

Lizard Communication

by

David Scott Steinberg

Department of Biology
Duke University

Date: _____

Approved:

Manuel Leal, Supervisor

Susan Alberts

Vikas Bhandawat

Leo Fleishman

Sönke Johnsen

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Biology in the Graduate School
of Duke University

2015

ABSTRACT

Lizard Communication

by

David Scott Steinberg

Department of Biology
Duke University

Date: _____

Approved:

Manuel Leal, Supervisor

Susan Alberts

Vikas Bhandawat

Leo Fleishman

Sönke Johnsen

An abstract of a dissertation submitted in partial
fulfillment of the requirements for the degree
of Doctor of Philosophy in the Department of
Biology in the Graduate School of
Duke University

2015

Copyright by
David Scott Steinberg
2015

Abstract

The evolution of animal signals is driven largely by characteristics of the signaling environment and properties of receiver sensory systems. Selection favors signal traits that increase the probability that a signal will stimulate the sensory systems of intended receivers, but not potential predators, under average environmental conditions. However, environmental conditions often fluctuate, which means that a given signal property may not be equally effective at all times. One potential mechanism that an organism might employ to overcome this challenge is to modulate its signal properties as environmental conditions change in order to maintain stimulation of the receiver sensory system. In this dissertation, I explore the possible role of signal modulation using the motion detection and communication systems of tropical *Anolis* lizards.

In order to assess the possible role of signal modulation in the communication behavior of anoles, it was necessary to determine the properties of their motion detection systems. In Chapter 2, I tested whether motion detection properties are conserved across species of anole. I adapted a behavioral assay to quantify the spatial parameters of the motion detectors of three species of Puerto Rican *Anolis* lizards, with each preferring a distinct structural habitat type. I then compared the results to data previously collected for anoles from Cuba, Puerto Rico, and Central America. Results

indicated that all species share a minimum amplitude threshold for detecting moving objects and exhibit multiple peaks in relative response to various motion amplitudes. Fine-scale interspecific differences in the number and values of response peaks were not correlated with structural niche. Overall, the study suggests that the motion detection systems of *Anolis* lizards are relatively conserved, which may help explain shared features of movement-based signals in anoles.

For mobile organisms, the spatial relationships of signaling individuals and intended receivers can be fluid. Such fluctuation in the distance between signalers and receivers can greatly impact signal efficacy, but it is unclear exactly how animals cope with this problem. In Chapter 3, I investigated whether signal modulation can serve as an effective strategy to cope with variation in the spacing of receivers in the environment by tuning a signal to maintain stimulation of the receiver sensory system. I evaluated this hypothesis by testing the use of modulation in the tropical lizard *Anolis gundlachi* in Puerto Rico. I first characterized the motion detection properties of the sensory system of *A. gundlachi* in the laboratory. I then measured the physical properties of movement-based headbob displays given during staged social encounters under natural conditions. I found a significant positive association between the maximum amplitude of headbob displays and the physical distance to intended receivers. Modulation occurred in response to small-scale changes in signaler–receiver distance, and signalers gave displays that fell within a range of amplitudes predicted to optimally

stimulate the visual system of *A. gundlachi*. These findings strongly suggest that modulation of the physical properties of motion-based signals can be an effective mechanism to tune signals to both characteristics of receiver sensory systems and receiver distance, and can serve as a behavioral strategy to cope with relatively frequent changes in the spacing of individuals.

Although signaling individuals must effectively capture and hold the attention of intended conspecific receivers, they must also limit eavesdropping by potential parasites or predators. However, predation pressure can vary over the course of an individual's lifetime, or over the course of a day, thereby altering signal efficacy. In Chapter 4, I tested the hypothesis that prey can modulate the physical properties of their signals or their display behavior in order to decrease conspicuousness and potentially limit predation risk. To do so, I conducted a manipulative experiment in nature to determine the effect of predation pressure on the properties of movement-based signals and the display rate of the semiarboreal lizard *Anolis sagrei*. I found that male anoles reduced the maximum amplitude of headbob displays but not the proportion of time spent signaling on islands onto which predators were introduced, in comparison to males from control islands lacking the predator. Characteristics of the motion detection system and social behavior of *A. sagrei* show that this reduction in amplitude also decreases signal active space, which might alter the reproductive success of signaling individuals. I suggest that future studies of predator-prey interactions consider the risk

effects generated by changes in signals or signaling behavior to fully determine the influence of predation pressure on the dynamics of prey populations.

Dedication

For my family.

