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Responses of *Anolis grahami* Males to Manipulations of Species Identity and Components of Displays in Lizard Robots

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Abstract: Many animal species use stereotyped displays to attract the opposite sex and to intimidate same-sexed rivals. Research aimed at understanding display recognition, function, and usage can be aided through the use of animal robots that allow one side of signaler–receiver interactions to be controlled. Manipulation of displays in ways that do not occur in nature has the potential to determine the boundaries of display recognition, as well as to provide insights into the manner in which animal display contests are structured. We describe two experiments that extend previous work on display recognition in the lizard *Anolis grahami*. In the first experiment, we used robots to determine the relative importance of body coloration and headbob display structure for species recognition. The results showed that subjects responded more strongly to robots having both conspecific appearance and display structure than to robots that deviated in those characteristics from the conspecific stimulus. In the second experiment, we explored the effect of removing display components on subjects' responses, where subjects witnessed a conspecific robot exhibiting a typical display (headbobs followed by dewlap pulses), or a deficient display consisting only of headbobs or dewlap pulses. Contrary to expectation, subjects in the headbobs-only treatment spent more time headbobbing than dewlapping in response; whereas, those in the dewlap-only treatment spent more time dewlapping than headbobbing. Interactive robots could be used in future investigations of the functions of different display components, as well as to examine the rules by which lizard display contests are conducted in nature.

Key words: Animal contests; Bermuda; Communication; Dewlap color; Headbob display; Signal function; Species recognition

Many remarkable examples of animal signals involve stereotyped performances of acoustic or visual displays used in species recognition, male agonistic competition, and mate attraction (e.g., Darwin 1871; Andersson 1994; Bradbury and Vehrencamp 2011). Given that animal displays often occur in contexts where the signaler and receiver interact, each individual might influence the actions of the other. Therefore, the ability to control the behavior of one participant in a dyad provides a powerful tool for studying display behavior. As dynamic models, robots can closely mimic the behavior of real animals and simultaneously achieve stimulus control. Moreover, robots permit manipulation of display characteristics beyond the limits of natural variation. Such manipulations facilitate explorations of display design and function that otherwise would be impossible to achieve.

Numerous genera of lizards are known to engage in visual displays of motion and color that convey information about species identity, territory ownership, condition, and reproductive state (e.g., Carpenter and Ferguson 1977; Cooper and Greenberg 1992; Ord and Stamps 2009). With its ~400 species, the genus *Anolis* has served as a showcase for the evolutionary diversification of visual displays, primarily through interspecific variation in headbob display structure and dewlap color patterns (e.g., Jenssen 1977; Macedonia and Clark 2003; Ord and Martins 2006; Nicholson et al. 2007; Losos 2009). In the present study, we add to research that has employed computerized robots to address questions about species recognition or assessment of display component function in *Anolis* (Ord and Stamps 2008, 2009; Partan et al. 2011; Macedonia et al. 2013) and *Sceloporus* (Martins et al. 2005; Smith and Martins 2006; Kelso and Martins 2008; Thompson et al. 2008; Nava et al. 2012).

Our previous findings showed that adult male *Anolis grahami* exhibited a stronger "dewlapping" response (repeated extensions and retractions of a throat fan) to a robot exhibiting both conspecific headbob display structure and dewlap coloration, than to robots where either of those traits was altered (Macedonia et al. 2013). Here, we describe two experiments that extend this earlier research. In Experiment 1, we tested the relative importance of species-specific appearance versus headbob display structure for species recognition in *A. grahami*. In Experiment 2, we examined how displays having only one of two components (headbob displays or dewlap pulses) affects subjects' responses, compared with displays containing both components.

Materials and Methods

Subjects and Study Area

Our study species, *A. grahami,* has been resident on Bermuda since it was introduced from Kingston, Jamaica, in 1905 (Wingate 1965). This species frequently occurs together with one or two other naturalized *Anolis* species—*A. extremus* from Barbados and *A. leachi* from Antigua and Barbuda—both of which appear to have been unintentionally introduced to Bermuda in the early to mid-1940s (Wingate 1965; Losos 1996; Macedonia and Clark 2003). Adult male *A. grahami* and *A. extremus* are similar in size (~65–70 mm snout–vent length [SVL]) and ecology, but differ in thermal preference: whereas *A. grahami* prefers direct sun, *A. extremus* prefers shade; in contrast, *A. leachi* is a larger, heliophilic species (~90–100 mm SVL; Schoener 1970; Losos 1996; Macedonia and Clark 2003).

