

Assessing display variability in wild brown anoles *Anolis sagrei* using a mechanical lizard model

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Abstract Signals used for species identity ought to be highly stereotyped so as to facilitate immediate recognition by conspecifics. It is surprising therefore to find variability in putative species signature displays. The brown anole *Anolis sagrei* has a high degree of variability in its signature bobbing display. In this study we collected descriptive data on variability in the temporal structure of wild brown anole bobbing patterns, finding that no two displays analyzed had the same temporal structure, and we also tested whether wild brown anoles prefer the signature display over an alternate display pattern by using mechanical robot playbacks in the field. As a response metric we assessed whether or not the lizards showed social responses (pushup, dewlap extension, or head-nod) in response to the robotic presentations. We found that the lizards responded slightly more to the signature than to the alternate pattern, providing support for the idea that despite the variability seen in displays, the signature pattern is meaningful to them. We tested two other independent variables: speed of the display and elevation of the robot during its display, neither of which was significant. Dewlap extensions were given predominantly by adult males and were more likely to be given in the breeding season than the nonbreeding season. Pushups and head-nods were given equally by males and a combined class of females and juveniles, and were not seasonal. Head-nods increased after the robot turned off, suggesting that they may be used in a conversational turn-taking style during communication [*Current Zoology* 57 (2): 140–152, 2011].

Keywords Species recognition, Ethorobotics, Visual signals, Territoriality, Signature display, Sex differences

One function of communication in animals is for species identity. Correct identification of species is important for individuals to find appropriate mates and to direct aggressive and affiliative social signals toward appropriate receivers. Species identity can be advertised in myriad ways, commonly involving vocal, visual or chemical signals. We expect that species-specific behaviors that are involved in species identity will be highly stereotyped across individuals and populations, to facilitate correct signal recognition. It is surprising, therefore, to find a species for which the putative signature display is not stereotyped. Anole lizards are a case in point. The best-studied anoles have highly stereotyped species-specific displays, called signature patterns (Jenssen, 1971; Stamps and Barlow, 1973; Jenssen, 1977). At least one species of anole, however, has such a high degree of variability in display behavior that it cannot be said to have a signature pattern (*Anolis opalinus*; Jenssen, 1979). In this case it has been proposed that selection for a species signature was relaxed due to evolved changes in body size and morphology that served to identify species without reliance on be-

havior (Jenssen, 1979). In the current study we examine the display behavior of the brown anole *Anolis sagrei* for which a signature pattern has been reported (Scott 1984) but which, like *A. opalinus*, has so much variability in display behavior that a reevaluation of the importance of the signature pattern is warranted.

Communication displays of many species of Anoline lizards have been extensively documented since the pioneering work of Evans (1938), Carpenter and Grubitz (1961), Jenssen (1971), Stamps and Barlow (1973), and Crews (1975). The typical display involves a series of rapid movements in which the head and/or the body is jerked quickly up and down with a particular temporal pattern. These movements can be graded, from only head movement to the bending of the front legs or of all four legs in synchrony. The displays are variously termed “headbob,” “bob,” or “pushup” displays (we will use the latter term) and are used in territorial defense, courtship, and aggression (Scott, 1984; Martins, 1993; Decourcy and Jenssen, 1994; Paterson, 2002). Much individual variability has been observed in display behavior, and in some species the variability within an

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individual is even greater than that between individuals (Jenssen, 1978, 1979; Macedonia and Clark, 2003; reviewed by Scott, 1984). Signature displays can be stereotyped across a number of variables, including the number of bobs, the duration and amplitude of each bob, the duration of the intervals between bobs, the length of the pause between display series, and how many series are performed in sequence. In addition to the signature display, lizards have other non-species-specific displays, such as head nodding and postural changes (McMann, 2000; Macedonia and Clark, 2003).

Animal communication displays can be studied by observing natural behavior or by simulating the display and recording subjects' reactions to these simulations. From the reactions we can begin to infer the function of the display. Stimuli used in experimental simulations of visual displays have varied from two-dimensional cut-outs or dummies (Tinbergen, 1948; see Rowland 1999 for review) to video playbacks (Rosenthal, 1999; Uetz and Roberts, 2002) and computer animation (Woo and Rieucou, 2008) to mechanized 3-dimensional models or "robots" of the animal display that are presented to live recipients (Michelson et al., 1992; Patricelli et al., 2002, 2006; Narins et al., 2003, 2005; Partan et al., 2009, 2010; see below for references to lizard robots).

Ethorobotics (the use of robotic or mechanical animals to study animal behavior, Partan, 2004) provides a useful method for the study of communication for many reasons. Most obviously, robots are three dimensional, providing an opportunity for recipients to perceive shadows and other depth cues, and they can be easily presented in a field setting, where high ambient light levels may preclude the use of other playback techniques aimed at visual systems, such as video playback (although see Clark et al., 1997). With a computer-controlled robot, as with computer animation, we can create new strings of behaviors in orders and combinations that, while they may occur naturally, may be rare or difficult to catch on recorded media. Multiple sources of information can also be varied systematically to test the function of the variations. Visual displays, for example, can be manipulated along dimensions of color and shape, as well as amplitude, speed and pattern of movement, and they can be combined with audio signals from embedded speakers. Such manipulations allow researchers to tease apart how multiple components of display contribute to overall display function, which is important to our understanding of how animals use complex displays (Partan and Marler, 2005).

Early work with lizard dummies was done by Hunsaker (1962), who made wooden models of lizards in the *Sceloporus torquatus* group. He reported anecdotally that males in breeding condition would respond to models that were bobbed up and down in a courtship display pattern. Hunsaker (1962) went on to create a mechanized plastic lizard model of *Sceloporus mucronatus*, with a motor and cam that moved the model up and down. He gave seven females the choice of approaching a model that bobbed in a species-typical pattern or a model that bobbed randomly. They all preferred the former, supporting the hypothesis that bobbing patterns are important in species recognition.