Contents

Abstract.....	iv
List of Tables	xi
List of Figures	xii
Acknowledgements	xiv
1. Introduction	1
2. Visual motion detection in <i>Anolis</i> lizards	5
2.1 Introduction.....	5
2.2 Methods.....	8
2.2.1 Focal Species.....	8
2.2.2 Motion Detection Experiment.....	10
2.2.3 Data Analysis	14
2.2.4 Ethical Note	14
2.3 Results	14
2.4 Discussion	18
3. Sensory system properties predict signal modulation in a tropical lizard.....	24
3.1 Introduction.....	24
3.2 Methods.....	28
3.2.1 Study species and site	28
3.2.2 Laboratory experiment: characterizing motion detector properties.....	29
3.2.3 Field experiment: testing for distance-based signal modulation.....	30

3.2.3.1 Experimental design	30
3.2.3.2 Video analysis.....	32
3.2.4 Statistical analysis.....	33
3.2.5 Predicting the range of amplitudes that maximize signal detection	34
3.2.6 Ethical note	34
3.3 Results	35
3.3.1 Laboratory experiment	35
3.3.2 Field experiment	36
3.4 Discussion	40
4. Predation-associated modulation of movement-based signals by a Bahamian lizard .	47
4.1 Introduction.....	47
4.2 Methods.....	52
4.2.1 Study site and experimental design.....	52
4.2.2 Data collection.....	53
4.2.3 Video analysis	55
4.2.4 Predicting the conspecific signaling active space	56
4.2.5 Statistical analysis.....	57
4.2.6 Ethical note	57
4.3 Results	57
4.4 Discussion	63
References.....	70
Biography	86

List of Tables

Table 1: Raw experimental data for three species of *Anolis* lizard. The ecomorphological class, sample size (N), and number of individuals that responded to each stimulus are presented for each species. The 0° column represents the control trial. 17

Table 2: Mean \pm one SEM perch height, proportion of time spent signaling, maximum headbob amplitude, and number of bobs per display for each island. Sample sizes are given in parentheses. The number of visits to each island and number of total hours spent on each island during the filming of spontaneous headbob displays are also provided. 62

List of Figures

- Figure 1: A phylogeny including the *Anolis* species considered in this study. Relationships are based on Brandley & de Queiroz (2004) and Nicholson et al. (2005). 9
- Figure 2: Schematic of the laboratory set-up for the motion detection experiment in plan (left) and perspective (right). A subject lizard (A) is maintained in a plastic test cage (B) with transparent walls and a horizontal wooden dowel rod (C, diameter = 19 mm). The edge of the dowel is located 3 mm from the front wall. The cage is then placed so that the eye of the lizard is located 17.5 cm from a black target (D). The target is attached to a thin white cylinder that is moved by a Haydon Kerk linear actuator stepper motor. The motor is enclosed in a white box (E). A bare 72 watt (1490 lm) halogen light bulb hangs 45 cm above the target, with light diffused by a square of translucent vellum located 30 cm below the bulb (bulb and vellum not shown). A white, wooden board [F, 130 x 46 cm (l x w)] serves as both a background for the target and a blind for the experimenter. Prior to the..... 12
- Figure 3: The relative responses of five species of *Anolis* lizard to moving stimuli with differing amplitudes. Each point indicates the proportion of individuals in a species that responded to a given motion amplitude relative to the number of..... 15
- Figure 4: Schematic of the field set-up for the *Anolis gundlachi* receiver distance experiment. The 'receiver' (A) is introduced to the territory of the 'signaler' (B). One camcorder (C) films the behavior of the receiver, while another camera (D) films the headbob display of the signaler. 31
- Figure 5: 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. 36
- Figure 6: 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 signaler. For each display, the trace follows the head position of the lizard along a linear axis (*y* axis, mm) over time (*x* axis, s)..... 38
- Figure 7: 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 signalers also increases. The majority of headbob displays

have maximum amplitudes that fall within the range of predicted values (shaded regions) for maximal stimulation of the receiver's motion detection system. 39

Figure 8: Mean perch height of male *Anolis sagrei* in both control (nonpredator) and experimental (predator) treatments. Values are the mean and one SEM for each treatment; $N = 9$ 58

Figure 9: Behavior of male *Anolis sagrei* in both control (nonpredator) and experimental (predator) treatments. (a) Proportion of time spent signaling. (b) Number of head bobs per display. Values are the mean and one SEM for each treatment; $N = 9$ 59

Figure 10: Change in the physical properties of head bob displays given by male *Anolis sagrei* in response to the presence of *Leiocephalus carinatus* and its effects on the signaling active space. (A) Maximum amplitude of headbob displays given in both control (nonpredator) and experimental (predator) treatments. Values are the mean and one SEM for each treatment; $N = 9$. (B) Illustration of the differences in conspecific active signaling space of *A. sagrei* on predator and nonpredator islands. The active space of a typical headbob display from a lizard on a predator island (solid line; 3.7 m) is smaller than the active space of a typical display from a lizard on a nonpredator island (dashed line; 5.8 m). Circles demarcate the area within which an anoline receiver would be maximally stimulated by a typical signal given by a lizard on a predator island (solid circle) and a typical signal given by a lizard on a nonpredator island (dashed circle), assuming that the signaling lizard is located at the center of the circle. The x- and y-axes are used simply to scale the two circles in meters. 60

