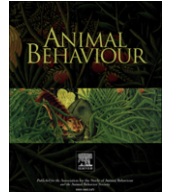


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# Animal Behaviour

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## Sensory system properties predict signal modulation in a tropical lizard

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Two common challenges faced by signallers, which can affect signal efficacy and are intrinsic to the communication process, are (1) that intended receivers are often inattentive and (2) that the spacing of animals in a habitat is relatively fluid. Signal modulation has been proposed to be an effective strategy to cope with these challenges by providing a mechanism to maintain signal efficacy. We evaluated this hypothesis by testing the use of modulation in the tropical lizard *Anolis gundlachi*. We characterized the motion properties of the sensory system and measured the physical properties of movement-based headbob displays given during staged social encounters under natural conditions. We found a significant positive association between the maximum amplitude of headbob displays and the distance to intended receivers. Modulation occurred in response to small-scale changes in signaller–receiver distance, and signallers gave displays that fell within a range of amplitudes predicted to optimally stimulate the visual system of *A. gundlachi*. Our findings strongly suggest that modulation of the physical properties of motion-based signals can be an effective mechanism to tune signals to the combined effects of characteristics of receiver sensory systems and receiver distance, and can serve as a behavioural strategy to cope with relatively frequent changes in the spacing of individuals.

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Communication is a fundamental component of social interaction, and therefore, understanding the possible factors that can affect signal efficacy (i.e. the ability of a signal to rapidly elicit a response from a receiver) is a central theme in animal behaviour. Studies have shown that signal efficacy depends on the ecological conditions under which the signal is given, as well as the properties of receiver sensory systems (e.g. Alberts 1992; Endler 1992; Fleishman 1992; Leal & Fleishman 2004; Siddiqi et al. 2004; Endler & Mielke 2005; Stuart-Fox et al. 2007; Ratcliffe & Nydam 2008). Moreover, signallers commonly face two challenges intrinsic to the communication process during most social interactions: (1) intended receivers are often inattentive, because they either are engaged in other activities or are simply unaware of the presence of the signaller (Guilford & Dawkins 1991); (2) spacing of animals in a habitat is relatively fluid, leading to frequent changes in the distance between signallers and intended receivers (see Peters & Allen 2009, and references therein). Elucidating how animals are able to cope with these problems to achieve signal efficacy is an area of much debate, in part because the answer to this question requires a sufficient understanding of the sensory system properties of the

organism in question. Such sensory data are limited for most organisms.

Fluctuations in spatial conditions present a challenge for communication because in most cases signal efficacy is sensitive to changes in the distance between individuals (Dusenbery 1992; Bradbury & Vehrencamp 1998). Signalling animals may cope with this problem in two major ways. First, individuals may produce signals of categorically different form depending on the distance to intended receivers (i.e. short versus long communication) (Stamps & Barlow 1973; Palombit 1992; Titus 1998; Krams 2001; de la Torre & Snowdon 2002). Alternatively, signallers may produce signals with the same general design irrespective of receiver distance, but modulate certain physical properties to achieve efficacy when receiver distance changes (Brumm & Slater 2006). One advantage of signal modulation is that it provides the opportunity for signals to be fine-tuned to receiver distance along a continuous scale. At the present, empirical support of distance-based modulation has come from only a handful of taxa (e.g. zebra finches, *Taeniopygia guttata*: Brumm & Slater 2006; fiddler crabs, *Uca perplexa*: How et al. 2008). However, whether this modulation increases the likelihood of signal detection by tuning a signal to the properties of the receiver sensory system remains largely untested.