More recently researchers have successfully used mechanical or robotic lizards to elicit reactions from lizards both in the lab (Martins et al., 2005; Smith and Martins, 2006, both with sagebrush lizards *Sceloporus graciosus*) and in the field. Thompson et al. (2008) studied the reactions of wild *S. graciosus* to presentations of a robotic lizard model that were paired on some trials with chemical signals. Ord and Stamps (2008, 2009) studied species recognition and the effect of visual background noise on display structures of *Anolis gundlachi*, also using a robotic lizard model in the field.

The displays of the brown anole *Anolis sagrei* show a high degree of variability along a number of dimensions. However, it has been suggested by Scott (1984) that despite this variability, *A. sagrei* does have a species-specific signature display pattern; she found that out of 24 territorial displays shown by three males, 12 of the displays were the signature pattern. The other half were variations on the pattern involving more or fewer bobs at various points in the display, including some variability in timing of long and short bobs. Scott (1984) also reported that out of seven courtship displays documented, only one of them was the signature display. There was, therefore, much variability, with fewer than 50% of *A. sagrei* displays having the signature pattern. Scott's (1984) study site was located just 50 km north-east of our site (although by land it would be approximately 75 km because our site, in Saint Petersburg, FL, is on a peninsula), so we expected to find similar patterns and variations in our population.

There have been remarkably few quantitative studies of variability in *A. sagrei* display patterns since Scott's (1984) work. A notable exception is the work of McMann (2000) who described head nodding and bobbing displays in *A. sagrei* on artificial habitats at another Florida site (approximately 400 km southeast of our

site). He also presented a Display-Action-Pattern (DAP) graph of a bobbing display for *A. sagrei*, which depicted the same temporal bobbing pattern as Scott's (1984) signature pattern, albeit with a slightly slower overall timescale, but he did not report data on frequency of occurrence of this display. McMann (2000) reported variability in the number of bobs included in bobbing displays (means ranged from 2 to 14 bobs), but he did not report data on variability in terms of temporal patterns of bobbing within the display.

The main goal of our study was to determine whether the putative signature pattern of brown anoles is recognized in our population and responded to preferentially above other display variations. We also assessed the efficacy of using a mechanical lizard model to elicit social responses from brown anoles in the field, as well as collected data on natural signal structure in this population. To test signature display recognition, we compared responses of wild lizards to two display patterns: the species signature pattern described by Scott (1984) and McMann (2000), and a second, nonsignature pattern we observed locally at our field site. We constructed a mechanical lizard model and programmed it with the two display patterns. Our goal was to compare the efficacy of the two patterns in eliciting social responses (head-nods, pushups, dewlap displays) from conspecifics. We hypothesized that if the species-specific signature pattern described by Scott (1984) is important in our population of lizards, the lizards would respond more strongly to this pattern than to the alternative. If we found no difference, this could call into question the longevity or generalizability of the signature pattern, with implications for the evolution of species recognition displays.

1 Materials and Methods

1.1 Subjects, location, time of year

The subjects were wild brown anoles *Anolis sagrei*. We conducted tests on and around the University of South Florida Saint Petersburg campus in St. Petersburg, Florida. Lizards were unmarked. We reduced the likelihood of resampling the same individuals by moving to a new location, at least 10 m away, for each new test. *A. sagrei* home ranges are fairly small in the Bahamas, averaging 3.7 m² for females and 17.6 m² for males (Schoener and Schoener, 1982), although they are larger in Cuba, approximately 37 m² (Evans, 1938). Since our field sites in Florida were located in developed areas on a college campus and nearby streets, many of the testing locations were along hedgerows and other narrow linear

habitat strips. Scott (1984) saw brown anoles along fences and hedgerows in Florida at approximately 6 m intervals, so we estimate that our 10-m sampling rule was sufficient to avoid resampling individuals.

We ran a set of trials for every solitary brown anole that we found, regardless of its age or sex. Adult males were large and dark, often had dorsal and/or nuchal crests, and had comparatively large and colorful dewlaps. Females and juveniles of both sexes were difficult to distinguish from one another and therefore were pooled together. They were smaller and less dark than adult males, and their backs often had a white stripe down the center and sometimes a diamond-shaped pattern.

We collected data for one year, from July 2005 through June 2006, in every month except December. Because some months had fewer data points than others, we lumped months for analysis into two 6-month seasons: the breeding season, March–August, and the non-breeding season, September–February. These seasonal designations are based on Lee et al. (1989), who found testis mass of *A. sagrei* in Florida to be higher from March to August than from September through February (see Fig. 1 in Lee et al., 1989).

1.2 Description of robot

Our lizard robot was made from a rubber lizard painted with acrylic paints to appear similar to a local *A. sagrei* male (Fig. 1). Its snout-vent length (SVL, from the tip of its nose to the base of its tail) was 50 mm, corresponding to the typical adult male *A. sagrei* found in Florida of 39–64 mm SVL (Tokarz, 1985). The head was 15 mm high in a resting position, and up to 21 mm when displaying. Its feet were attached to the substrate with adhesive. The robot was perched on a covered wire frame designed to resemble a root of a tree, painted to approximate the local terrain, and adorned with locally collected dried leaves, sand, and dirt. A metal hook secured to the center of the chest of the lizard, extended



Fig. 1 Lizard robot

The dark color and nuchal and dorsal crests are typical of adult male morphology.

downward through a small hole in the substrate into a hidden cavity below that housed a mini servo motor. The chamber housing the motor was soundproofed with foam, but the soundproofing did not eliminate all motor noise. We were not concerned about the remaining motor noise, however, because Martins et al. (2005) found that their lizards *Sceloporus graciosus* did not respond to motor noise, and there is no evidence to suggest that noise would affect *A. sagrei*. The motor moved the lizard up and down in a motion approximating a fairly vigorous two-legged pushup, including the tail movement of a natural display. The motor was activated via a 12.2-m cable that ran to a control box with three switches: on/off, speed, and pattern, described below.