Acknowledgements

This dissertation would not have been completed without the support, guidance, and encouragement of my mentor, Manuel Leal. My committee members – Susan Alberts, Vikas Bhandawat, Leo Fleishman, and Sönke Johnsen – also provided invaluable advice on all aspects of this work. My friends and colleagues in the Leal lab – especially Brian Powell, Alex Gunderson, Maria Campano, and Ellee Cook – helped improve the quality of my research in both the field and lab. Maria Campano, Angela Les, Dustin Owen, Jonathan Steinberg, and Arthur Steinberg toiled in the field to assist in data collection. Holland Steinberg offered unparalleled moral support and practical assistance with figures. Anne Lacey made life in graduate school run a bit more smoothly. Jason Kolbe, Jonathan Losos, Tom Schoener, and Dave Spiller were collaborators on the Bahamas project. John Endler and Mike Ryan helped improve the quality of the Bahamas manuscript with insightful comments. Staff members at El Verde Field Station in Puerto Rico, Mata de Platano Field Station in Puerto Rico, and La Selva Field Station in Costa Rica supplied logistical support. Permission for fieldwork was granted by the Bahamas Ministry of Agriculture, the Bahamas Environment, Science, and Technology Commission of the Ministry of the Environment, Ministerio de Ambiente, Energía y Mares de Costa Rica, and Departamento de Recursos Naturales y Ambientales de Puerto Rico. Funding was provided by the National Science Foundation

(Graduate Research Fellowship), Duke University's Graduate School (James B. Duke Fellowship, Bass Fellowship, International Research Dissertation Travel Award), Duke University's Department of Biology (Causey Fund), Duke University's Center for Latin American and Caribbean Studies (Mellon Research Travel Grant), the North Carolina Academy of Science (Robert R. Bryden Award), the Duke Chapter of Sigma Xi (Sally Hughes-Schrader Travel Grant), the Organization for Tropical Studies (Tyson Fellowship), and The Herpetologists' League (E.E. Williams Research Grant).

1. Introduction

Selection favors signal designs (i.e., physical properties or forms) that increase the probability that intended receivers will detect and respond to the signal (Guilford and Dawkins 1991, 1993), while limiting the probability of detection by unintended receivers (e.g., predators or parasitoids) [Endler 1992, Endler and Basolo 1998]. The evolution of signal design, therefore, is influenced by factors that impact signal detectability, such as characteristics of the sensory systems of receivers, as well as the physical and social conditions of the signaling environment (Hailman 1977, Guilford and Dawkins 1991, Endler 1992, Endler and Basolo 1998, Akre et al. 2011). Over the last several decades, researchers have identified a number of aspects of the signaling environment that are particularly important in shaping signal design. These include habitat spectral quality (e.g., Marchetti 1993, Leal and Fleishman 2004, Doucet et al. 2007), background noise level (e.g., Douglas and Conner 1999, Feng et al. 2006), predator presence and/or density (e.g., Endler 1980, Ryan et al. 1982), and the spatial relationship of signalers and receivers (Wiley and Richards 1978, Brumm and Slater 2006).

Many of these environmental conditions fluctuate over the lifetime of an individual or even over the course of a day, which can have obvious consequences for the effectiveness of a particular signal design (Bro-Jørgenson 2010). Organisms can deal with these fluctuations in a three major ways. First, if the signal design is invariant, an animal can restrict its display activity to particular times or locations at which conditions

are "ideal" for communication with that design (e.g., Zelick and Narins 1985, Endler and They 1996). Alternatively, an animal relying on a signal with an invariant design can couple that signal with signals of different design or sensory modality (i.e., communicate using multicomponent signals or multimodal displays) to increase the probability that intended receivers will detect the signaling individual under a variety of signaling conditions (Partan and Marler 2005, Wilgers and Hebets 2011). This redundancy will safeguard the display against random fluctuations in noise level in one communication channel (Rand and Williams 1970, Wiley 1983, Krebs and Dawkins 1984). Finally, if an animal uses a dynamic signal (e.g., acoustic or movement-based), it can modulate certain physical properties of the signal to compensate for immediate changes in conditions of the signaling environment (Potash 1972, Cynx et al. 1998, Brumm et al. 2004, Peters et al. 2007). Theoretically, exhibiting such flexibility in signal design (or signal modulation) is the most advantageous strategy because the design can be fine-tuned to maintain optimal detectability even as conditions fluctuate along a continuous scale (Ord et al. 2010).