Our understanding of the natural history, signalling behaviour and sensory biology of *Anolis* lizards makes them an ideal model system for evaluating the potential use of signal modulation as

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a mechanism for achieving signal efficacy when the distance between interacting individuals changes during social interactions (*Anolis* visual system reviewed in: Fleishman 1992; Fleishman et al. 2009; natural history of *Anolis* reviewed in: Losos 2009). Male anoles often patrol their territories, and as a result, the spatial relationships of territorial males and neighbours, rival males and potential mates is fluid (Stamps 1977a; Jenssen & Nunez 1998; Jenssen et al. 2001). When signalling to these other individuals, anoles communicate using dewlap flashes and motion patterns of the head, or headbobs, which can be either nondirected (i.e. spontaneous 'assertion' displays broadcast to unseen lizards in the surrounding habitat; Jenssen 1977; Stamps 1977b; Fleishman 1992), or directed towards specific individuals during courtship or aggressive encounters (i.e. 'challenge' displays; Greenberg & Noble 1944; Jenssen 1977). Although headbobs often show a high degree of stereotypy in temporal pattern (Jenssen 1977), certain physical properties of these displays (e.g. amplitude, velocity/speed) have some degree of plasticity. Fleishman (1988a) showed that male *Anolis aeneus* modulate headbob amplitude, velocity and acceleration depending on social context (e.g. close-range challenge displays versus long-range assertion displays), and Stamps & Barlow (1973) found that under laboratory conditions *Anolis aeneus* tended to include relatively higher-amplitude movements in their displays when receivers were farther away. However, assertion and aggressive displays were not differentiated when evaluating changes in the relative amplitude of *A. aeneus* headbobs. Studies have also demonstrated that some species of West Indies anoles can adjust the speed of assertion displays to account for fluctuations in environmental noise (Ord et al. 2007, 2010).

Recent work on motion detection in *Anolis sagrei* (Fleishman & Pallus 2010; Pallus et al. 2010) suggests that much of the headbob modulation documented (i.e. specifically changes in the amplitude of displays) can be explained by sensory constraints imposed on physical properties of headbobs. The probability that a moving stimulus will elicit the visual grasp reflex in a receiver (i.e. a reflexive shift of gaze that brings the image of the stimulus onto the fovea where it receives direct attention; Ingle 1982) depends on the pattern, duration and apparent amplitude of a movement (i.e. the distance the object travels at the eye, measured in degrees visual angle; Fleishman & Pallus 2010; Pallus et al. 2010). Specifically, abrupt, square wave-like movements within a particular range of apparent amplitudes (0.2–0.8° for *A. sagrei*) that occur in less than 100 ms maximally stimulate anoline motion detectors. Because nearly all movements in the early portion of *Anolis* headbob displays are completed in less than 100 ms (Fleishman & Pallus 2010), the detectability of a motion signal largely depends on its apparent amplitude along with the specific range of apparent amplitudes that maximally elicit the visual grasp reflex in receivers. Knowing this range of 'optimal' amplitudes, then, provides us with the opportunity to make robust predictions about how an individual should modulate its motion displays in the face of changes in receiver distance to stimulate the receiver sensory system effectively. However, whether the motion detection properties of *A. sagrei* are representative of those of other *Anolis* species is currently unknown.

Here we tested the hypothesis that male *Anolis gundlachi* modulate the amplitude of their initial headbob displays in response to changes in receiver distance to achieve high detection probabilities (Fleishman & Pallus 2010). To test this hypothesis, we first characterized the motion detector properties of *A. gundlachi*, namely the range of apparent amplitudes that maximally stimulate the visual grasp reflex in this species. Second, we tested whether distance-based modulation occurred under natural conditions. If modulation is used as a strategy for achieving signal detectability, then we predicted that (1) the amplitude of movement-based

signals would be positively correlated with receiver distance and (2) the amplitude of movement-based signals would fall within the predicted range of amplitudes that maximally elicit the visual grasp reflex (i.e. grab the attention) of receivers.

## METHODS

### Focal Species

*Anolis gundlachi* is a medium-sized, sexually dimorphic (females to 45 mm, males to 75 mm; Rivero 1978; Schwartz & Henderson 1991) and highly territorial lizard, restricted to the wet, deep-shade forests of Puerto Rico (Schwartz & Henderson 1991). Male *A. gundlachi* are most commonly observed within 3 m of the ground on the trunks of large-diameter trees (Rand 1964; Rodríguez-Robles et al. 2005). From these perches, territorial males signal to conspecifics in the surrounding habitat using motion patterns of the head and dewlap (Ruibal 1965; Ord et al. 2007).