Robot Construction

Body and dewlap creation.—We constructed a conspecific robot body and dewlap to resemble our study species,

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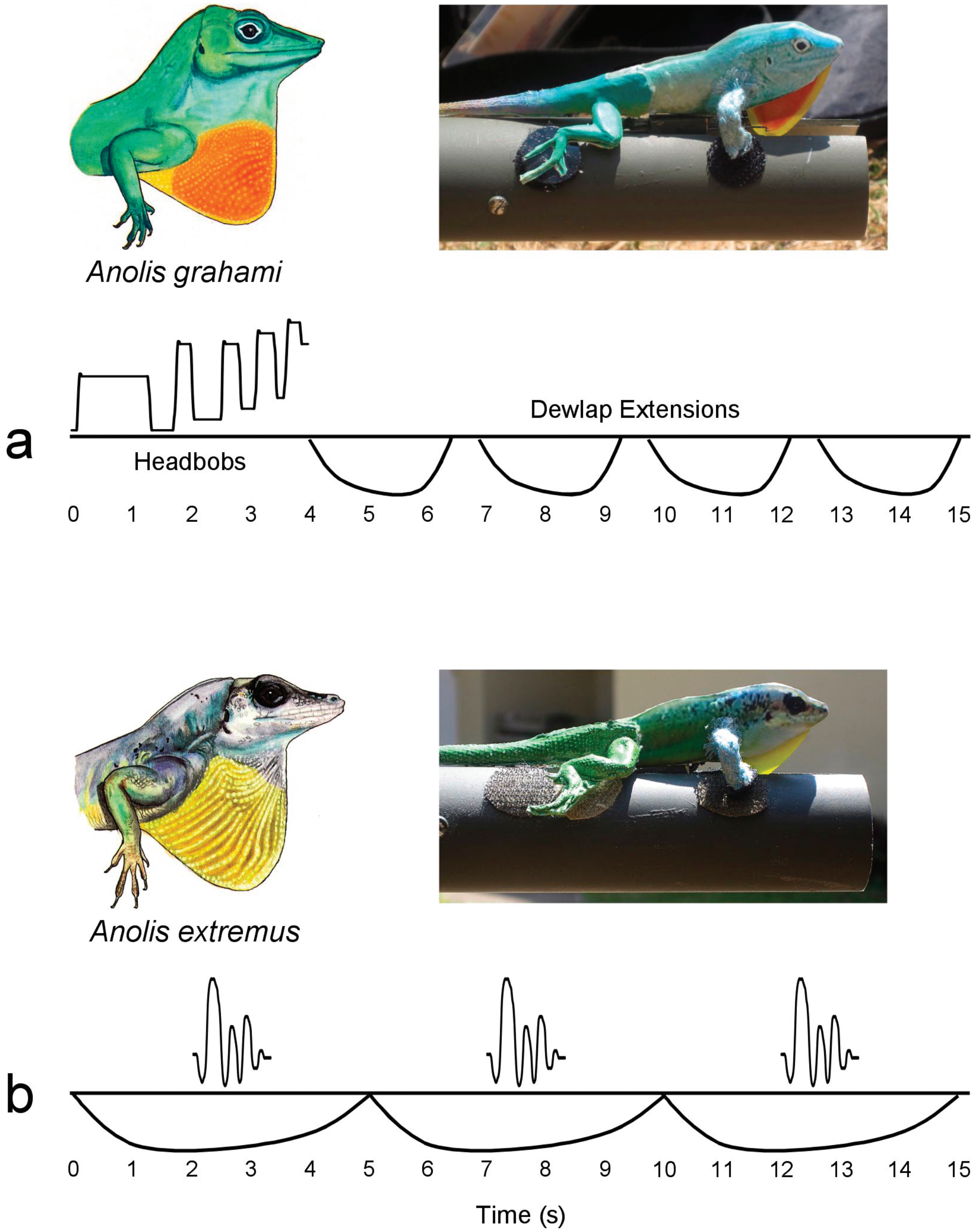

FIG. 1.—(a) Illustration of *Anolis grahami* coloration with photo of *A. grahami* robot (above), and *A. grahami* robot headbob and dewlap display (below). (b) Illustration of *Anolis extremus* with photo of *A. extremus* robot (above) and *A. extremus* robot headbob and dewlap display (below). Relative head amplitude (y-axis) is plotted against time (x-axis). *Anolis* portrait illustrations modified from Schwartz and Henderson (1985).

A. grahami, as well as a heterospecific robot body and dewlap to resemble *A. extremus*. Excluding the hind limbs and tail of each robot, which were made of airbrushed latex cast from lizard specimens (see Macedonia et al. 2013), each robot body was carved from a thick wooden dowel and attached to a servomotor pushrod. Anterior to the hind limbs, robots were covered with an image created in Adobe Photoshop® from photos of the study species (Fig. 1). These images were mirrored and joined together at the body midline. Final images were printed onto adhesive-backed fabric and molded around the wooden body, which, together with the latex hindquarters, was attached to the polyvinyl chloride (PVC) perch. Dewlaps were fashioned from white, semitransparent guitar picks that fit into a slot carved in the neck of the robot body. A small hole that was drilled into the guitar pick was secured to a hinge pin that allowed it to pivot and extend. A second small hole in the pick allowed insertion of a thin wire that was attached to the pushrod, which in turn was attached to a servomotor.