The role that signal modulation plays in the short-term (i.e., immediate or over a lifetime) adaptation of animals to signaling environments in flux has received increasing attention recently (e.g., Verzijden et al. 2010, Proppe et al. 2011), but little is known about the contextual or taxonomic generality of the strategy (e.g., Brumm and Slabbekoorn

2005). In this dissertation, I use *Anolis* lizards as a model system for further investigating the use of signal modulation in animal communication systems.

Anoles communicate visually using two channels: color and motion. In anoles, color, particularly that of the dewlap, seems to be relatively invariant over the lifetime of an individual. Movement-based signals of *Anolis* (i.e., motion patterns of the head, or head bobs; Jenssen 1977), on the other hand, appear to be quite flexible (Ord et al. 2010). Furthermore, recent studies have identified the parameters of moving stimuli that are important for the detection of motion by one species of anole (Pallus et al. 2010). This work provides a foundation upon which further characterization of the *Anolis* motion detection system can be built, and allows for the development of specific predictions about which physical properties of a signal should be adjusted, and how they should be adjusted, when conditions of the signaling environment change.

In Chapter 2, I characterize the spatial parameters of visual motion detectors in several species of *Anolis* lizard from Puerto Rico in an effort to determine whether the sensory system is conserved in this clade. In Chapter 3, I test whether anoles in the wild can modulate the amplitudes of their movement-based displays to maintain stimulation of the receiver sensory system in the face of changes in signaler-receiver distance. I use sensory system data to predict the extent of modulation that might be expected. A version of this chapter was published as: Steinberg, D. S. & Leal, M. 2013. Sensory system properties predict signal modulation in a tropical lizard. *Animal Behaviour*, 85,

623–629. Finally, in Chapter 4, I assess the ability of Bahamian anoles to modulate their motion signals in response to different levels of predation pressure. Predation pressure has been known to be a strong selective force in the evolution of displays across a wide variety of sensory modalities. This assessment utilized a large-scale manipulation of lizard communities in nature. A modified version of Chapter 4 was published as:

Steinberg, D. S., Losos, J. B., Schoener, T. W., Spiller, D. A., Kolbe, J. J. & Leal, M. 2014.

Predation-associated modulation of movement-based signal by a Bahamian lizard.

Proceedings of the National Academy of the Sciences USA, 111, 9187–9192.

2. Visual motion detection in *Anolis* lizards

2.1 Introduction

Biologists have long been interested in how organisms sense and respond to stimuli in their environments. A general pattern that has emerged from this research is that, regardless of sensory modality, perception is influenced by physical characteristics of the stimulus, environmental conditions under which perception occurs, and properties of the sensory system (see Dusenbery 1992 and references therein).

The perception of visual stimuli has been a major area of inquiry in sensory ecology. Much of this work has focused on coloration (e.g., Endler 1978, Endler 1983, Briscoe & Chittka 2001, Leal & Fleishman 2002, Lucas et al. 2003, Osorio & Vorobyev 2005). However, for visually oriented organisms, the process of visual motion detection is also crucial to survival and reproduction, allowing for the assessment of risk (e.g., Schleidt 1961, Layne 1988, Wisenden & Harter 2001), location of food sources (e.g., Martel and Dill 1995, Zaret 1980), and identification of potential mates (e.g., Zeil & Zanker 1997, Martins et al. 2005) or rivals (e.g., Mizutani et al. 2003). Despite the importance of motion detection to many organisms' daily activities, the degree of interspecific variation in the perception of visual motion remains largely unexplored.

Theoretical and empirical evidence suggest that the neural circuits that drive elementary motion detection in vertebrates are likely Reichardt or 'correlation-type' motion detectors (Reichardt 1961, Borst & Egelhaaf 1989, Haag et al. 2004, Pallus et al.

2010). Under this model, whether a particular moving stimulus effectively attracts the attention of an individual depends on the pattern and displacement of a movement, along with the time it takes for the movement to be completed (Reichardt 1961, Borst & Egelhaaf 1989). However, neither the spatial nor temporal parameters of motion detectors are inherent to the correlation model, but instead may be determined by response properties of neurons in the retina (Borst & Egelhaaf 1989). The extent to which these parameters vary across species is currently unknown, as are any potential selective pressures that might be responsible for generating any such variation.

Studies addressing the evolution of sensory systems across species have revealed two main patterns. First, properties of sensory systems may diverge extensively, even between closely related species, often in response to interspecific differences in habitat preference. This finding has been particularly common in aquatic organisms, in which divergence in photoreceptors or spectral sensitivity between species is correlated with interspecific differences in conditions of the signaling environment (see Boughman 2002 and references therein). Second, sensory system properties may remain highly conserved across species living in distinct habitat types (e.g., Ache & Young 2005, Neuhofer et al. 2008).

