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Original Article

Species recognition of color and motion signals in *Anolis grahami*: evidence from responses to lizard robots

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Male *Anolis* lizards exhibit an impressive diversity of dewlap color patterns and motion displays. These traits are thought to mediate species recognition, but direct experimental support is limited. It is also unclear if and how color and display behavior each may contribute to the signaling of species identity. We used a programmable robotic lizard to manipulate these signal components independently in *Anolis grahami*. Four robot variants were used: a control treatment that displayed the conspecific (orange) dewlap color and headbobbing sequence, 2 treatments that differed from the control only in dewlap coloration (light or dark blue), and a fourth treatment that differed from the control only in headbob display pattern (reversed headbob display structure). Artificial dewlaps were calibrated in color and brightness to the *A. grahami* visual system using a computational model. We presented robots to 102 adult male subjects and quantified their responses for durations of dewlap pulsing and headbob displays. Subjects spent significantly more time pulsing their dewlaps in response to control (conspecific) robot displays than to treatments that deviated from the control either in dewlap color or in headbob display structure. Our findings implicate both morphology and behavior as functional components of social signaling in *A. grahami*, thus underscoring the complex, multicomponent nature of anoline displays.

Key words: ***Anolis,*** **dewlap coloration, headbob display, lizard robots, species recognition.** *[Behav Ecol]*

INTRODUCTION

Species recognition is a fundamental problem for animals in social contexts such as mate choice and intra-sexual competition. This problem is magnified in adaptive radiations where related and phenotypically similar species occur sympatrically (Williams and Rand 1977; Ryan and Rand 1993). One solution to the problem of species recognition has been the evolution of species-specific displays that minimize costly identification errors. For example, the "reproductive character displacement" hypothesis (Brown and Wilson 1956) expects that the strongest selection for premating isolation will be experienced by sympatric congeners, and it predicts the rapid divergence of socio-sexual signals among such taxa (e.g., Marshall and Cooley 2000; Höbel and Gerhardt 2003).

With nearly 400 species, the genus *Anolis* has provided an excellent system for exploring the evolution of species identity signaling (Losos 2009). Male anoles possess 2 principal visual displays that function as advertisement signals. First, like many other kinds of lizards (e.g., Carpenter and Ferguson 1977), anoles exhibit stereotyped motion signals in which the body is vertically displaced in a repeated up–down fashion. These "headbob" or "push-up" displays may function to announce territory ownership, intimidate rivals, or attract mates (Jenssen 1977).

A second display involves extension and retraction of the "dewlap"—a colorful, fan-like flap of gular skin. Although males of some species extend and hold their dewlaps outstretched for a period of time, in other species, the dewlap is repeatedly extended and retracted to deliver "pulses" of conspicuous coloration (e.g., Gorman 1968). Differences in the ambient light spectrum arising from habitat variation have an influence on dewlap coloration (e.g., Fleishman 1992), but additional factors must contribute to the enormous diversity of color patterns observed in anoles (Nicholson et al. 2007; Fleishman et al. 2009; Ng et al. 2012). For example, an association between genetic divergence and character displacement in dewlap coloration has been shown in several population studies of anoles (Webster and Burns 1973; Glor and Laport 2011; Ng and Glor 2011). The results of at least 1 study have suggested that character displacement also may occur in headbob display patterns (Jenssen and Gladson 1984).

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Use of robots to investigate signal production rules and signal recognition

In the 1960s, several researchers used painted wood models that were made to perform push-up displays, either by pulling a string or via a motorized system of wheels and pulleys (reviewed in Jenssen 1970). In most of these experiments, subjects appeared to attend to display details, as a decrease in responsiveness was observed when displays were altered from the conspecific form. More recently, advances in miniaturized electronics have inspired the use of realistic animal-mimicking robots in behavioral experiments (e.g., fish: Faria et al. 2010; frogs: Narins et al. 2003, 2005; lizards: Martins et al. 2005; Smith and Martins 2006; birds: Patricelli et al. 2002, 2006; Göth and Evans 2004; squirrels: Rundus et al. 2007; Partan et al. 2009, 2010, 2011).