Artificial dewlap coloration.—To create the dewlap color patterns for *A. grahami* (orange dewlap with yellow edge) and *A. extremus* (solid yellow), we used the same orange and yellow permanent markers that had been applied to white, modified guitar picks in a prior robot experiment (i.e., Macedonia et al. 2013). Although the simulated dewlap colors differ somewhat in spectral shape from the actual dewlap

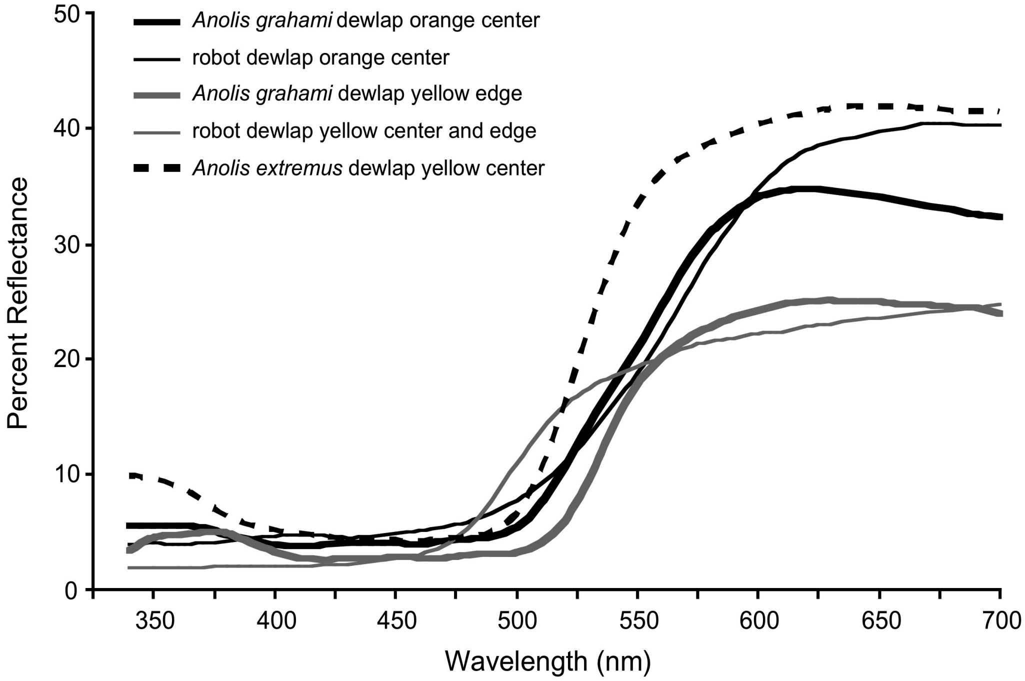

FIG. 2.—Reflectance spectra of *Anolis grahami* and *A. extremus* actual dewlaps and artificial robot dewlaps. Center and edge samples from actual males' dewlaps are means: *A. grahami* dewlap center (n = 23) and edge (n = 9), *A. extremus* dewlap center (n = 8). Artificial dewlap spectral curves are single samples. For details on the acquisition of these spectra, see Macedonia et al. (2013).

colors (Fig. 2), the choice of markers was based on the perceived intensities of the colors to our subjects, as determined using a computational model of *A. grahami* spectral sensitivity (see Macedonia et al. 2013 for details). The inks used to create the artificial dewlap colors reflected an amount of ultraviolet light similar to the dewlaps of both *A. grahami* and *A. extremus* (~10% or less at 350 nm; Fig. 2).

Hardware.—Two servomotors (Futaba S9001), housed inside a camouflage-painted plastic box, independently controlled headbob motion and dewlap extension or retraction in the robots (photos in Fig. 1). Commands were sent to the servomotors via a Midi v1.2 control board, which was secured within the housing. A PVC pipe, extending forward from the housing, held pushrods that were attached to the servomotors and to the robot. The robot and control system were powered with a Lithium-ion battery.