1.3 Test conditions and programming

The lizard was controlled by a “Stamp” controller, programmed using “Basic Stamp” software (by Parallax). We programmed two main movement patterns, each with a series of five bobs (or pushups). The patterns were designed using observational analyses of the bobbing patterns of local *A. sagrei*, which include both short and longer duration bobs. The order of bobs for each series is indicated in Fig. 2. The first pattern was randomly chosen from one of many patterns observed locally. In pilot observations we noticed very low consistency in the timing of pushups in a display, and we did not observe any one pattern that occurred more frequently than any other pattern. We therefore chose a random lizard pushup pattern to mimic in our robot, to represent a local variant. The second pattern that we programmed into the robot was the putative signature pattern described by Scott (1984), and also depicted by McMann (2000) as the species-specific stereotyped pattern. Scott (1984) specified that the *A. sagrei* signature display consisted of a series of bobs beginning with two quick bobs, followed by a long bob, a short bob, and finally a variable number of medium-length bobs. She considered “bob” displays to be a graded signal ranging from a headbob, to a pushup with the front legs only, to a full four-legged pushup. Our robot displayed a signal that appears closest to a two-legged pushup. Both Scott

(1984) and McMann (2000) depict more than five bobs in their DAP graphs, but we used five in our study because in the putative signature pattern, the first five bobs were always the same but the number of additional bobs beyond five was variable (Scott, 1984; McMann, 2000). Each series of five bobs was followed by a 2-s pause, after which the series repeated for the duration of the trial (1 min; see below).

We also tested the significance of display speed with two versions of each display. The faster version used a short bob with duration 0.5 s and a long bob with duration 1.0 s. This speed approximated natural speeds; a recent meta-analysis by Ord and Martins (2006) described short bobs as <0.5 s, and long bobs as >0.5 s. For our slower version we programmed a short bob with duration 0.8 s and a long bob with duration 1.3 s. We were interested in display speed because captive video playback work with Jacky dragons *Amphibolurus muricatus* found that video males with faster displays elicited higher response levels from observers, up to the point at which the display rate exceeded the population average (Ord and Evans, 2003).

Following the robotic playback studies by Narins et al. (2003, 2005), we considered each condition to be a type of control for the other conditions, in the sense that a differential response to the different conditions would indicate that the subjects were distinguishing between them. By using a robot to present the stimuli, we controlled for all extraneous factors inherent in using live animal presentations. In other words, nothing varied between our stimuli except for the pattern presented, so if the response of the subjects differs by condition, it should be due to the variation in the stimuli.

1.4 Trial protocol

A trial began when we found a new location with a new *A. sagrei* lizard. We placed the robot approximately 2 m from the lizard in an open, highly visible location. We randomly varied the elevation of the robot lizard, because other studies have shown that perch height reflects dominance (Tokarz, 1985) and resident lizards react differently to intruders introduced at different elevations (Calsbeek and Marnocha, 2006). We set up a

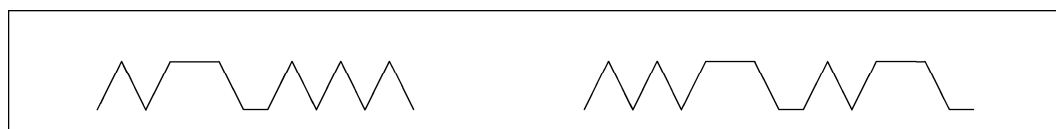


Fig. 2 Robot pushup display patterns

Line indicates relative height of top of head during display (y axis: height of head; x axis: time). Left: Pattern 1, one of a number of variations observed locally at our field site. Right: Pattern 2, the putative signature pattern reported by Scott (1984) and McMann (2000). See text for temporal information, as both patterns were replicated in an overall faster and slower version.

video camera (Sony DCR-TRV17) on a tripod and began filming the live lizard. After at least a 1-min acclimation period, trials began. Trials consisted of a 1-min pretest phase (no robot movement), followed by a 1-min test phase (the robot moves in one of the four conditions), followed by a 1-min post-test phase (no robot movement). We analyzed data only from lizards that were in view for at least 45 s of every 60-s phase of the trial. As long as the subject lizard remained in the area, we proceeded immediately to the next condition, through each of the four conditions in random order. The “post-test” phases and subsequent “pretest” phases could therefore also be considered “intertrial intervals” for a lizard who remained in the testing area. During development of the data collection protocol we tried different durations of robot movement, starting with 5 min and reducing it to 2 min and finally to 1 min. The 1-min trial duration simulated live lizard behavior more accurately than longer trials. If the subject remained in the area after completing one set of all four conditions, we ran the entire set again, in re-randomized order.

1.5 Behavioral coding from video

All videotapes were digitized and then analyzed using The Observer Videotape Analysis program (Noldus), which allowed us to document the time of occurrence of the behavioral responses. Two videotape analyses were conducted. One analysis was designed to collect detailed descriptive data on the timing of pushup bout displays by adult males (tapes were scored by T. Adi). For this analysis, we configured the Observer to code the behaviors “body up” and “body down” and played the tapes frame by frame to extract detailed timing information on pushup sequences. We defined a bout of pushups as a series of up-and-down movements of the body, including leg flexion, separated by at least 5 s from the next up-down body movement. This 5-s rule was also used by McMann (2000) to define an *A. sagrei* display bout.

The main videotape analysis was of the responses to the robotic playbacks. For this analysis, behaviors coded that will be discussed here were dewlap display (extension of the colorful flap of skin at the throat), pushup (flexion of the front legs or all four legs, causing the body and sometimes the tail to move up and down) and head-nod (movement of just the head up and down). Behaviors were coded by researchers that were blind to experimental condition as well as to onset and offset times of trials. Two of us (VP, SB) scored the tapes for this analysis; interobserver reliability was 82% (number of agreements divided by total number of agreements

plus disagreements; note that the Noldus Observer program is conservative in its measure of reliability because it considers precise time windows as well as identity of behavior; in addition, this reliability figure included a number of additional behaviors that were coded but not discussed in this paper).

1.6 Statistical analyses

Data was extracted from the Observer using custom software (written in Perl by D. Anderson) that converted the data from the format produced by the Observer into comma-delimited data that was imported to Excel and SPSS for analysis. Alpha was set at 0.05.