### Study Site

The study was conducted at the El Verde Field Station (Universidad de Puerto Rico) in the Caribbean National Forest, Luquillo Mountains, Puerto Rico (elevation = 360 m). The habitat is dominated by *Dacryodes excelsa* (tabonuco) and *Prestoea acuminata* var. *montana* (sierra palm) (for detailed description of site, see Leal et al. 1998) and supports a dense population of *A. gundlachi* (Reagan 1991; Leal et al. 1998).

### Laboratory Experiment: Characterizing Motion Detector Properties

Our characterization of the motion detector properties of *A. gundlachi* closely follows the paradigm used in Fleishman (1986) and Pallus et al. (2010). Briefly, we captured male *A. gundlachi* around the El Verde Field Station, in the same area as our behavioural experiments (see below), and transferred them to a laboratory at the Mata de Plátano Field Station (Universidad Interamericana de Puerto Rico, Recinto de Bayamón). Lizards were housed in transparent, plastic test cages (23 × 16 × 17 cm, with a horizontal wooden perch) for 24–72 h prior to experimentation. Each individual was presented with nine total motion detection trials (eight experimental + one control) that each consisted of a black cylindrical target (diameter = 5 mm, height = 5 mm) moving in a single cycle, 0.8 Hz, square wave-like pattern (duration of each movement = 0.066 s) against a white background. Trials differed only in the amplitude of motion (0.1, 0.25, 0.5, 0.75, 1.0, 1.25, 1.75 or 2.5° visual angle). Any shift in gaze (via eye or head movement) by an individual towards the stimulus within 3 s of the end of target motion was scored as a positive response (i.e. detection of the stimulus), while absence of a gaze shift was scored as a negative response. To control for random eye movements, each lizard was also presented with a control trial, during which the target was set in motion, but was visually obstructed (= 0° visual angle in Fig. 1). Trials were separated from one another by at least 1 h to avoid habituation and were presented in random order, and the experimenter was blind to the amplitude of motion being presented during each trial. A more detailed description and schematic of the experimental set-up can be found in the Supplementary Material (Fig. S1).

### Field Experiment: Testing for Distance-based Signal Modulation

#### Experimental design

Data were collected during 15–21 July 2011 at El Verde Field Station. To induce directed visual displays from potential signallers,

we introduced tethered adult males (receivers) into the territories of other adult male *A. gundlachi* (signallers) (sensu Evans 1938; also see Supplementary Fig. S2). First, we captured a receiver and secured it to the surface of a small, transparent box (15 × 30 cm) with a piece of dental floss tied around its waist. The floss restricted the movement of the lizard to the top of the box, but did not otherwise impede its behaviour. With the box attached to the top of a small tripod, we placed the receiver in the immediate vicinity of the tree trunk on which the signaller was perched. A minimum of 20 m separated the site of receiver capture and the territory of the signaller to avoid the possibility of confounding effects of familiarity on behaviour (Qualls & Jaeger 1991; Paterson & McMann 2004). Using a Canon GL2 mini-DV camcorder secured to a tripod approximately 5 m from and at a height level with the signaller, we then filmed the first motion display directed towards the receiver.