Headbob display programming.—Robots were programmed with midi controller data to perform headbob displays and dewlap extensions or retractions, which were based on mean values from display analyses in Macedonia and Clark (2003). *Anolis grahami* performs asynchronous displays (sensu Ord et al. 2013), in which headbobbing and dewlapping exhibit little overlap in time (Fig. 1a). In this species, a headbob display is followed by a series of dewlap pulses, although one or more dewlap pulses might precede the initiation of headbobbing (see fig. 1 in Macedonia and Stamps 1994). In addition, *A. grahami* exhibits two variants of the headbob display (Type A and Type B) that differ primarily in interbob pause durations (see Jenssen 1981; Macedonia and Clark 2003). We chose the Type A form for our conspecific robot displays, because this display type is performed in all display contexts (male alone, male–male, and male–female); thus, it fits the definition of a species-typical signature display (e.g., Jenssen 1978). The robotic *A. grahami* display lasted 15 s and consisted of a headbob display (~4 s) followed by four dewlap pulses (~11 s) and a 15-s pause (Fig. 1a). This sequence was repeated twice per minute for 10 min. The other stimulus species, *A. extremus,* performs synchronous displays (sensu Ord et al. 2013), in which the dewlap is slowly extended and held open during the brief headbob display, and then is retracted (Fig. 1b). In contrast to *A. grahami, A. extremus* exhibits only one type of headbob display (Macedonia and Clark 2003). Our *A. extremus* robot display began with a dewlap extension that lasted ~2 s before the brief (~1 s) headbob display was performed, which was followed by the slow retraction (~2 s) of the dewlap (Fig. 1b). A series of three consecutive 5-s displays, followed by a 15-s pause, was repeated 2×/min for 10 min. Total display time therefore was the same for both species (i.e., 5 min of display over a 10-min trial period).

Robot presentation protocol.—Adult male *A. grahami* (≥60 mm SVL) were located by scanning tree trunks for territorial individuals in the head-down survey posture (e.g., Stamps 1977). Once a suitable male was found, the stimulus robot, secured to a tripod, was moved to a position ~2 m from the subject. A video camera was secured to another tripod and set ~2 m behind the robot such that, when possible, the subject and robot stimulus could be seen together in the video frame. During this time period, the experimenters moved slowly and carefully so as not to alarm the subject. If preparation for a trial (~5 min) did not cause the subject to flee or display, the trial was initiated by triggering the robot's display sequence from a laptop computer. Subjects were recorded for 12 min from the start of the presentation, unless the subject fled or some other event required early termination of a trial. Choice of stimulus was based on a predetermined constrained random approach—the presentation order of the four robotic stimuli to four consecutive subjects was randomized, with each