Since not all lizards stayed for a complete set of four trials, while others stayed for more than four trials, our full data set included unequal contributions from different individuals. We therefore created two different subsets of the data for analysis that included equal contributions from each individual. One subset of data included first trials only, so that each lizard was included and contributed one trial to the database. This data was analyzed in two ways: first, the presence and absence of behavior patterns shown in response to the robotic displays were analyzed with a binary logistic regression and chi-square contingency tests. Five independent variables were used: pattern and speed of robotic display, elevation of robot in the substrate, season, and sex of responding lizard. Second, the frequencies of each dependent variable (the three behaviors coded) were analyzed in relation to the independent variables, using analysis of variance (ANOVA) tests. The other subset of data included only those lizards who stayed for one full set of four trials, which allowed us to run a repeated measures ANOVA design, using test condition as our repeated measure, and each behavior as a dependent variable.

2 Results

We tested 87 lizards over the course of a year. We eliminated data from ten of the lizards because they either ran off before the trial began or exceeded a maximum time (15 s) that they were allowed to be out of view during the trial, and we omitted another five lizards because there were conspecifics in view during their tests, which may have affected their behavior. Of our final set of 72 lizards, 40 were adult males and 32 were females or juveniles.

2.1 Descriptive analysis of adult male pushup displays

Seventeen of the 40 adult males that were tested performed pushup displays. The total number of pushups

per male ranged from 1 to 138 (median 25, mean 28.94, SD 31.32), and the number of pushup bouts per male ranged from 1 to 26 (median 3, mean 5.41, SD 6.08). The number of pushups per bout ranged from 1 to 13 (median 5, mean 5.35, SD 2.63; Fig. 3a). In order to compare our work to the data on lizard-to-lizard communication from McMann (2000) and Scott (1984), we also calculated the range of mean number of pushups per bout per lizard, which was 1–9.67 (Fig. 3b).

The variability in timing of pushups within a bout is depicted in Fig. 4, in which one bout is diagrammed for each male (bouts to code were chosen randomly for each male, using a random number generator at random.org). None of the 17 randomly selected bouts had the exact same temporal pattern and the same number of

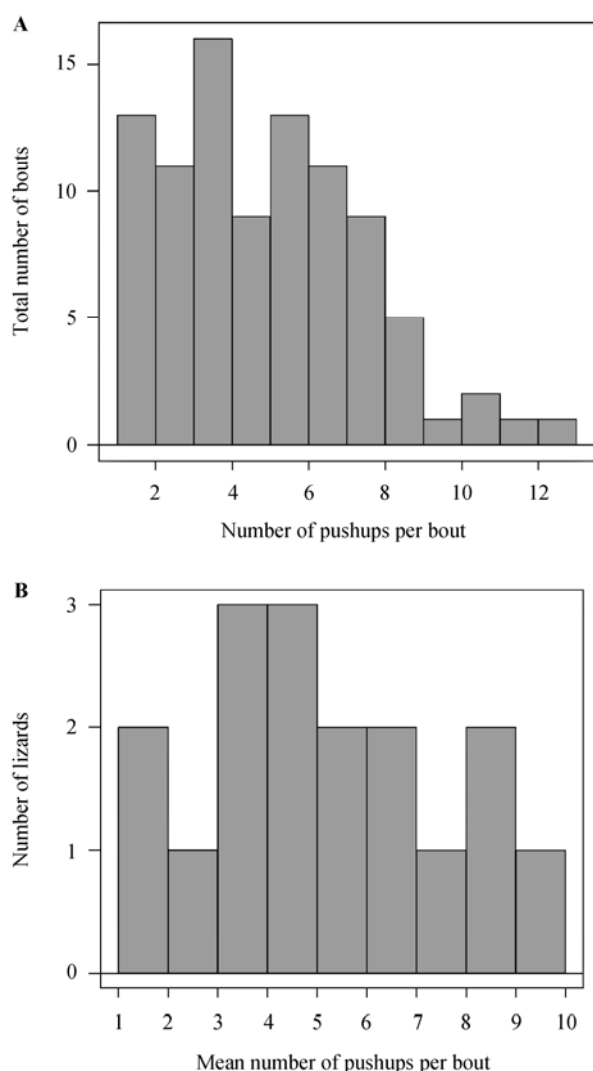


Fig. 3 Number of pushups per bout, for all 17 adult males who gave pushups during the study

A. Distribution of raw number of pushups per bout, for each bout; **B.** Distribution of mean number of pushups per bout, for each lizard.

pushups as any other bout. Only one of the bouts had the temporal features described by Scott (1984) and McMann (2000) as the “signature” display (see first five bobs for lizard #70 in Fig. 4).

2.2 Experimental test results

As described in the methods section, we ran analyses on two sets of experimental data. First-trial data were available for 72 lizards, randomly distributed among experimental conditions (pattern 1, fast, $n=19$; pattern 1, slow, $n=12$; pattern 2, fast, $n=22$, pattern 2, slow, $n=19$). Of these 72 lizards, 37 remained in the testing area for one full set of all four conditions. These lizards received each condition in randomized order, without replacement, over the first four trials, so for this subset of 37 subjects we also conducted repeated measures tests over condition.

2.3 Presence of social responses: correlated with pattern of robot display

We categorized each of the 72 lizards according to whether or not they showed any social behavior during the test or post-test phase of the first trial (i.e., any time after the robot was first turned on, during and up to 1 min after the first trial). Social behavior included all three dependent variables analyzed: dewlap extension, pushup and head-nod. Twenty-three lizards showed social behaviors during this time period; 49 did not. A binary logistic regression analysis including all five independent variables as covariates (pattern and speed of display shown by robot, elevation of robot, sex of subject, and season), found a nonsignificant trend in favor of the signature pattern, but the other four independent variables were clearly nonsignificant (Table 1). We analyzed the pattern data with chi-square tests and found that a significantly higher proportion of lizards showed a response to the signature pattern than to the alternate ($\chi^2_{df=1} = 3.969$, $P=0.046$, Fig. 5). When the dependent variables (the three response behaviors) were analyzed separately, dewlapping ($\chi^2_{df=1} = 7.08$, $P=0.008$) and pushups ($\chi^2_{df=1} = 4.28$, $P=0.039$) occurred significantly more to the signature pattern than the alternate, but head-nods ($\chi^2_{df=1} = 2.29$, $P=0.131$) did not.