Due to their species richness and reliance on vision for most daily activities, lizards in the genus *Anolis* provide a unique opportunity to evaluate broad patterns in sensory ecology, particularly the evolution of visual system traits (Losos 2009).

Furthermore, in the West Indies, species co-vary in morphology and ecology, and can be grouped into ecomorphological categories based on these traits (Williams 1972, 1983).

Such 'ecomorphs' have evolved independently repeatedly across the anole radiation, are somewhat restricted to relatively distinct structural microhabitats, and exhibit suites of behavioral, morphological, and physiological adaptations to their particular structural niches (Losos 2009). This existence of ecomorph classes allows for an exploration of how environmental factors might shape sensory system properties. Finally, a considerable amount of work already has been conducted on the *Anolis* eye in general (e.g., Underwood 1970, Fleishman 1992) and on motion detection in particular (e.g., Fleishman 1992).

Recently, Fleishman and colleagues (Fleishman and Pallus 2010, Pallus et al. 2010) identified the likely temporal and spatial constants of correlation-type elementary motion detectors in the Cuban brown anole, *Anolis sagrei*. The temporal constant was exceedingly short, probably due to the fact that most important movements in a natural, daytime scene (i.e., the movements of other animals, both prey and potential predators) are typically rapid. Square wave-like or jerky movement patterns that caused the image of the stimulus to move quickly from one receptor to its partner receptor were the most effective stimuli (Fleishman & Pallus 2010). More recently, Steinberg and Leal (2013) measured the spatial parameters of the motion detection system of the Puerto Rican *Anolis gundlachi* and found a pattern relatively similar to that of *A. sagrei*. The

congruence of the results suggests that motion detection systems might be relatively conserved in the *Anolis* clade.

Here we evaluated the hypothesis that motion detection systems are conserved across species of anole, even when those species occupy distinct structural niches, which could potentially drive divergence in motion detection systems due to differences in visual background motion. We quantified the motion detection systems of multiple species of Puerto Rican *Anolis* lizards, with each preferring a distinct structural habitat type. We then compared the results to data previously collected for anoles from Cuba, Puerto Rico, and Central America.

2.2 Methods

2.2.1 Focal Species

Anolis cristatellus, *A. evermanni*, and *A. krugi* are closely related lizards endemic to the Puerto Rican island bank (Figure 1; Brandley and de Queiroz 2004, Nicholson et al. 2005). Anoles, including those species studied here, communicate to conspecifics with highly stereotyped motion patterns of the head and/or dewlap (Ruibal 1965, Philibosian 1975, Ortiz and Jenssen 1982, Schwartz and Henderson 1991, Ord et al. 2007). The head-bobbing portions of these displays often consist of extremely rapid linear movements (Ord et al. 2007, Fleishman and Pallus 2010) that are highly conspicuous to correlation-type elementary motion detectors (Fleishman and Pallus 2010).

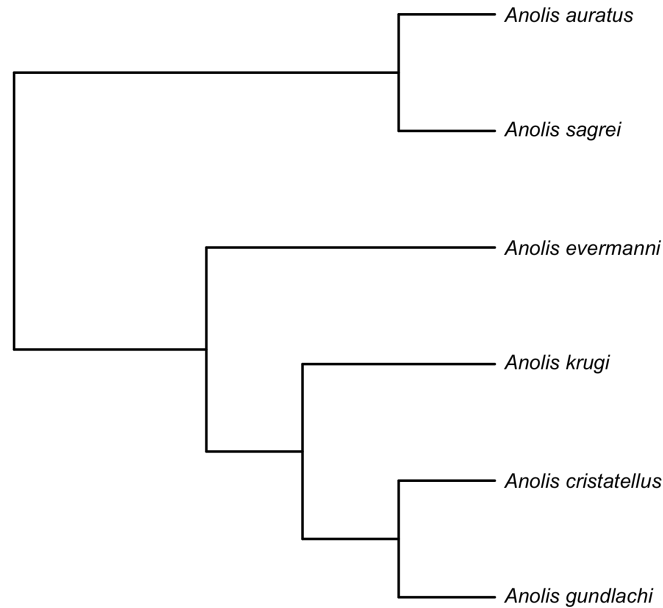


Figure 1: A phylogeny including the *Anolis* species considered in this study. Relationships are based on Brandley & de Queiroz (2004) and Nicholson et al. (2005).