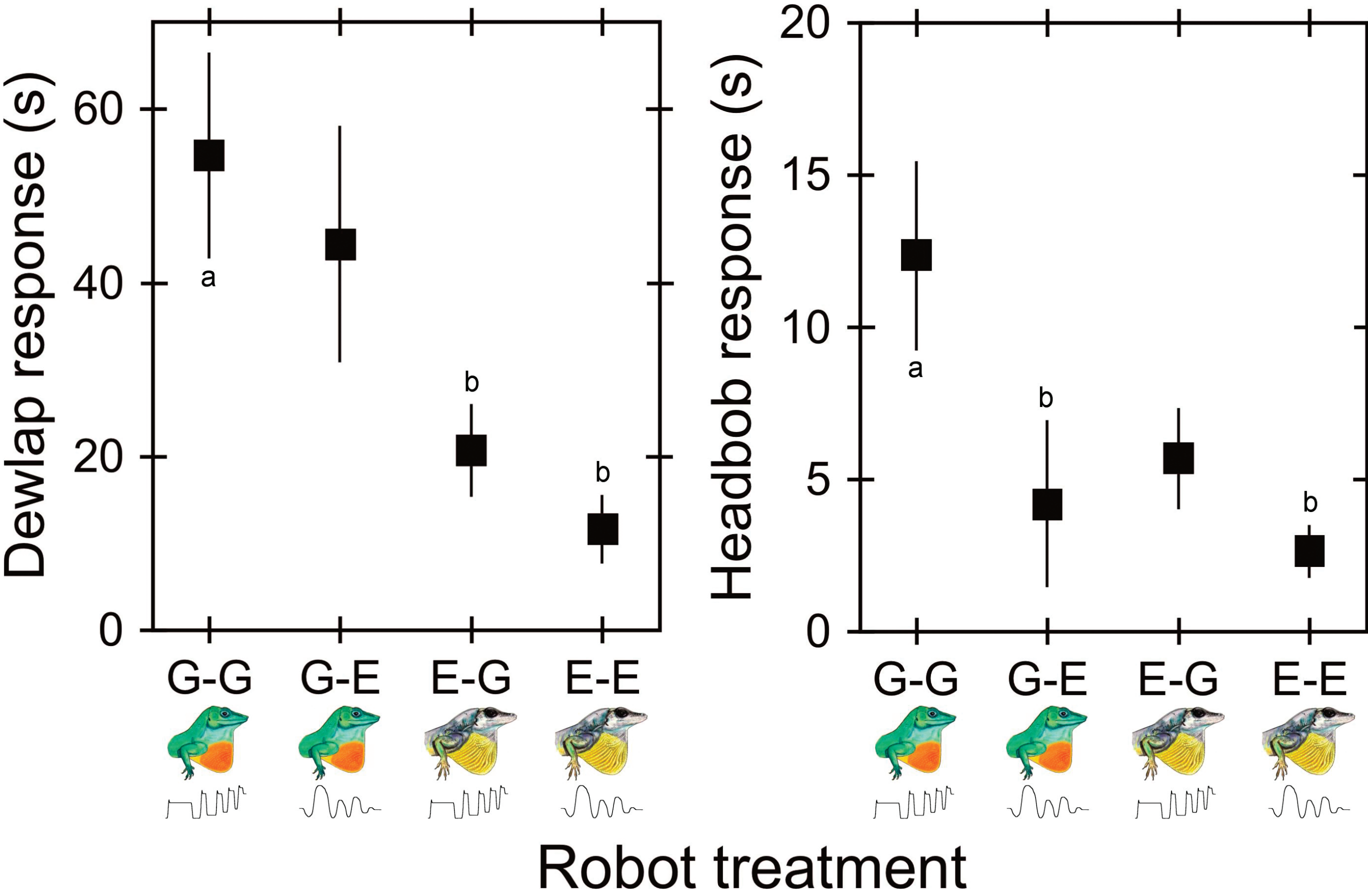

FIG. 3.—Dewlap (left) and headbob (right) responses to the four robot treatments in Experiment 1. The durations that subjects spent performing each response are reported means ± 1 SE (whiskers). Values with different letters are significantly different at $P < 0.005$ for the dewlap response, and $P < 0.05$ for the headbob response. X-axis labels: first letter denotes species represented by robot body, and second letter denotes species' display (e.g., G–E = *Anolis grahami* body and dewlap performing *A. extremus* display characteristics).

subject being tested with one stimulus type only. This process was repeated for each block of four subjects. We conducted most of our robot presentations in nature parks and along the Old Railway Trail, where subjects were relatively abundant, and where we could carry out experimental trials without much disturbance.

Experimental Design

Experiment 1 quantified subject display behavior in response to different combinations (conspecific versus heterospecific) of body and display characteristics. Our four treatments included (1) *A. grahami* body with *A. grahami* display (G–G); (2) *A. grahami* body with *A. extremus* display (G–E); (3) *A. extremus* body with *A. grahami* display (E–G); and, (4) *A. extremus* body with *A. extremus* display (E–E; Fig. 1). We predicted that the less similar a robot appeared to, or displayed like, a conspecific male, the less responsive subjects would be, in the order as follows: G–G > G–E or E–G > E–E. We had not used a heterospecific robot body in previous work; therefore, we made no prediction about the relative strength of subject responses to a conspecific body with a heterospecific display versus a heterospecific body with a conspecific display. In Experiment 2, we examined the independent influences of conspecific headbob and dewlap displays on subject responses. We predicted that a conspecific display, which typically includes a headbob display followed by a series of dewlap pulses (H + D treatment), would elicit more responses from subjects when compared with presentations of either headbob-only displays or dewlap-pulses-only displays. (See video clips of displays performed by robot models in the Supplementary Materials available online).

Statistical analysis.—We used durations of dewlapping and headbobbing as response measures, both of which were log-transformed prior to analysis to satisfy assumptions of normality. For both experiments we ran one-way analyses of variance (ANOVA) on each of the two measures to detect the treatment effects on subject responses. Subsequent pairwise comparisons were made with protected Tukey Honestly Significant Difference tests. Statistical tests were conducted with SPSS (v21.0, IBM Inc., Armonk, New York).

RESULTS

Experiment 1

Of 145 adult male lizards that received robot presentations, 67 subjects ($\overline{X}$ + SE; 16.8 + 2.3 subjects per treatment) responded either with dewlap pulsing, headbob displays, or both. One-way ANOVAs indicated significant main effects of treatment on durations of subject dewlapping ($F_{3,63} = 6.46$, $P < 0.001$) and headbobbing ($F_{3,24} = 4.93$, $P = 0.008$) responses. Results of protected post hoc tests revealed significant differences in the duration of subject dewlapping between the conspecific body with conspecific display (G–G), and both treatments with the heterospecific body (E–G