To date, several studies have used robots to ask questions about signal production and perception in *Anolis*. For example, Ord and Stamps (2008) created a highly realistic robot of the Puerto Rican anole *Anolis gundlachi* and conducted a field presentation experiment to examine the effects of "background noise" on display structure. Partan et al. (2011) later used a robot to test *Anolis sagrei* subjects for the preference of a previously described "signature" headbob display pattern over a locally prevalent variant.

Most relevant to the work presented here, Ord and Stamps (2009) used *A. gundlachi* robots to study the species recognition value of headbob displays. The robots were programmed to perform conspecific displays as well as those of *Anolis grahami*—a species with which subjects had no familiarity. Presentations to approximately 50 free-ranging *A. gundlachi* males failed to reveal a significant difference between responses to the conspecific and heterospecific display patterns, regardless of whether the robotic display included dewlap extension in a species-specific manner (see Ord and Stamps 2009 online appendix). The authors argued that their inability to demonstrate species recognition in *A. gundlachi* could not be attributed to similarity between the conspecific and heterospecific displays, nor to low statistical power. Ord and Stamps (2009) suggested further that, given multiple physical and behavioral cues available to make species recognition judgments, it may not be surprising that an *A. gundlachi* robot elicited normal responses from subjects despite the novel motion patterns.

In sum, robotics holds much potential for asking a variety of questions about production and perception of visual displays in lizards. Although useful insights already have been gained, seemingly conflicting results among studies suggest that more research is required on a greater diversity of species before generalities can be formed.

Here, we use computerized robots to assess the relevance of headbob display morphology and dewlap coloration for species recognition in a Bermudian population of *A. grahami*. This species, which evolved on Jamaica with 5 other congeners (Jackman et al. 2002), was introduced to Bermuda in 1905, where it has co-occurred with 2 other introduced *Anolis* species since the 1940s (Wingate 1965). Evolution in sympatry is predicted to favor rapid divergence (i.e., species specificity) in multiple components of species/sex advertisement signals, with individuals expected to respond strongly to conspecific signals. We tested these predictions by altering independent components of *A. grahami* color and motion displays (i.e., dewlap coloration and headbob display structure) and analyzing the outcomes of our robot presentations to free-ranging adult male subjects.

MATERIALS AND METHODS

Subjects and study area

Anolis grahami from Kingston, Jamaica were purposefully introduced onto Bermuda in 1905 (Wingate 1965), where they have an island-wide distribution (Losos 1996). Robots were presented to 102 adult male *A. grahami* over a 2-week period in May 2010 at 1) Blue Hole Park and Coney Island Park in Hamilton Parish, 2) Clearwater Beach Park in St. George's Parish, 3) the Bermuda Botanical Garden in Paget Parish, and at several locations in nearby areas of Bermuda where this species was abundant.

Robot construction

Hardware

Two Futaba S9001 servomotors, which were used to independently control the dewlap extension and push-up display of the robot, were secured inside a camouflage-painted 20 L × 16 W × 14 H-cm plastic box. The box also contained a Yost Engineering ServoCenter Midi v1.2 control board that communicated midi controller messages to the servomotors. In the field, midi controller messages were sent to the input of the ServoCenter from an iPod Touch (model A1213) using a Line 6 MIDI Mobilizer. To simulate a lizard perched on a branch, a 35-cm long piece of 2.5-cm diameter camouflage-painted polyvinyl chloride (PVC) pipe was attached to the front of the plastic protection box. Aligned inside the PVC pipe were two 30-cm pushrods that were sleeved inside plastic tubing for smooth motion. These pushrods were attached to the servomotors at 1 end and to the robot at the other end.

Robot skeletons were constructed using 5-mm diameter copper tubing that was bent into the shape of the spine and head for supporting the latex skin (see Construction of the robot body and dewlap). The copper skeleton was secured posteriorly via the plastic sleeve that extended from the front of the servomotor that controlled the robot dewlap. The skeleton was secured anteriorly to an eyelet that was attached to a pivot. The pivot was positioned within the PVC pipe beneath the robot and was connected to the pushrod that ran to the servomotor and controlled the push-up display.