Although all three species can be found in sympatry, they inhabit distinct structural microhabitats. In the ecomorphological parlance of the *Anolis* literature, *A. cristatellus* is a ‘trunk-ground’ anole that typically perches on moderate- to large-diameter tree trunks within 2 m of the ground (Rand 1964, Losos 1990). *Anolis krugi* is a ‘grass-bush’ anole usually found less than 1 m from the ground on small-diameter trunks and stems, and *A. evermanni* is a ‘trunk-crown’ lizard that occupies large-diameter trunks and branches in the forest canopy (Rand 1964, Losos 1990). These differences in perch height and diameter also contribute to differences in vegetation

structure, such as cluttering or complexity (Powell and Leal 2013), which could affect the qualities of the motion environments of the various ecomorphs.

2.2.2 Motion Detection Experiment

We captured male lizards in their natural habitat in Puerto Rico (*A. cristatellus* in Guánica State Forest, *A. evermanni* in the vicinity of El Verde Field Station, and *A. krugi* in the forest surrounding Mata de Plátano Field Station) and immediately transferred them to a laboratory.

We measured the spatial motion detector properties of the three species under the same protocol followed by Steinberg and Leal (2013) for *A. gundlachi*. Fleishman and colleagues originally developed a similar methodology to characterize motion detection parameters of *A. auratus* and *A. sagrei* (Fleishman 1986, Pallus et al. 2010). Briefly, once in the laboratory lizards were maintained in transparent, plastic test cages (23 x 16 x 17 cm, with a horizontal wooden perch) for 24–48 h prior to the experiment. During testing we presented each subject with nine motion detection trials (eight experimental and one control) that consisted of a black cylindrical target (diameter = 5 mm, height = 5 mm) moved against a white background by a programmable linear actuator stepper motor in a single cycle, 0.8 Hz, square wave-like pattern (duration of each movement = 0.066 s). Trials were identical except for amplitude of motion (0.1, 0.25, 0.5, 0.75, 1.0, 1.25, 1.75 or 2.5° visual angle). A more detailed description and schematic of the experimental set-up can be found in Figure 2 and Steinberg and Leal (2013).

When the image of an object with particular motion characteristics travels across the peripheral retina of an organism, it elicits a shift in gaze known as the 'visual grasp reflex' (Ingle 1982, Fleishman 1992). The gaze shift foveates the object, thereby focusing an individual's direct attention on it (Ingle 1982). We considered any shift in gaze via eye or head movement by an individual towards the stimulus within 3 s of the end of target motion as a positive response (i.e. an indication of stimulus detection), and the absence of a gaze shift as a negative response. To account for random eye movements, we subjected each individual to a control trial, during which the target was set in motion with a randomly chosen amplitude, but was visually obstructed ($= 0^\circ$ visual angle in Fig. 3). Trials were separated from one another by at least 1 h to avoid habituation and were presented in random order, with the experimenter blind to the amplitude of motion being presented during each trial.