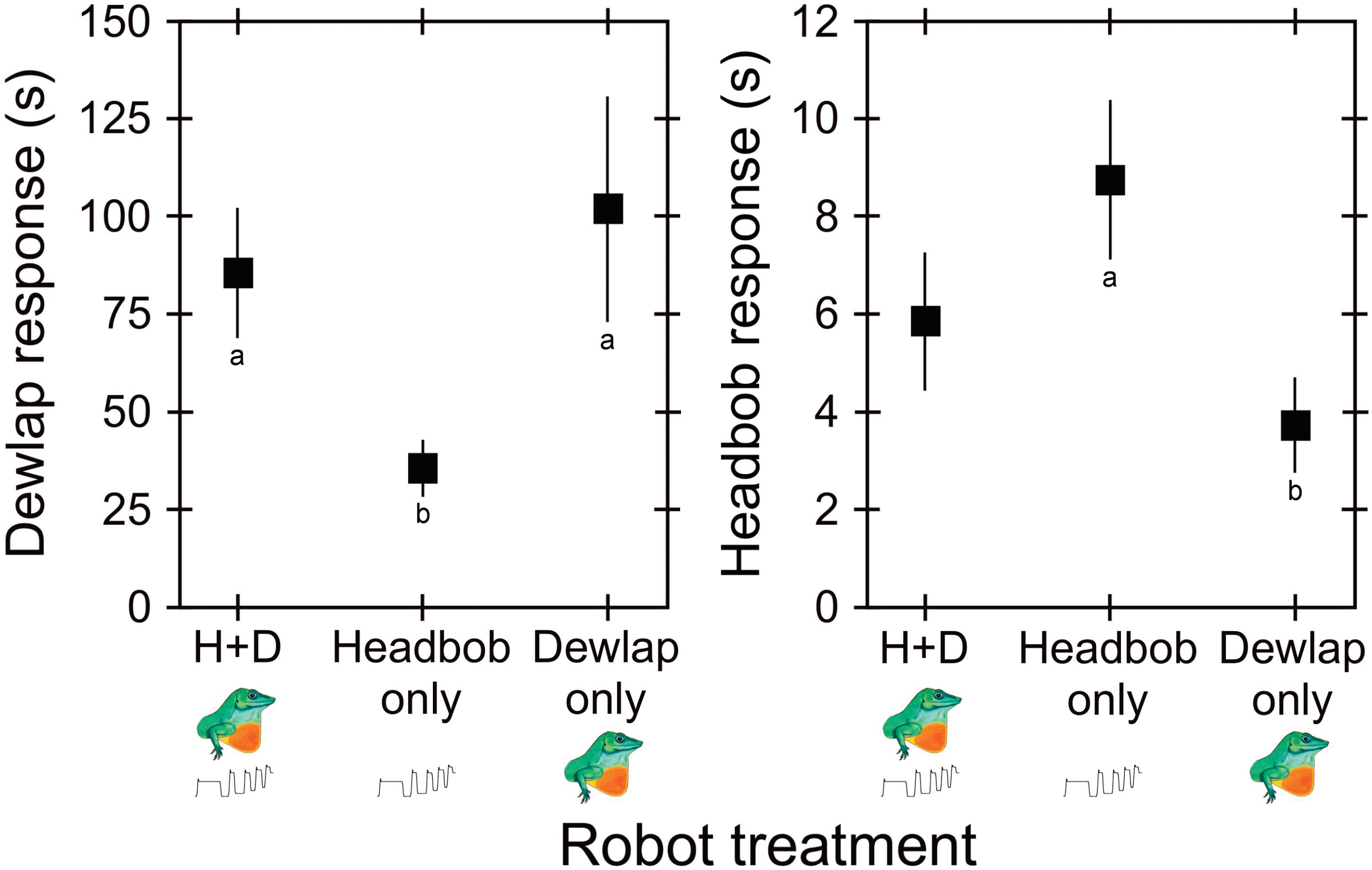

FIG. 4.—Duration of dewlap (left) and headbob (right) responses to the three *Anolis grahami* robot treatments in Experiment 2: H + D (headbob plus dewlap display), Headbob (headbob only), and Dewlap (dewlap only). Values are reported as means ± 1 SE (whiskers), with letters indicating significant differences at $P < 0.01$.

and E–E); values in other pairwise comparisons were similar (Fig. 3). Durations of subject headbobbing differed significantly between the G–G treatment and the two treatments with the heterospecific headbob display (E–G and E–E); values in other pairwise comparisons were similar (Fig. 3).

Experiment 2

Of 112 adult male lizards that received robot presentations, 66 subjects ($\overline{X}$ + SE; 21.0 + 4.0 subjects per treatment) responded with dewlap pulses, headbob displays, or both. One-way ANOVAs revealed significant main effects of treatment on durations of dewlapping ($F_{2,60} = 6.46$, $P = 0.003$) and headbobbing ($F_{2,23} = 3.77$, $P = 0.04$). Interestingly, whereas subjects in the headbob-only treatment spent more time headbobbing than dewlapping, subjects in dewlap-only treatment spent more time dewlapping than headbobbing (Fig. 4).

Discussion

Experiment 1

The results of Experiment 1 were consistent with our hypothesis that subjects would respond more strongly to the conspecific robot with conspecific display than to experimental stimuli with heterospecific display and/or appearance. Results also tended to follow our specific prediction that subject responses would decrease with decreasing stimulus similarity to the full conspecific treatment (G–G), although the response means of only a few of the pairwise comparisons were different (Fig. 3).