During each display we measured maximum wind speed with a hand-held anemometer (JDC Electronic SA, Yverdon-les-Bains, Switzerland, Skywatch® GEOS N°11; resolution = 0.1 m/s) because background motion may impact signal properties of *A. gundlachi* (Ord et al. 2007). We also filmed the behaviour of the receiver throughout the trial using a tripod-mounted Canon ZR950 mini-DV video camera to control for receiver behaviour (see Supplementary Fig. S2). Following each display, we placed a ping-pong ball of known diameter at the site of the display to serve as a standard that could later be used to convert head-movement distances to real units (i.e. mm). We then measured the straight-line distance between the signaller and receiver at the time of display using a laser distance meter (Leica Geosystems, Atlanta, GA, U.S.A., Disto™ D5; error = ±1.5 mm). We only staged encounters in which the linear distance between the signaller and receiver was less than 3 m because signal efficacy is predicted to be more sensitive to modulation at relatively short distances (Fleishman & Pallus 2010). We also measured the snout–vent length (SVL) of the lizards when possible (some signallers escaped before capture) and marked them before releasing them at their original site of collection. No individual served as a signaller or receiver more than once, and all interactions were staged between 0800 and 1800 hours, a period during which *A. gundlachi* is active (M. Leal, personal observation).

#### Video analysis

We restricted video analysis to the first 10 s of the first display given by each signaller to (1) minimize contextual differences between trials (i.e. all trials began with a signal given to a potentially inattentive receiver that had not yet responded to the signaller) and (2) focus on the portion of the display that was likely to contain alerting components important for detection (Wiley 1983; Fleishman & Pallus 2010). We converted video clips of each visual display to a format appropriate for the motion analysis software VideoPoint 2.5 (Lenox Softworks, Inc., Lenox, MA, U.S.A.), which allows users to superimpose a rotatable Cartesian coordinate system onto a sequence of video frames. We then plotted the position of the snout of the lizard on every frame (30 frames/s). Next, we measured the diameter of the ping-pong ball standard in pixels and converted the Cartesian coordinate system to real units. After unit conversion, we rotated the coordinate system such that the vertical (*y*) axis was aligned with the apparent axis of maximal head motion (= maximum amplitude) and the origin was centred on the perch below the head of the lizard. Because this alignment was achieved by eye, an underestimate of maximum head amplitude was possible. To reduce the likelihood of encountering this error, we also rotated the coordinate system 5 degrees to the right and left of our original alignment and then compared the maximum head amplitudes given by all three alignments (rotation typically resulted in a shift in calculated amplitude of less than 0.5 mm). We used only data obtained from the alignment that yielded the largest

maximum head amplitude to generate a time–motion graph for each display (Carpenter & Grubitz 1961; Carpenter 1965). This graph provided an illustration of the temporal pattern of head movements along with the amplitude of each movement. We also analysed the video footage of the receivers to record their behaviour.

#### Statistical Analysis

We used Spearman rank correlations to test for associations between the maximum amplitude of displays and distance, wind speed and signaller body size (SVL). We used a Bonferroni correction to account for multiple comparisons, with  $\alpha = 0.0125$ . The sample size for the amplitude × body size correlation was smaller than the sample sizes for the other correlations because not all signallers could be captured following the trials. All statistical tests were performed in R (R Development Core Team 2009).

#### Predicting the Range of Amplitudes That Maximize Signal Detection

The visual angle ( $\theta$ ) of a movement (i.e. apparent amplitude) varies predictably with distance according to the simple tangent function:  $\theta = \tan^{-1}(S/D)$ , where *S* is the amplitude of a signal and *D* is the distance between the signal and the eye of the receiver (McIlwain 1996; Land & Nilsson 2002). Coupling this information with the fact that there is a limited range of apparent amplitudes that maximally stimulate the motion detectors of receivers (see Introduction and Results), we predicted the range of headbob amplitudes that *A. gundlachi* should produce when a potentially inattentive receiver is located at a particular distance from the signalling individual.

#### Ethical Note

This study was conducted with all necessary permits from Departamento de Recursos Naturales y Ambientales de Puerto Rico (2012-IC-065). We followed the Recommendations for the Care of Amphibians and Reptiles (Pough 1991) in the humane treatment of all animals, and our research was approved by the Institutional Animal Care and Use Committee of Duke University.