Construction of the robot body and dewlap

To construct life-like lizard replicas, we commissioned an exhibit preparator at the Museum of Natural History, University of Michigan. Two freshly preserved adult male *A. grahami* were positioned in a natural display pose and cast in Plaster of Paris (USG® No. 1 Moulding Plaster, Chicago, IL). Once dry, the lizard specimens were removed, and the molds were brushed with multiple coats of liquid latex rubber (Woodland Scenics® Linn Creek, MO) to create latex-positive models. These latex lizard replicas were then airbrushed to achieve the subtleties of the *A. grahami* body color pattern (live lizards and high-resolution photos were used for reference).

Dewlaps for the robotic lizards were fashioned from 0.50-mm white semitransparent guitar picks (Steve Clayton, Inc., Talent, OR). Using a life-size photograph of an *A. grahami* with dewlap fully extended, the shape of its dewlap was transferred to the guitar pick, which then was trimmed to size. A small hole was drilled into the posterior-upper region of the plastic dewlap so that it could be attached to a hinge pin in the neck region of the copper tubing skeleton. This design allowed the dewlap to both pivot and extend. A second hole was drilled into the posterior-bottom region of the artificial dewlap to allow for the attachment of a thin wire. This wire was connected to the pushrod that was attached to the dewlap-controlling servomotor.

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Dewlap spectral reflectance measurements

Anolis grahami dewlap reflectance spectra ($N = 23$ adult males) were obtained at a 45° angle relative to the target surface using a custom-made, flat, black plastic probe holder that fit over a reflectance probe (Ocean Optics R400-7). One arm of the reflectance probe was attached to a deuterium/halogen light source (AIS Mini-DT); the other arm was attached to an Ocean Optics USB4000 portable spectrometer that was interfaced with a notebook computer running Ocean Optics Spectra Suite (v 4.1) software. To calculate percentage of reflectance, a diffuse white spectralon reflectance standard (WS-1-SL; Labsphere Inc. North Sutton, NH) was scanned prior to gathering spectral data from each spectral sample, and dark noise was subtracted from the signal.

Visual modeling of artificial dewlap color treatments

A computational model of *A. grahami* spectral sensitivity was used to choose permanent marker inks for the artificial dewlaps, based on how those colors might appear to our lizard subjects. First, following equations for A1 visual pigments in Govardovskii et al. (2000), approximate Gaussian absorbance curves were generated from λ_{max} values for each of the 4 visual pigments that had been determined with microspectrophotometry (Loew et al. 2002). Absorbance spectra of oil droplets associated with the visual pigments were provided by Ellis Loew at Cornell University. Normalized visual pigment absorbance spectra were then multiplied by their associated oil droplet transmission spectra to calculate the spectral sensitivity function of each of the 4 cone classes. These curves are shown normalized to the curve with the highest peak (Figure 1A).

To visually model our study species' perception of the artificial dewlap color treatments, each cone class function (extracted at 10-nm intervals from 340–700 nm) was multiplied by a given dewlap reflectance spectrum over the same range of wavelengths. These spectra included the mean center and edge reflectance of the *A. grahami* dewlap, which served as reference spectra for selecting the permanent markers that we used to color the artificial dewlaps. The sum of each cone class output was then calculated and "corrected" by multiplying each sum by the reciprocal area under the corresponding spectral sensitivity curve. This correction is required to satisfy the assumption that the neural stimulation of each cone class is equal in response to a "white" stimulus (see Fleishman and Persons 2001). The grand sum of the corrected summed outputs across the 4 cone classes is equivalent to stimulus perceived intensity, or, "brightness" (Table 1).