In an earlier experiment, we showed that subjects exposed to a conspecific robot performing reversed headbob display structure responded with fewer dewlap extensions than subjects presented with a normal display structure (Macedonia et al. 2013). Therefore, we anticipated that subjects in this study would perform fewer dewlap extensions to a robot with a conspecific body and a heterospecific headbob display (G–E). Although the G–E treatment did evoke less dewlapping in subjects than did the G–G treatment, variance in response to both treatments rendered them statistically similar (Fig. 3). Nevertheless, dewlapping by subjects in response to the G–G treatment was greater than to the E–G or E–E treatments (Fig. 3).

The failure to show strong discrimination in subject dewlapping responses between the G–G and G–E treatments might have resulted from our use in this stimulus of the *A. extremus* dewlap motion pattern rather than the *A. grahami* dewlap motion pattern. In *A. extremus,* the dewlap is extended prior to the initiation of the headbob display and is retracted only after the headbob display is completed; in contrast, *A. grahami* usually does not extend the dewlap during the headbob display, but instead performs a variable number of dewlap pulses following the headbob display (see video clips in the Supplementary Materials available online). As a consequence, subjects witnessing the G–E stimulus saw the *A. grahami* dewlap 1.7 times longer (15 s total) than they did for the full conspecific (G–G) stimulus (9 s total). Given that *A. grahami* attends strongly to the dewlap (see Macedonia et al. 2013), it seems possible that increased duration of dewlap visibility in the G–E treatment could have resulted in increased responsiveness of subjects to this stimulus.

Experiment 2

This experiment explored the influence of separate and combined display components on subject responses. We hypothesized that subjects would display more to the conspecific robot performing a typical display sequence (headbob display followed by dewlap pulses) than to the headbob-only or dewlap-only treatments. Contrary to expectation, subjects witnessing only one display component (either headbobs or dewlap extensions) responded more with that same component than did subjects exposed to the robot performing both display components. This outcome indicates that *A. grahami* males might take into account a bias in the use of headbob displays or dewlap extensions by an opponent (cf. Tokarz et al. 2003). This finding invites further study in which a more interactive robot stimulus is used. In our experiments, the sequence and timing of displays performed by the stimulus robots followed a script that, once set in motion, continued to completion without influence from subjects. Other researchers have used the same technique of presenting lizard robots with preprogrammed displays to investigate issues ranging from recognition of display pattern to effects of display syntax, learning, and sex on subjects' responses (e.g., Smith and Martins 2006; Nava et al. 2012). A fundamental characteristic of animal contests, however, is that they frequently take the form of escalating sequential assessments where one opponent's behavior is influenced by that of its challenger (reviewed in Arnott and Elwood 2009).

To date, use of an interactive experimental paradigm in which the display of a stimulus lizard is based on the previous response of a subject, has been limited to video playbacks with Jacky Dragons (*Amphibolurus muricatus* [e.g., Ord and Evans 2002; Van Dyk and Evans 2008]). These studies have progressed the understanding of the dynamics of lizard display contests by varying the display of a stimulus lizard to be aggressive, submissive, or matched to a subject's behavior. Interactive robots could provide the same level of stimulus control while circumventing problems arising from interspecific differences in spectral sensitivities (e.g., Fleishman et al. 1998; Fleishman and Endler 2000). Moreover, whereas video playbacks are difficult to conduct under field conditions (although see Clark et al. 1997), interactive robots are ideal for investigating the rules by which sequential assessment in lizard contests is structured in nature.

In sum, our results have shown that *A. grahami* male subjects are sensitive to both the species identity of a challenger and the structure of its displays. In addition, responses of subjects in our second experiment indicate that contestants might bias their use of display components in the direction of a component bias in a challenger's displays. Although the significance of this apparent bias is not yet clear, using interactive robots might further elucidate the rules by which display contests are structured and opponents are sequentially assessed in lizards and other animals.

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Supplementary Data

Supplementary material associated with this article can be found online at http://dx.doi.org/10.1655/Herpetologica-D-14-00044.S1.

Literature Cited

Andersson, M. 1994. Sexual Selection. Princeton University Press, USA.

Arnott, G., and R.W. Elwood. 2009. Assessment of fighting ability in animal contests. Animal Behaviour 77:991–1004.

Bradbury, J.W., and S.L. Vehrencamp. 2011. Principles of Animal Communication, 2nd edition. Sinauer Associates, Inc., USA.

Carpenter, C.C., and G.W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles. Pp. 335–554 in Biology of the Reptilia, vol. 7, Ecology and Behaviour, A.C. Gans and D.W. Tinkle (eds.), Academic Press, USA.

Clark, D.L., J.M. Macedonia, and G.G. Rosenthal. 1997. Testing video playback to lizards in the field. Copeia 1997:421–423.

Cooper, W.E., and N. Greenberg. 1992. Reptilian coloration and behavior. Pp. 298–422 in Biology of the Reptilia, vol. 18: Physiology, E, Hormones, Brain and Behavior (C. Gans and D. Crews, eds.). University of Chicago Press, USA.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. Murray, UK.