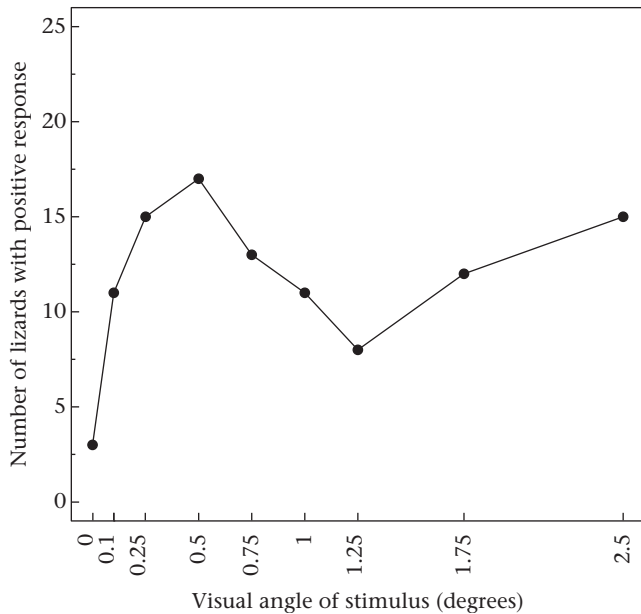
## RESULTS

#### Laboratory Experiment

Male *A. gundlachi* showed a clear peak in response to movements with apparent amplitudes in the range of 0.25–0.75° visual angle ( $N = 47$ ; Fig. 1). A second increase in motion detection appeared to occur at an apparent amplitude of 2.5° (Fig. 1). In *A. sagrei*, a similar pattern is observed and has been suggested to represent the possibility of multiple overlapping motion channels (Pallus et al. 2010). However, because of the uncertainty surrounding the existence or contribution of an additional motion channel, we used the distinct 0.25–0.75° peak for conservative predictions.

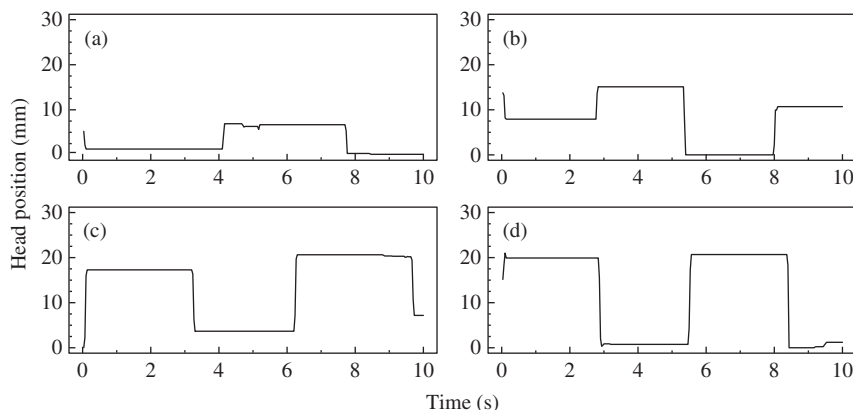
#### Field Experiment

A typical trial consisted of four phases. (1) The signaller, likely startled by the introduction of the apparatus holding the intended receiver (see Supplementary Fig. S2), retreated to the side of the perch opposite the receiver. (2) After 0.5 to 5 min, the signaller returned to the area around the perch and appeared to monocularly inspect the area occupied by the receiver, settling its gaze on the receiver within 1 min. (3) At the end of the previous phase, the



**Figure 1.** Total number of male *Anolis gundlachi* that positively responded to moving stimuli with different apparent amplitudes (in degrees of visual angle). Note: a visual angle of 0° indicates the control trial. Apparent amplitudes in the range of 0.25–0.75° are most frequently detected by individuals.