We found no significant differences between experimental conditions when we conducted ANOVAs on the raw frequencies of occurrence of behaviors in either data set (either first trial data or the lizards who got complete sets of all four trial types), likely due to the high number of nonresponders in the data set.

2.4 Phase of trial: head-nods increased after trial

As described above, there were three 1-min phases in each trial: a pretest minute during which the robot was

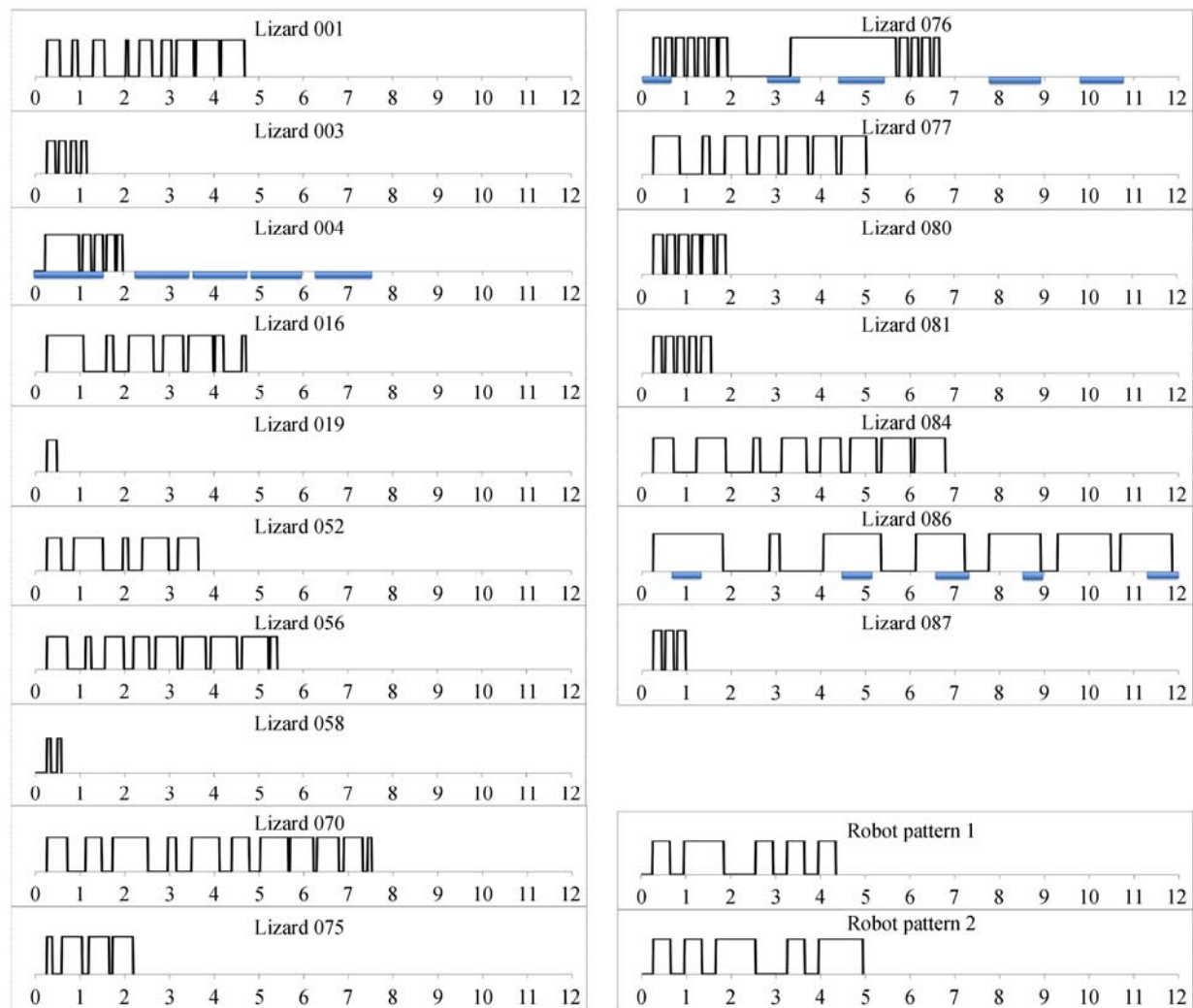


Fig. 4 Display Action Pattern graphs of pushup bouts (one bout for each male who gave pushups, randomly chosen from among that male's bouts)

The x-axis shows time in s; the y-axis shows relative height of the head and body (up or down). Three of the 17 bouts also had dewlap extensions; these are plotted with bars below the horizontal axis. Timing information was taken from frame-by-frame video analysis with Noldus Observer. Lizard numbers were ID numbers assigned in the field. At the bottom right of the figure are the two robot pushup patterns, on the same axes for comparison (pattern 2 is the putative signature pattern).

Table 1 Logistic Regression Predicting Presence of Social Responses from Pattern, Speed, Season, Sex, and Elevation

Predictor	B	SE	Wald	df	P	Exp(B)
Pattern	-1.098	0.586	3.514	1	0.061	0.334
Speed	-0.107	0.543	0.039	1	0.843	0.898
Season	0.025	0.670	0.001	1	0.970	1.025
Sex	-0.112	0.625	0.032	1	0.858	0.894
Elevation			1.742	2	0.419	
Elevation(1)	1.051	0.797	1.742	1	0.187	2.861
Elevation(2)	0.851	0.918	0.859	1	0.354	2.341
Constant	-1.034	0.825	1.574	1	0.210	0.355

inactive, a test minute during which the robot was activated, and a post-test minute during which the robot was again inactive. We ran a repeated measures ANOVA of phase and trial type, for head-nods, on the 37 animals who completed full sets of trials, and found an overall significant difference ($F_{2,72} = 3.540$, $P=0.034$, Greenhouse-Geisser corrected). Follow-up contrasts found that head-nods significantly increased after the trial, from the test phase to the post-test phase ($F_{1,36}=6.419$, $P=0.016$; Fig. 6). Pushups and dewlap extensions did not differ significantly by phase of trial.