Fleishman, L.J., and J.A. Endler. 2000. Some comments on visual perception and the use of video playback in animal behavior studies. Acta Ethologica 3:15–27.

Fleishman, L.J., W.J. McClintock, R.B. D'eath, D.H. Brainard, and J.A. Endler. 1998. Colour perception and the use of video playback experiments in animal behaviour. Animal Behaviour 56:1035–1040.

Jenssen, T.A. 1977. Evolution of anoline lizard display behavior. American Zoologist 17:203–215.

Jenssen, T.A. 1978. Display diversity in anoline lizards and problems of interpretation. Pp. 268–285 in Behavior and Neurology of Lizards: An Interdisciplinary Conference (N. Greenberg and P.D. Maclean, eds.). National Institutes of Mental Health, USA.

Jenssen, T.A. 1981. Unusual display behavior by *Anolis grahami* from Western Jamaica. Copeia 1981:728–733.

Kelso, E.C., and E.P. Martins. 2008. Effects of two courtship display components on reproductive behaviour and physiology in the sagebrush lizard. Animal Behaviour 75:639–646.

Losos, J.B. 1996. Dynamics of range expansion by three introduced species of *Anolis* lizards on Bermuda. Journal of Herpetology 30:204–210.

Losos, J.B. 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. University of California Press, USA.

Macedonia, J.M., and D.L. Clark. 2003. Headbob display structure in the naturalized *Anolis* lizards of Bermuda: Sex, context, and population effects. Journal of Herpetology 37:266–276.

Macedonia, J.M., and J.A. Stamps. 1994. Species recognition in *Anolis grahami* (Sauria: Iguanidae): Evidence from responses to video playbacks of conspecific and heterospecific displays. Ethology 98:246–264.

Macedonia, J.M., D.L. Clark, R.G. Riley, and D.J. Kemp. 2013. Species recognition of color and motion signals: Evidence from responses to lizard robots. Behavioral Ecology 24:846–852.

Martins, E.P., T.J. Ord, and S.W. Davenport. 2005. Combining motions into complex displays: Playbacks with a robotic lizard. Behavioral Ecology and Sociobiology 58:351–360.

Nava, S.S., L. Moreno, and D. Wang. 2012. Receiver sex differences in visual response to dynamic motion signals in *Sceloporus* lizards. Behavioral Ecology and Sociobiology 66:1357–1362.

Nicholson, K.E., L.J. Harmon, and J.B. Losos. 2007. Evolution of *Anolis* lizard dewlap diversity. PLoS One 2:1–12. DOI: 10.1371/journal.pone.0000274.

Ord, T.J., and C.S. Evans. 2002. Interactive video playback and opponent assessment in lizards. Behavioural Processes 59:55–65.

Ord, T.J., and E.P. Martins. 2006. Tracing the origins of signal diversity in anole lizards: Phylogenetic approaches to inferring the evolution of complex behaviour. Animal Behaviour 71:1411–1429.

Ord, T.J., and J.A. Stamps. 2008. Alert signals enhance animal communication in "noisy" environments. Proceedings of the National Academy of Sciences (USA) 105:18830–18835.

Ord, T.J., and J.A. Stamps. 2009. Species identity cues in animal communication. American Naturalist 174:585–593.

Ord, T.J., J.A. Stamps, and J.B. Losos. 2013. Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean *Anolis* lizards. Animal Behaviour 85:1415–1426.

Partan, S.R., P. Otovic, V.L. Price, and S.E. Brown. 2011. Assessing display variability in wild brown anoles *Anolis sagrei* using a mechanical lizard model. Current Zoology 57:140–152.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

Schwartz, A., and R.W. Henderson. 1985. A Guide to the Identification of the Amphibians and Reptiles of the West Indies, Exclusive of Hispaniola. Milwaukee Public Museum, USA.

Smith, C.B., and E.P. Martins. 2006. Display plasticity in response to a robotic lizard: Signal matching or song sharing in lizards? Ethology 112:955–962.

Stamps, J.A. 1977. The function of the survey posture in *Anolis* lizards. Copeia 1977:756–758.

Thompson, J.T., A.N. Bissell, and E.P. Martins. 2008. Inhibitory interactions between multimodal behavioural responses may influence the evolution of complex signals. Animal Behaviour 76:113–121.

Tokarz, R.R., A.V. Paterson, and S. McMann. 2003. Laboratory and field test of the functional significance of the male dewlap in the lizard *Anolis sagrei*. Copeia 2003:502–511.

Van Dyk, D.A., and C.S. Evans. 2008. Opponent assessment in lizards: Examining the effect of aggressive and submissive signals. Behavioral Ecology 19:895–901.

Wingate, D.B. 1965. Terrestrial herpetofauna of Bermuda. Herpetologica 21:199–219.

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