signaller oriented itself such that its body was presented laterally to the receiver. The signaller then produced its initial headbob display, generally a highly stereotyped square wave-like pattern resulting from combined motion of the head and body (see Fig. 2, Supplementary Video S1). Each head movement was completed in less than 0.066 s (in one to two video frames) and was followed by a similar movement every 2.5–4 s, with an average of three to five movements in the first 10 s of a display. Occasionally, the signaller produced a square wave-like headbob display with a different temporal pattern, but these patterns were not restricted to a particular range of distances. (4) After the initial display, the signaller moved closer to the receiver, while continuing to display. These displays were often characterized by slow lifting of the head and body, prolonged extension of the dewlap, and use of static modifiers associated with aggressive or threat behaviour, such as nuchal crest extension, lateral compression and darkening of the body (Rand 1967; Jenssen 1977; Ortiz & Jenssen 1982). For the signaller, this final stage appeared to represent a transition from an initial alert display to aggressive signalling.



**Figure 2.** Representative time–motion graphs for directed headbob displays of four male *Anolis gundlachi* to receivers located (a) 66 cm, (b) 93 cm, (c) 150 cm and (d) 202 cm away from the signaller. For each display, the trace follows the head position of the lizard along a linear axis (Y axis, mm) over time (X axis, s).

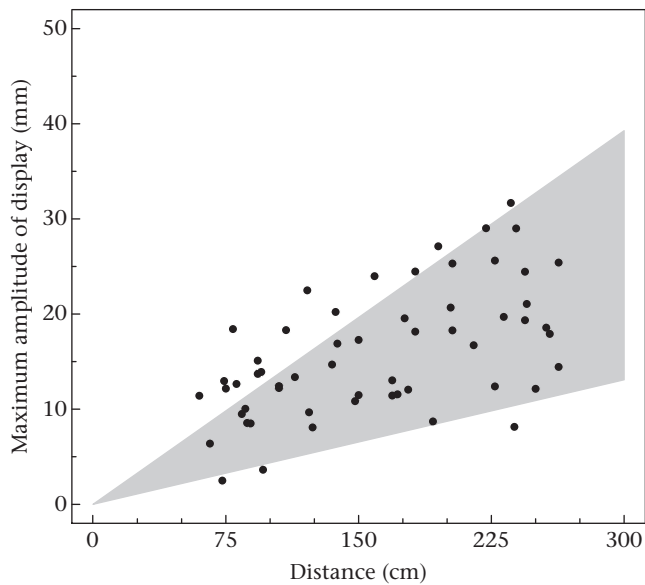
Matching observations reported by Ruibal (1965) in his experiment with *A. gundlachi*, the receivers in this study remained motionless prior to the displays of the signallers in all trials. Therefore, the first signal given by the signaller should not have been influenced by the signalling behaviour of the receiver. Wind speed also had no significant effect on the maximum amplitude of the display given by the signaller (Spearman rank correlation:  $r_s = -0.078$ ,  $N = 57$ ,  $P = 0.563$ ). Similarly, body size of the signaller had no effect on display amplitude (Spearman rank correlation:  $r_s = 0.189$ ,  $N = 45$ ,  $P = 0.213$ ). However, the distance between the signaller and receiver had a significant positive effect on the maximum amplitude of the display. As the distance between the signaller and receiver increased, so did the maximum amplitude of the display given by the signaller (Spearman rank correlation:  $r_s = 0.547$ ,  $N = 57$ ,  $P < 0.001$ ; Fig. 3).

Furthermore, signallers gave displays that fell within a range of amplitudes predicted to optimally elicit the visual grasp reflex of the receivers in 68% (39 of 57) of the trials (Fig. 3).

## DISCUSSION

Studies of animal communication have shown that sensory systems are a major selective force in the evolution of signal design (Alberts 1992; Endler 1992; Phelps & Ryan 2000; Stoddard 2002; Feng et al. 2006; Fuller 2009; Akre et al. 2011). Here we demonstrate that during staged encounters under natural conditions, male *A. gundlachi* modulate the amplitude of their movement-based signals (headbob displays) as a function of the distance to potentially inattentive receivers. Observed changes in the amplitude of headbobs are those expected based on the motion detection properties of *A. gundlachi* (see Fig. 3) and are in accordance with the predictions of a recently developed biologically based motion detection model (Fleishman & Pallus 2010; Pallus et al. 2010), suggesting that modulation is used to tune signals to the properties of receiver sensory systems. Signal tuning is commonly discussed in the context of sexual selection (e.g. Ryan 1998; Boughman 2001), and our study reveals that the ability of signallers to tune the physical properties of their displays can also be an important mechanism in a broader social context.