To create the robot "conspecific" dewlap treatment, we sought orange (Prismacolor Premier, Burnt Ochre, PM-93) and yellow (Sharpie: Yellow 30035) permanent marker inks that produced spectral shapes and perceived intensities similar to those of the actual *A. grahami* dewlap. We next chose colors for the robot "heterospecific" dewlaps that differed dramatically in spectral shape from those of the *A. grahami* dewlap. We used 2 blue permanent marker inks (light blue dewlap: Prismacolor Premier, True Blue, PM-39; dark blue dewlap: Prismacolor Premier, Navy Blue, PM-45) and created a white rim on both treatments from the unaltered semitransparent white color of the 0.5-mm thick guitar picks used to fashion all the dewlaps (Steve Clayton, Inc., Talent, OR). We purposefully chose blue permanent markers that, when applied to our artificial dewlaps, either were much greater (light blue) or much weaker (dark blue) in brightness than our orange conspecific treatment (Table 1). This "bracketing" of novel dewlap color brightness (around conspecific dewlap brightness) reduced the likelihood that subjects might respond to overall differences in dewlap brightness, rather than to differences in spectral shape. Although we could not closely match the spectral shapes of the light blue and dark blue permanent markers, both colors are distinct from the conspecific dewlap colors (Figures 1B and 2A).

Transmission of light through the dewlap can affect perception of dewlap brightness and, to a lesser degree, hue (e.g., Fleishman et al. 2006). For 2 reasons, however, we did not include transmission in our calculations of perceived dewlap intensity. First, habitat physical structure (forest geometry), sun angle (e.g., low or high, same side or opposite side of the dewlap relative to the viewer) and sky clarity (e.g., clear or cloudy) all affect the dewlap radiance reaching a viewer's eye (e.g., Fleishman 2000; Leal and Fleishman 2002, 2004; Fleishman et al. 2009). Given that anoles are required under natural conditions to recognize dewlap color patterns with changes in illumination, they may have relatively broad tolerances for what falls within the acceptance region for a species- (or population-) specific dewlap color pattern. Second, the treatments in this study were designed to assess the influence of hue and brightness separately on dewlap color recognition in a coarse manner, as opposed to fine-scale discrimination among similar dewlap colors. We, therefore, simplified our task of modeling dewlap brightness perception by using standardized dewlap reflectance.

Headbob display pattern programming

Anolis grahami produces 2 variants of the headbob display: Type A and Type B (Jenssen 1981). These displays are plotted as amplitude × time "display action pattern" graphs (Carpenter and Grubitz 1961), in which headbobs and pauses are divided into units. The primary difference between Type A and Type B displays in *A. grahami* lies in the duration of the pauses between vertical head motions: comparatively long pauses between head motions in units 2, 6, and 8 of the Type A display are virtually absent in the Type B display (Jenssen 1981; Macedonia and Clark 2003). This species also exhibits population-level variation in headbob display morphology (Jenssen 1981), where individuals from south-central Jamaica (e.g., Kingston) exhibit a square wave-like, plateau-shaped display that contrasts with the "spiked" display form seen elsewhere on Jamaica (Macedonia and Clark 2003). We, therefore, used the plateau form of the headbob display as the conspecific pattern for robot displays.

Robots were programmed with midi controller data to perform headbob displays and dewlap pulses using the Logic Pro (v. 9.1 for Macintosh OS) software program. Type A and Type B display sequences were programmed in an alternating sequence, such that both display variants were performed once per minute over a period of 10 min (Figure 2B). The programmed sequence followed the pattern: Type A display—4 dewlap pulses—20-s pause—Type B display—4 dewlap pulses—20-s pause. This pattern was repeated for 10 min. For our reverse headbob display treatment, we used the same sequence of events in the same order, but we reversed the morphology (time-structure) of each headbob display pattern (Figure 2B). To present this robotic display sequence in the field, the midi controller data were exported from Logic Pro and recorded directly to an iPod Touch, using the input of the Line 6 MIDI Mobilizer.