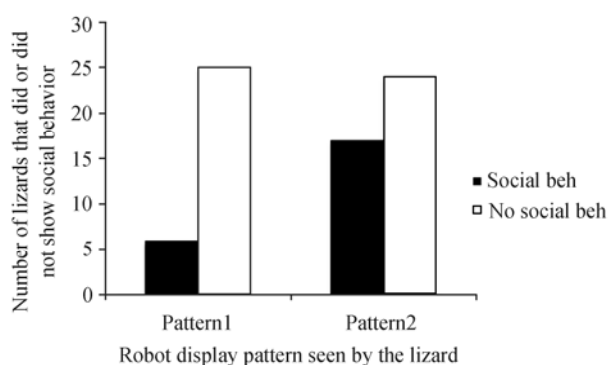


Fig. 5 All first trials for all 72 lizards, showing in which experimental condition the lizards showed social responses

The y-axis shows number of lizards that did or did not respond with social behavior (dewlap, pushup, head-nod) during or in the 1 min after the robot's display. Pattern 1 was observed locally; pattern 2 is the putative signature pattern. Lizards showed more social responses to pattern 2 than to the alternate pattern ($\chi^2_{df=1} = 3.969$, $P=0.046$).

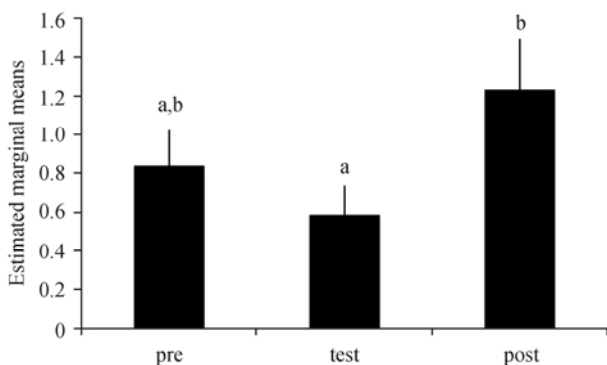


Fig. 6 Mean (and SE) head-nod behaviors in the 37 lizards that each received a full set of four trials, by phase of trial

Data for the different experimental conditions is pooled. Test and post-test phases significantly differed ($F_{1,36}=6.419$, $P=0.016$).

2.5 Age/sex class: males gave more dewlaps

Behaviors observed varied by age/sex class (Fig. 7a). Analysis of the first trial data found that adult males ($n=40$) performed significantly more dewlap extensions than did the combined class of females and juveniles

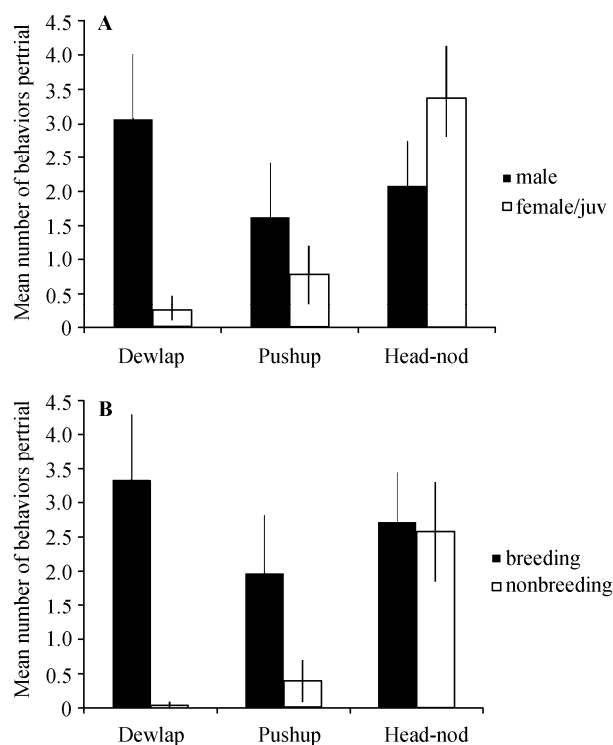


Fig. 7 First Trial Data: Mean and SE of dewlap, pushup, and head-nod behaviors performed by lizards during the first trials only (3 min of data per trial)

Data for the different experimental conditions is pooled, and all individuals (both responders and nonresponders) are included in each graph. (A) Sex differences: comparison of the behavior of males ($n=40$) and females/juveniles ($n=32$). (B) Seasonal differences: comparison of behavior during breeding ($n=39$) and nonbreeding ($n=33$) seasons. Dewlap use differed significantly between males and females ($F_{1,70} = 6.893$, $P = 0.011$) and between seasons ($F_{1,70} = 9.838$, $P = 0.003$).

($n=32$) ($F_{1,70} = 6.893$, $P = 0.011$). The number of pushup and head-nod displays did not differ significantly between adult males and females/juveniles.

2.6 Season: dewlapping was highest in the breeding season

Examination of the data on a month-by-month basis revealed that more dewlapping and pushup behaviors occurred in May and June than in the other months; head-nods were more evenly spread across the year. Since some months had too few subjects tested to analyze statistically (range of lizards tested per month, that were included in the first trial analysis of 72 lizards, was 1–19), we lumped months into seasons, as described in the methods section. When months were lumped, we found that only dewlapping behavior was significantly seasonal: it was higher in the breeding season than in the nonbreeding season (One-Way ANOVA, $F_{1,70} = 9.838$, $P = 0.003$; Fig. 7b).

3 Discussion

In this study of the responses shown by wild brown anoles to a conspecific robot displaying pushup patterns, we found that the lizards were more likely to show social behavior in response to the signature pattern described by Scott (1984) and McMann (2000) than they were to one of a number of variations found locally. The lizards attended to the behavior of the robot, being more likely to wait to show head-nods until after the robot's display ended than to head-nod during the display. We also found sex differences and seasonal differences in behavior, discussed below.