The underlying principles of visual motion detection have been suggested to be relatively conserved across taxa (Borst & Egelhaaf 1989). However, the degree of variation in motion detector parameters (i.e. spatial and temporal) is largely unknown. Our study demonstrates that the motion detection properties of the sensory system of *A. gundlachi* (Fig. 1) are similar to those reported for *A. sagrei* (Pallus et al. 2010). Whether this pattern of conservatism in



**Figure 3.** Correlation between receiver distance and maximum amplitude of headbob displays in *Anolis gundlachi*. As receiver distance increases, the maximum amplitude of headbob displays given by signallers also increases. The majority of headbob displays have maximum amplitudes that fall within the range of predicted values (shaded region) for maximal stimulation of the receiver's motion detection system.

detection parameters is a general one remains to be seen and requires direct experimental testing. However, the overall structure of visual displays in *A. gundlachi* (i.e. square wave-like motion) and the predictive power of the motion detection model are in agreement with the hypothesis that motion detector properties might account for the typical pattern of head movement in anoles (Fleishman & Pallus 2010). Future studies should evaluate the properties of moving stimuli that maximize the probability of detection by species known to produce headbobs that might be considered deviations from the general square wave-like pattern (e.g. *Anolis barbouri*: Jenssen & Feely 1991; *Anolis stratulus*: Fleishman & Pallus 2010). Such deviations could be generated by divergence in sensory system properties or pressures imposed by distinct signalling environments (e.g. Peters 2010).

Numerous studies have shown that the physical properties of animal signals have evolved to be conspicuous against the average background (e.g. Endler 1992; Leal & Fleishman 2002; Peters & Evans 2003; Derryberry 2007; Uy & Stein 2007; Fleishman et al. 2009). Recent work has also demonstrated that individuals are capable of adjusting these properties to maintain signal conspicuousness in the face of fluctuations in background characteristics (Slabbekoorn & Peet 2003; Peters et al. 2007; Bermúdez-Cuatmatzin et al. 2011). In the case of movement-based signals in anoles, conspicuousness is achieved via the production of square wave-like motion patterns at the commencement of display bouts, which are highly detectable against the typically sinusoidal motion of vegetation (Fleishman 1988b). These displays can be adjusted in response to changes in background noise levels, probably to maintain detectability (e.g. Ord et al. 2007; Peters et al. 2007; Ord & Stamps 2008). Here we provide evidence for another context for signal modulation: the fluid nature of spatial relationships of individuals in a habitat. We found that individuals adjusted the maximum amplitude of their headbobs in response to the distance of potentially inattentive receivers, on a relatively fine spatial scale (Fig. 3).

For a territorial animal, fine-scale distance-based signal modulation should be highly advantageous. For example, in anoles,

including *A. gundlachi*, males patrol their territories relatively frequently, resulting in frequent shifts in distances between individuals. A failure to correct for these fluctuations could affect an individual's ability to attract potentially inattentive mates in the surrounding habitat. Similarly, an unmodulated signal might fail to immediately and effectively advertise territorial occupation to potential rivals, leading to costly close-range agonistic encounters (Jenssen 1977; Fleishman 1992; Bradbury & Vehrencamp 1998). Because of the potential benefits associated with modulation, we predict that distance-based modulation might be relatively common. If this is so, the relative paucity of examples in the literature may result from the small number of experiments conducted at the distance scale that is appropriate for a particular taxon. For example, a recent study failed to find evidence for a correlation between nearest-neighbour distance and headbob speed within species of anole (Ord 2012). One possible explanation for this finding is that the study focused on long-range signals given across a range of receiver distances at which fine-scale modulation is not expected to provide much benefit in terms of enhanced detectability (Fleishman & Pallus 2010).