Experimental protocol

Adult male lizards (≥60-mm snout-vent length) were located by walking slowly and scanning tree trunks. Once a subject was located, the robot was moved to a distance ~2–4 m perpendicular to the lizard's

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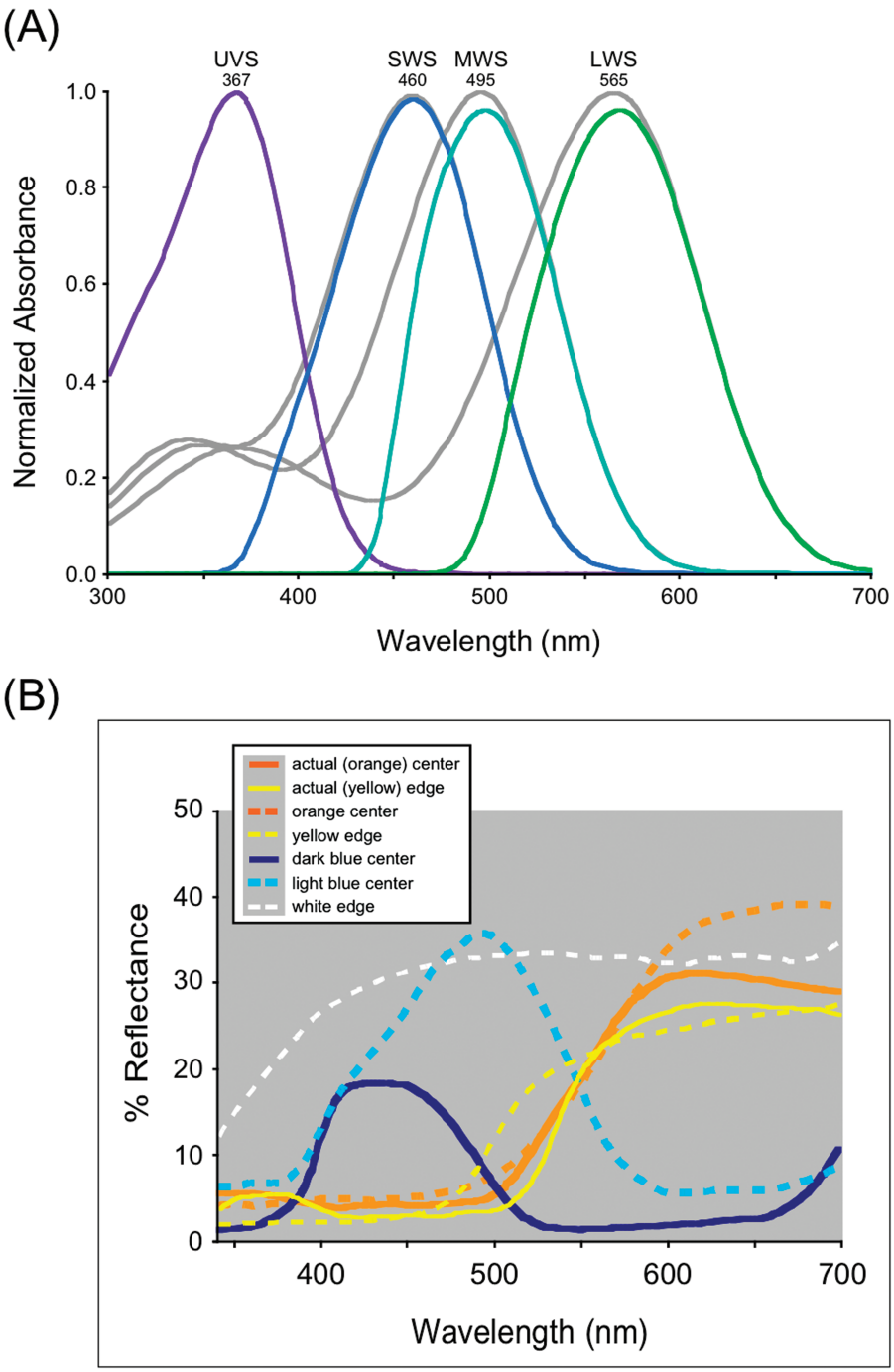

Figure 1

(A) Relative photon catches for each cone class in *Anolis grahami*. Black curves depict cone capture areas, obtained by multiplying smoothed, normalized visual pigment. Absorbance curves times their associated smoothed, normalized oil droplet transmission spectra. Grey curves depict cone capture areas prior to oil droplet filtering (the oil droplet associated with the UVS cone is transparent and has no impact on absorbance). Numbers above each curve indicate peak wavelength absorbance for each visual pigment in the absence of filtering by oil droplets. Visual pigment and oil droplet data are from Loew et al. (2002). Curves were generated using absorbance templates for A1-based visual pigments using the equations of Govardovskii et al. (2000). (B) Reflectance spectra of the (actual) *A. grahami* male dewlap and of the 3 color treatments used for artificial dewlaps.