Natural variability in display behavior was high in that no pushup display pattern observed in a randomly selected sample (of one bout from each male) had the same temporal structure as any other pattern observed. The lizards responded to the robotic presentations in a naturally appropriate manner, evidenced by the finding that the mean number of pushups per bout was similar to the mean number of bobs per bobbing display reported by McMann (2000) and Scott (1984) in their studies of *A. sagrei* lizard-to-lizard communication. Our male lizards gave a range of 1–13 pushups per bout, with a range of means of 1–9.67 pushups per bout, and McMann's lizards showed an overall range of means of 2–14 bobs per display. The male lizards studied by Scott (1984) had a mean of 11.1 bobs per display. It is worth noting that our robot performed only 5 pushups per bout, so if our lizards were inclined to match the robot's display, this may have lowered our mean ranges of pushups per bout. There is some evidence of display matching in the green anole *A. carolinensis* (McMann, 1993), but there is evidence against display matching in the Sagebrush lizard *Sceloporus graciosus* (Smith and Martins, 2006), and no evidence for it yet in *A. sagrei* (McMann, 2000). The rate of dewlap displaying shown by our males in response to the robotic presentations was also biologically appropriate, in that 17.65% (3 of 17) of the display bouts randomly chosen for detailed analysis included dewlap extension, corresponding to the male lizards studied in the natural context by Scott (1984), in which 23% of bobbing displays included dewlaps (comparable data is not available in McMann, 2000).

One primary goal of our work was to determine the degree to which the brown anoles in our study responded to the specific signature pattern described by Scott (1984) and McMann (2000) as opposed to another temporal variant of the bobbing display. We found that the presence and absence of social responses was corre-

lated with pattern of the robot display: responses, particularly pushup and dewlap extensions, were more likely during and after the signature display than the alternate pattern. This suggests that the signature pattern may, despite the high variability seen in pushup displays, hold significance for this population of anoles, as was stated by Scott (1984) and suggested (by using the same signature pattern to show the stereotyped display for *A. sagrei*) by McMann (2000).

Preference for the putative signature display was not strong, however, in that the response frequency data, containing detailed information on the number of bobs or dewlaps in the response, did not correlate with pattern type. One possible reason for this may have been that there were so many nonresponders in the data set that the differences washed out. Other reasons may have been due to our choice of nonsignature pattern to use as our comparison stimulus. We chose one nonsignature pattern to use, randomly, from our pilot observations of local lizards. From our post-hoc analysis of male pushup displays (see Fig. 4), it is apparent that there were other patterns we could have chosen as our "local alternate" which would have been more temporally different from the putative signature pattern than the one we used. We could also have taken a different approach by programming a variety of alternate nonsignature patterns that would have been called up at random, to test against the signature pattern. This would be an interesting design for a follow-up study. Without more observational data on the prevalence of each temporal variant in the population, it is not apparent which variant(s) to use. It is worth reiterating that of the 17 pushup displays randomly chosen for detailed analysis, none showed the same temporal pattern as any other, and only one showed the putative signature pattern. We were somewhat surprised, therefore, to have found any preference at all for the signature pattern. A follow-up study that documents the prevalence of local patterns more widely and uses a robot programmed to test a variety of these patterns would be very interesting.

Another factor that may have affected our results was that the duration of the two patterns that we programmed into our robot was slightly different. Although both the "signature" and the alternate, nonsignature pattern included the same number of bobs, the "signature" pattern had one longer bob than the nonsignature, resulting in a pattern that was roughly a half second longer. This slight increase in duration may have been enough to cause the lizards to respond more to this pattern than to the alternate pattern. McMann (2000) has emphasized

that these display patterns are used for territoriality and aggression; it is possible that longer patterns may indicate higher arousal (although this must be tested). In our case, a difference of a half a second is not likely to have been highly salient (one display was roughly 4.5 s and the other just under 5 s), but this can be tested in future studies either by using comparison stimuli of the same duration, or multiple stimuli that randomly vary in duration. In addition, both the “signature” and our alternate pattern included just five bobs, because the first five bobs of the signature are thought to be more stereotyped than any subsequent bobs that may be tacked onto the basic display (Scott, 1984; McMann, 2000). It is possible that if we had included a variable series of trailing bobs in addition to the first five, we may have obtained stronger results.

Ord and Stamps (2009) found no differences in response of live anoles *Anolis gundlachi* to a robotic lizard model that displayed either the correct species signature pattern or the pattern of a heterospecific lizard. They suggested a number of possible reasons for this, concluding that species recognition is mediated by a complex set of factors, not easily tested for with a simple metric of higher responses expected to an appropriate signal.

It is also possible that the lizards in our population simply did not have a strong preference for the signature pattern. This is highly plausible, given the high degree of variability seen in pushup patterns. If this idea is supported by further studies, then the idea that there is one preferred “signature” display that has one specific temporal pattern may not be valid for *A. sagrei*. It also may be that we need to test the validity of signature patterns with different methods, or that the pushup display is used more in contexts of aggression (e.g., McMann, 2000) than in species recognition. Traditionally, however, lizard displays have been considered broadcast signals that advertise territory ownership and/or species identity, as well as ritualized aggression (Jenssen, 1977), so it may be that both species recognition and aggression are compatible explanations for this type of display.

There is evidence that there can be population differences in the signature pattern in other anole species such as *A. nebulosus* (Jenssen, 1971), *A. grahami* (Jenssen, 1981; although see Macedonia and Clark, 2003), *A. conspersus* (Macedonia and Clark, 2001), and even *A. carolinensis* (Bloch and Irschick, 2006), and so it is possible that the local alternative patterns that we saw may represent an evolved local shift in the species

signature in this population. This is unlikely, however, given the proximity in space and time of Scott (1984) and McMann (2000)’s studies to our own. Scott’s (1984) observations were collected in 1979 in Tampa, FL, and McMann’s (2000) observations were collected in 1995 in Miami, FL, and they show almost identical display patterns to one another. Our observations were made 10 years later, in St. Petersburg, FL (50 km southwest of Tampa, and 400 km northwest of Miami), likely not enough time (or distance) for the evolution of a new signature.