Our results also support the less intuitive prediction of the motion detection model that signallers should use smaller amplitudes as they get closer to receivers, not simply to save energy or be less visible to predators, but because the visual grasp reflex is less responsive to movements over a certain maximum amplitude (Fleishman & Pallus 2010). At first glance, any decrease in the amplitude of motion displays designed to alert potentially inattentive receivers seems counterintuitive. In fact, it is commonly suggested that individuals should produce alert displays with physical properties that maximize both the active space of the signal and the likelihood of detection by receivers, particularly in noisy conditions (see Ord & Stamps 2008 and references therein). Thus, if *A. gundlachi* males are capable of producing displays with maximum amplitudes greater than 30 mm, why would they ever produce displays that are 10 times as small with significantly smaller active spaces? To answer this question, it is important to keep two issues in mind. First, studies of signals designed to grab the attention of receivers often focus on displays broadcast to unseen individuals located an unknown distance from the signaller (e.g. Wiley & Richards 1978). In these instances maximization of active space may indeed be advantageous. However, signals must also capture the attention of specific receivers, which often are inattentive and located at known distances. Second, when a receiver is maximally sensitive to a range of a given signal property (as opposed to being characterized by a threshold sensitivity), there is often both a lower and upper limit of efficacy for that property. Thus, the observed modulation of headbob amplitude in this study is necessary to ensure that the signal is large enough to reach an intended receiver at a known distance, while remaining below the upper limit of the optimal sensitivity range (Fleishman & Pallus 2010).

A close examination of Fig. 3 reveals that 32% of the displays had amplitudes greater than predicted based on the response properties of *A. gundlachi*. This lack of total congruence is not unexpected considering that our data were collected in a natural habitat with many sources of potential noise. In fact, it is surprising that a relatively simple motion detection model was able to predict small changes in the amplitude of headbob displays with a high level of accuracy even under such noisy conditions. Therefore, the apparent overshoots simply may be necessary to overcome variation in the viewing angle of the receiver that would impact the perceived size of a movement (Rosenthal 2007), or background motion that may impact detection of a signal (Ord et al. 2010). Alternatively, males may simply misjudge receiver distance due to inherent inefficiencies in the possible mechanism(s) used for distance

estimation. The observation that individuals were able to estimate distance at such fine scale is somewhat surprising, because this is an area of research for which very little is known in anoles and in lizards in general (but see Ott et al. 1998, 2004). Further testing under controlled laboratory conditions might prove useful in evaluating possible mechanisms used in judging distance.

Here we demonstrate experimentally fine-scale distance-based signal modulation by *A. gundlachi* under natural conditions. Our results also show that modulation results in head movements that are more likely to be detected by an inattentive receiver. These findings contribute to the expanding narrative of signal flexibility in *Anolis* lizards (Stamps & Barlow 1973; Fleishman 1988a; Ord et al. 2007, 2010) and in species across a diverse set of taxa (e.g. frogs: Zelick & Narins 1985; mammals: Brumm et al. 2004; agamid lizards: Peters et al. 2007; birds: Verzijden et al. 2010; insects: McNett et al. 2010; spiders: Sullivan-Beckers & Hebets 2011). Recent work on anoles has concentrated on the plasticity of headbob displays, particularly display speed, serving as an effective strategy to compensate for changes in the speed of background vegetation movement, light levels in the habitat and average nearest-neighbour distances (Ord et al. 2007, 2010; Ord 2012). However, since anoline headbob displays often consist of movements that are completed within one frame of video when recorded at 30 frames/s, which is the film speed used in previous studies, there is an ambiguity as to whether observed differences in speed are in actuality a result of subtle changes in amplitude (Fleishman & Pallus 2010). In the context of these recent studies, our findings suggests that amplitude, not speed per se, is the property under selection to increase signal detectability.

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## Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2012.12.025.

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