head-on view so that the robot dewlap and headbob displays were readily visible to the subject. A digital video camera was secured to another tripod, positioned ~2 m behind the stimulus robot and in-line with the male subject, capturing both in a single field of view. If the subject did not flee or display throughout the setup (ca. 5 min), we triggered the robot's display sequence from a laptop computer, thus initiating the trial. The display portion of each trial lasted 10 min, after which we continued to record subject responses for an additional 2 min. We conducted ~25 robots presentations per treatment and used a constrained random approach whereby treatments were presented to subjects, as encountered, according to a repeated random sequence.

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Table 1

Visual modeling of *Anolis grahami* relative photon catches (×100) in response to reflectance of actual and artificial dewlaps

Source	UVS	SWS	MWS	LWS	Sum	Perceived intensity
A. grahami dewlap						
Orange center	5.152	4.974	13.633	23.944	47.703	1.000
Yellow rim	4.390	3.455	9.702	17.766	35.314	0.740
Robot dewlaps						
Orange center	4.317	5.990	13.561	23.792	47.660	0.999
Yellow rim	2.105	5.030	16.267	19.508	42.911	0.900
Light blue center	8.491	26.870	26.486	15.602	77.450	1.624
Dark blue center	4.747	13.727	2.910	2.268	23.652	0.496
White rim	20.150	30.927	33.135	32.828	117.040	2.453

Brightness (perceived intensity) values are normalized relative to the sum of the cone outputs for the *A. grahami* dewlap orange center. UVS: ultraviolet-sensitive, SWS: short-wavelength-sensitive, MWS: medium-wavelength-sensitive, LWS: long-wavelength-sensitive. See text for details.

Statistical analysis

Data on subjects' responses were extracted directly from video recordings. We explored the effect of stimulus (robot) treatment in a semihierarchical manner by first contrasting whether subjects responded to the stimulus with headbobbing or dewlapping, and second, for responders only, by contrasting the duration of each behavior. "Responders" in this analysis were subjects that exhibited headbob displays or dewlap pulses in response to the displays of the robot. Given our a priori prediction that stimuli departing in color or behavior from the control (conspecific) would elicit fewer or weaker responses from subjects, we embedded in our analysis the planned contrast: control responses versus responses across all other treatments. This contrast also recognizes the 1 × 2 "hanging control group" nature of our design.

We conducted all analyses within a generalized linear modeling framework, in which parameters were estimated using restricted maximum likelihood techniques. This approach is more versatile than least squares, both in the range of response distributions that can be modeled and in its freedom from restrictive assumptions such as homoscedasticity (Agresti 1996). It also incorporates nonlinear (canonical) link functions, a point of potential importance in that it allows for nonlinear scaling of the probability distribution underlying subject response behaviors across stimulus treatments (Agresti 1996). We have no a priori grounds to expect that such scaling should be linear with respect to our treatments. We analyzed whether subjects reacted to the robots and the duration of those responses, by comparing the fit of variously parameterized models in analyses using binomial (logit-link) and normal (log-link) response distributions and link functions, respectively. Log-likelihood ratios were evaluated for significance against the chi-squared distribution with k-1 degrees of freedom, whereby k is the change in estimated parameters across models. Data were analyzed using Statistica v7.0.

RESULTS

Robots were presented in closely similar numbers of trials per treatment to 102 lizards (Table 2). Overall, 56 (55%) subjects responded by dewlapping, 41 (40%) by headbobbing, and 60 (59%) engaged in both behaviors. We found no evidence that treatment influenced a subject's probability of responding (Table 2). However, among the 60 subjects that did respond, treatment affected the duration of their dewlap pulsing (overall: $\chi^2_3 = 7.948$, $P < 0.05$; planned contrast: $\chi^2_1 = 7.839$, $P < 0.01$) but not their headbobbing response (overall: $\chi^2_3 = 2.120$, $P = 0.548$; planned contrast: $\chi^2_1 = 0.697$, $P = 0.404$). Individuals dewlapped in response to conspecific (control) displays significantly longer than to robot presentations in which either dewlap color or headbob display structure was altered (Figure 2C).