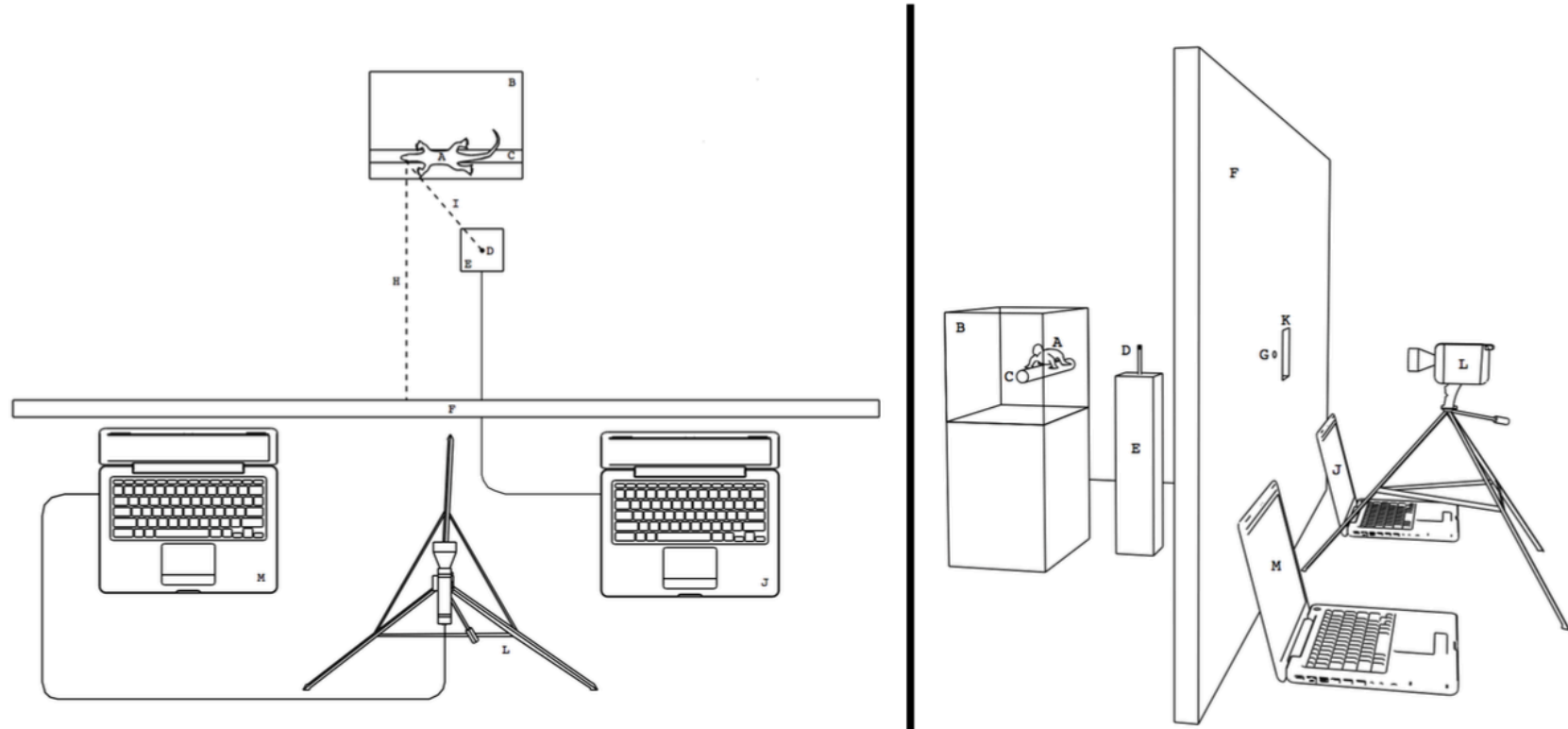


Figure 2: Schematic of the laboratory set-up for the motion detection experiment in plan (left) and perspective (right). A subject lizard (A) is maintained in a plastic test cage (B) with transparent walls and a horizontal wooden dowel rod (C, diameter = 19 mm). The edge of the dowel is located 3 mm from the front wall. The cage is then placed so that the eye of the lizard is located 17.5 cm from a black target (D). The target is attached to a thin white cylinder that is moved by a Haydon Kerk linear actuator stepper motor. The motor is enclosed in a white box (E). A bare 72 watt (1490 lm) halogen light bulb hangs 45 cm above the target, with light diffused by a square of translucent vellum located 30 cm below the bulb (bulb and vellum not shown). A white, wooden board [F, 130 x 46 cm (l x w)] serves as both a background for the target and a blind for the experimenter. Prior to the

trial, the lizard is encouraged to perch on the dowel rod by gently rotating the cage. A thin metal nail is then pushed through a small circular hole (G) in the blind to draw the gaze the lizard directly to its side along a line running perpendicular to the dowel (H). With its gaze on the nail, the target is located along a line (I) running 40 degrees from H. Fifteen seconds after the gaze shift, a laptop (J) is used to initiate movement of the target. The eye of the lizard is filmed through a small window (K, 6.5 x 6.5 cm) in the blind using a tripod-mounted camcorder (L). The camcorder is connected to another laptop (M) to magnify the image of the eye for easy characterization of the lizard's response. During control trials, a white blind is placed along line (I) to block the lizard's view of the target.

2.2.3 Data Analysis

We only included data from individuals that responded positively to at least one trial (*A. cristatellus*: $N = 36$, *A. evermanni*: $N = 30$, and *A. krugi*: $N = 50$). Based on this dataset, we quantified the relative responses of all three species to each stimulus trial. First, we determined the total number of individuals that responded to the stimulus amplitude that elicited the most positive responses (= maximum response). We then calculated the proportion of individuals that responded to each stimulus amplitude, relative to the maximum response. We also used data from previous studies to examine the relative motion detection responses of two additional species of anole (*A. gundlachi* from Steinberg and Leal 2013 and *A. sagrei* from Pallus et al. 2010). These anoles are included in the phylogeny shown in Figure 1.

2.2.4 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.

2.3 Results

The relative responses of *A. cristatellus*, *A. evermanni*, and *A. krugi*, to the eight experimental stimuli and control trial (0° visual angle) are presented in Figure 3 (a-c).

Several broad-scale similarities are apparent. Individuals of the three species exhibited an extremely limited response to the experimental trial with the smallest amplitude (0.1° visual angle), shifting their gazes two to three times less frequently than during the most stimulating trial. Relative responses then increased to an initial peak at 0.25° in *A. cristatellus* and *A. krugi* and 0.5° in *A. evermanni*. Responses peaked again at least once for all three species before eventually dropping during high amplitude trials (2.5°). Individuals of the three species responded approximately five times less frequently to the control trial than to the trial that elicited the most responses. Raw data for the responses of the three species to all trials are presented in Table 1.

