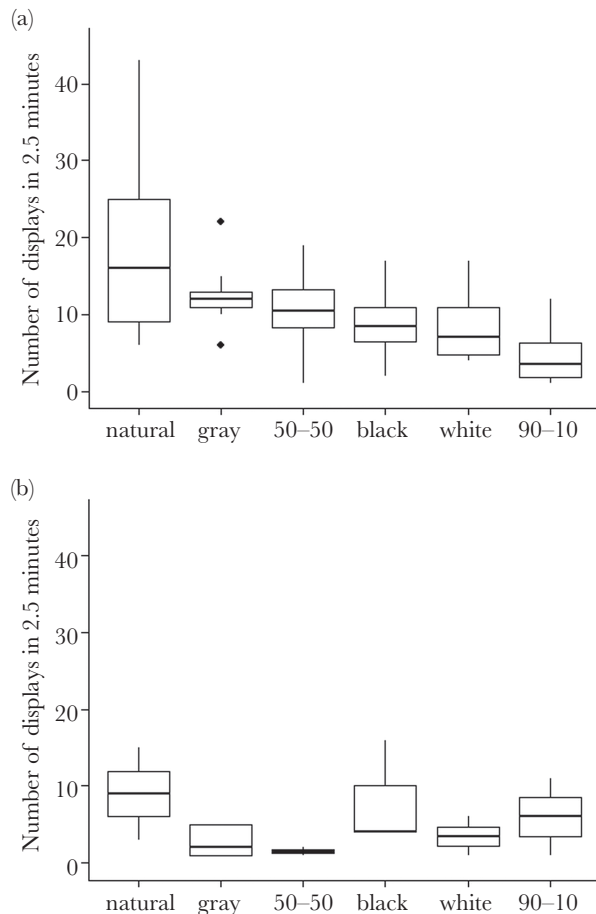


Figure 3
Boxplot showing the number of dewlap displays performed by lizards in 2.5 min following detection for (a) males and (b) females.

seems to affect the level of response once a male has decided to respond. Whether or not animals ultimately decide to respond to conspecific and non-conspecific signals can be affected by many factors and is a separate question to whether those animals discriminate differences in the signals presented (e.g., see Ord and Stamps 2009; Ord *et al.* 2011; Drury *et al.* 2015, for discussion). For example, our experiment revealed that the presence of a neighbor during robot presentations increased the likelihood of the focal lizard responding to the robot. This is consistent with many other taxa, in which the presence and sex of a neighbor has been shown to influence mating and territorial behavior (Matos and McGregor 2002; Striedter *et al.* 2003; Wich and Sterck 2003; Matos and Schlupp 2005). It suggests that recent or ongoing activity in the surrounding social environment can have an important motivating influence on an individual's decision to respond to any form of social stimulus.

Although species recognition is important in preventing costly heterospecific mating (Servedio and Noor 2003; Gröning and Hochkirch 2008), we did not find the same strong effect for females. Female reproductive status and motivation may strongly influence female response to a conspecific male signal (Shine 1980), so a lack of response does not imply that females are not using the dewlap signal in species recognition. Female receptivity to males is also likely to be influenced by many additional cues (body size, territory quality; Candolin 2003) that were absent in our stimuli. How females discriminate among conspecific males or choose areas to

establish home ranges will require further study, but our results suggest that reproduction in these lizards is likely centered on male–male competition for the monopolization of access to females, rather than female mate choice per se.

Research on the mechanisms leading to diversity in color signals in groups of closely related species has often focused on (among other things) selection for detectable signals in diverse visual habitats (i.e., Sensory Drive hypothesis: Endler 1992, 1993). Comparative studies on terrestrial species have shown some support for this hypothesis (Gomez *et al.* 2004; Leal and Fleishman 2004; Stuart-Fox *et al.* 2007; Fleishman *et al.* 2009; Macedonia *et al.* 2014). Furthermore, in a laboratory study on *Anolis cristatellus*, Fleishman and Persons (2001) found that visual flags (resembling dewlaps) with greater chromatic contrast or achromatic contrast were detected sooner than those with lower contrast; yet our field experiment showed that even large differences in achromatic contrast had no influence on detection. This suggests that in real-world conditions, the evolution of conspicuous signals is unlikely to be driven by selection for signal detectability alone. Instead, conspicuous signals may increase the reliability of information transfer during display (i.e., post detection; Endler 1993). That information may include cues on species or sex identity, individual condition or quality, motivational state, or any combination of these factors (Maynard Smith and Harper 2003).

The evolution of color signal diversity is therefore likely to be driven by multiple forms of selection and their interaction, and particularly the interaction between sexual and natural selection (Endler 1984; Stuart-Fox and Moussalli 2008; Chen *et al.* 2012; Heinen-Kay *et al.* 2014; Marshall and Stevens 2014) and sexual selection and species recognition (Ryan and Rand 1993; Ellers and Boggs 2003; Nicholson *et al.* 2007; Pryke and Andersson 2008; Rosenthal and Ryan 2011; Pike *et al.* 2014). Although signal detection is critical for effective communication (Fleishman *et al.* 2009), in *D. melanopogon*, achromatic contrast does not appear to be used in conjunction with motion-based display to increase signal detectability. Instead, the initial grasp reflex is likely to be primarily elicited by movement. Overall, therefore, our study provides no support for the hypothesis that diversity in signal design between groups of closely related species is due to the selection for detectability in different visual habitats. Signal design likely plays an important role in advertising species identity in *Draco*, and the need for improved species recognition is believed to have contributed to the evolution of signal complexity and diversity in communities with several sympatric congeners (Espmark *et al.* 2000). However, our results also highlight that a receiver's decision to respond to a signal depends on other factors as well, such as the presence of a neighbor or motivational state. This presents a challenge for playback experiments and the study of species recognition more generally, because consistent responses to both conspecific and non-conspecific signals could reflect lack of discrimination of species identity cues or a host of other factors that are unrelated specifically to discrimination (Ord and Stamps 2009).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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