Table 2

Probabilities of live male *Anolis grahami* responding across the 4 robot treatments

Robot treatment	N	Probability of Response: Headbobbing	Probability of Response: Dewlap pulsing
1. Control	25	0.40	0.64
2. Light blue	27	0.37	0.63
3. Dark blue	27	0.30	0.41
4. Reverse headbob	23	0.56	0.52
Contrasts			
Overall		$\chi^2_3 = 3.902$, $P = 0.272$	$\chi^2_3 = 3.815$, $P = 0.282$
Planned (1 vs. 2 + 3 + 4)		$\chi^2_1 = 0.000530$, $P = 0.982$	$\chi^2_1 = 1.121$, $P = 0.290$

We measured lizard responses in terms of "headbobbing," in which the head and anterior trunk region are bobbed in a repeated "up–down" motion (also including 4-legged push-ups), and "dewlap pulsing," wherein the dewlap is sequentially extended and retracted in a pulsing manner.

DISCUSSION

Selection to avoid costly heterospecific interactions has favored a great diversity of complex, multicomponent species advertisement signals. One putative example is headbob display structure and dewlap coloration in anoline lizards (Williams and Rand 1977). These displays have long been argued to deliver multiple redundant cues for species recognition, particularly in areas of multispecies sympatry (e.g., Williams and Rand 1977), or where diverged species have established zones of secondary contact (e.g., Glor and Laport 2011). As suggested by Nicholson et al. (2007), although dewlap color variation in *Anolis* communities may be no greater than would be expected by chance, the diversity of extant dewlap color and headbob display patterns could easily facilitate species identification.

Here, we used a computerized robotic stimulus to demonstrate a unique social signaling role for dewlap color and headbob motion components of male *A. grahami* displays. Our artificial dewlap color treatments were designed, first and foremost, as manipulations of color (hue) independent of luminance (brightness), thus allowing assessment of the importance of these signal features to species advertisement. *Anolis* dewlaps are viewed under a broad range of intensities of down-welling

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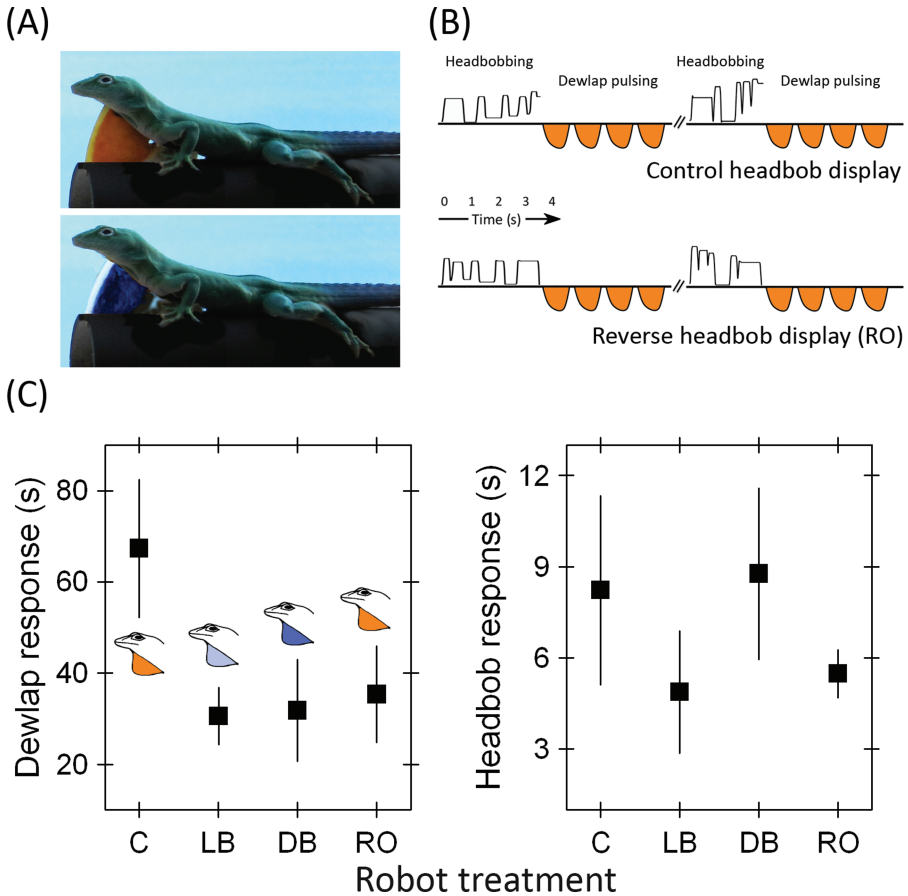