The variability in *A. sagrei* display patterns in Florida (Scott, 1984; McMann, 2000), and the presence of local alternatives at our site (see Fig. 4), might reflect the fact that there are no other *Anolis* species of similar size to *A. sagrei* in Florida, so discrimination of display patterns may no longer be under strong selection for species recognition. The green anole *A. carolinensis* is sympatric with the brown anole at our study location and throughout much of Florida, but it is smaller and distinctively colored so the two species are not easily confused. In addition, while *A. sagrei* are trunk-ground habitat specialists, *A. carolinensis* live higher in the tree canopies (Losos et al., 2003). It would be interesting to replicate our study in Cuba, which has a large *Anolis* fauna with sympatric heterospecific anole species similar in size to *A. sagrei*; one might predict stronger discrimination of the species-specific patterns in that case.

Sex differences in behavior are typical for *Anolis* lizards. Jenssen et al. (2000) reported that in the green anole *A. carolinensis* display rates of males were higher than display rates of females. Orrell and Jenssen (2003) found that in heterosexual contexts, *A. carolinensis* male and female display rates are actually equivalent, but in male-male contexts the display rate for males increases tenfold. We found that our *A. sagrei* males performed more dewlap displays than did females and juveniles, while pushups and head-nods did not differ between age/sex groups.

Seasonal differences are also important in *Anolis* behavior. Tokarz et al. (2002) found that *A. sagrei* dewlap displays were correlated with testosterone and were seasonal, occurring more highly in May, June and July, which are during the breeding season, than in October, November and December, which are outside of the breeding season. We also found that dewlap displays were seasonal, occurring more frequently during the breeding than the nonbreeding season. That dewlap extensions are more common during the breeding season suggests that they play a role in courtship or mating

behavior, although Tokarz (2002) and Tokarz et al. (2005) found no decrement in the mating success of lizards experimentally prohibited from extending their dewlaps. We did not find strong seasonality in pushup or head-nod behavior, or in the tendency of the subjects to respond to the signature versus the alternate pushup pattern.

The lizards in our study responded to the phase of the trials, indicating that they attended to periods when the robot was activated. In particular, head-nods increased after the robot finished its display. There was also a nonsignificant trend for head-nods to decrease during the robot's display. This suggests the possibility either that the lizards are "turn-taking" (alternating display patterns with one another, as described in Evans, 1991), or perhaps that head movements interfere with perception and the lizards suppress head-nods during conspecific displays in order to better perceive the display. However, pushup behavior (which also causes head movement) did not decrease when the robots were displaying; if anything, there was a trend for it to increase. More work should be done to clarify whether *A. sagrei* alternates displaying between lizards, and if so, why. Interactive video playbacks have provided a useful method to study turn-taking in lizards (Ord and Evans, 2002; Van Dyk and Evans, 2008); an interactive approach would be promising to try with robotic models as well.

Our results suggest that head-nods may have a different function than pushups and dewlap extensions, because they are less seasonal and more likely to occur in females/juveniles than are pushups or dewlap extensions. This finding is somewhat difficult to compare to other work because the literature is inconsistent in the use of terminology; as mentioned above, authors have variously used the terms "bob", "headbob" and "pushup" to refer to the stereotyped bobbing display (which we call pushup), and have only occasionally explicitly discussed a head movement that does not involve the rest of the body. Scott (1984) distinguished three types of bobs in *A. sagrei*: one was the stereotyped "signature display", another was a "quick rhythmic bobbing" used primarily by subordinate individuals, and the third was a "jiggling" display used in courtship (Scott, 1984, pp. 7–9). Our pushup behavior corresponds to Scott's signature bob, and our head-nod behavior likely corresponds to her rhythmic bobbing term. Tokarz (1985), in a study of *A. sagrei* dominance behavior, also distinguished between the stereotyped "challenge display," which we called pushups, and head-nods, which were likely the same as the "quick

rhythmic bobbing" reported by Scott (1984), as they were used by subordinate individuals. Our data supports this distinction, as we found head-nods to be used as much or more by females/juveniles than by adult males. McMann (2000) distinguished between "bobbing" and "nodding" displays of *A. sagrei*, probably corresponding to our pushup and head-nod, respectively; he found a more complex picture in which the proximity of an opponent affected the likelihood of bobbing versus nodding. Our lizard robots were placed approximately 2 m from the subject lizards, which would most likely be classified as "short distance" in McMann (2000)'s study of opponent proximity (his short distance interactions occurred within square enclosures that measured 2.4 m wide); in the short distance contexts, McMann (2000) found that resident lizards performed more bobbing displays relative to nodding displays than did new opponents. In addition, McMann and Paterson (2003) and Paterson and McMann (2004) found that the proportion of bobbing to nodding displays was higher for males in the periphery of their home ranges and for males interacting with nonneighbor males, respectively, suggesting that the bobbing display may be the more aggressive of the two display types. Finally, Simon (2007), in a study of *A. sagrei* display behavior under varying predation pressure, distinguished between "headbob" which included both head-nods and up-and-down movements of the forebody (the latter we would call a two-legged pushup), and "pushup" which included flexion of all four legs (which we called a four-legged pushup; we combined two- and four-legged pushups in our analysis).

For future work we are designing a dewlapping anole model so that multiple visual signal components can be manipulated in playbacks, and the role of the dewlap and its relation to the pushup in display behavior can be assessed (*cf.* Ord and Stamps, 2008, 2009). It would be interesting to design robotic models of anoles that are capable of finer movements that distinguish between head-nods and two- and four-legged pushups, to assess the importance of this dimension of display variability. It would also be interesting to build both male and female anole robots, so as to test intra- and intersexual communication separately. We also hope to see more documentation of the variability of natural *A. sagrei* display behavior, although as Jenssen (1979) found for *A. opalinus*, the high degree of variability may render this a difficult task.

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