Figure 2

(A) Robots exhibiting the control (top) and dark blue (bottom) dewlap color treatments. (B) Normal (top) and reverse (bottom) headbob display patterns with dewlap pulses (orange semicircles below graphs). See text for details. (C) Dewlapping and headbobbing responses by subjects to the 4 experimental treatments: C = control: orange dewlap, normal headbob displays; LB = light blue dewlap, normal headbob displays; DB = dark blue, normal headbob displays; RO = orange dewlap, reverse headbob displays. Results shown are treatment group means ± 1 standard error.

and side-welling illumination, where overall luminance may vary greatly both within and among different viewing situations (e.g., Fleishman et al. 2009). We, therefore, expected that, at least over an ecologically reasonable range of viewing conditions, dewlap hue would offer a more salient visual signal of species identity (and henceforth elicit stronger test subject responses) than dewlap brightness. Our subjects responded with less dewlapping to both blue-dewlap treatments ("LB" and "DB"; Figure 2C) than to the control treatment ("C"; Figure 2C), irrespective of dewlap brightness. This result indicates, as predicted, that dewlap hue has a primary effect on species recognition in *A. grahami*.

Our subjects also responded with less dewlap pulsing to novel (reversed) than to control (normal) headbob displays, supporting a species recognition role for these stereotyped motion signals in our study species. Interestingly, this outcome mirrors results of earlier video presentations to male *A. grahami* (Macedonia and Stamps 1994). We are uncertain why dewlapping by subjects was a stronger indicator of conspecific signal recognition (both color and motion) than headbobbing, but fewer subjects responded with headbob displays than with dewlap pulses and among-subject variance in time spent headbobbbing was large in most treatments (Figure 2C).

By comparison, in another study using an anole robot, *A. sagrei* male subjects indicated their preference for the species' "signature" headbob display (versus a locally prevalent variant), not only with greater amounts of dewlap pulsing but also with 4-legged push-up displays (Partan et al. 2011). This was a strong effect, equivalent in magnitude to ours (Figure 2C), and was detectable in spite of characteristically large variance in individual display structure (Scott 1984; McMann 2000). In contrast, *A. gundlachi* does not display the dewlap independently of headbobs/push-ups, and Ord and Stamps (2009) found no evidence that adult males distinguished between robots that performed a conspecific headbob display or a novel (*A. grahami*) one. This apparent among-species difference in providing evidence of signal recognition is perplexing, but it seems unlikely to be coupled to whether or not a species uses the dewlap independently of its headbob/push-up displays.

At present, too few *Anolis* species have been subjected to experiments employing robotic anoles to make many generalizations. Nevertheless, our results indicate that *A. grahami* males are sensitive to substantial departures away from conspecific dewlap coloration and headbob display pattern, and that the significantly elevated dewlapping response of subjects to the control treatment is consistent with a species recognition interpretation. Our results demonstrate as well that perceived dewlap brightness is unlikely to explain the substantially reduced dewlapping response to our blue-dewlap treatments. As we were unable to include all possible combinations of dewlap and headbob display manipulations in this study, future research may shed additional light on our understanding of color and motion signal recognition, function, and evolution in anoles.

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