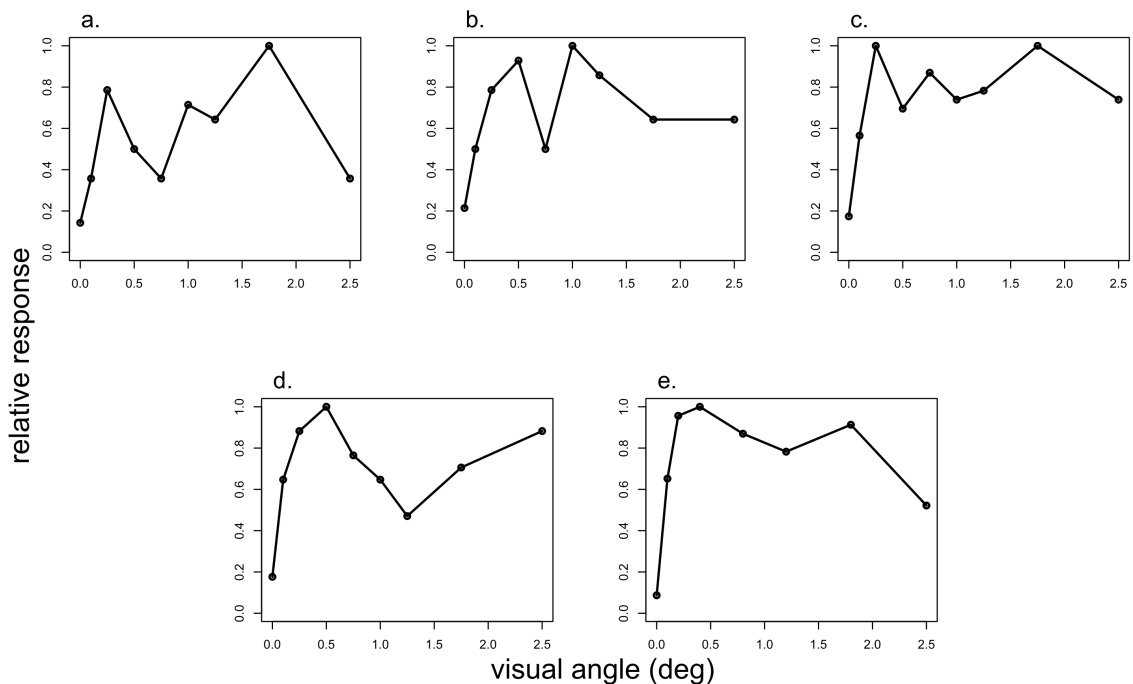


Figure 3: The relative responses of five species of *Anolis* lizard to moving stimuli with differing amplitudes. Each point indicates the proportion of individuals in a species that responded to a given motion amplitude relative to the number of

individuals in a species that responded to the most stimulating motion amplitude. Please note that 0° visual angle represents the control trial, during which the moving stimulus was visually obstructed from the test subject. Data for *A. cristatellus* (a), *A. evermanni* (b), and *A. krugi* (c) were collected during the course of this study. Data for *A. gundlachi* (d) are taken from Chapter 3 and Steinberg & Leal (2013), and those for *A. sagrei* (e) are from Pallus et al. (2010).

Although the motion detection curves of the species are similar in general pattern, they differ in some details, namely the precise number and values of their relative peaks (Figure 3). These differences in peak values and number show no obvious relation to ecomorph class (i.e., broad scale habitat preference) or shared evolutionary history.

Using data from previous studies, we have included in Figure 1 (d-e) relative response curves for another Puerto Rican ‘trunk-ground’ anole, *A. gundlachi* (Chapter 3, Steinberg and Leal 2013), and for a ‘trunk-ground’ anole from a separate radiation, the Cuban *A. sagrei* (Pallus et al. 2010). These curves suggest that the motion detection responses of *A. gundlachi* and *A. sagrei* are similar to those of the three species measured in the present study. One prominent difference is that the response of *A. gundlachi* does not plummet during the 2.5° amplitude trial.

Table 1: Raw experimental data for three species of *Anolis* lizard. The ecomorphological class, sample size (*N*), and number of individuals that responded to each stimulus are presented for each species. The 0° column represents the control trial.

Species	Ecomorph	<i>N</i>	0°	0.1°	0.25°	0.5°	0.75°	1.0°	1.25°	1.75°	2.5°
<i>Anolis cristatellus</i>	Trunk-ground	36	2	5	11	7	5	10	9	14	5
<i>Anolis evermanni</i>	Trunk-crown	30	3	7	11	13	7	14	12	9	9
<i>Anolis krugi</i>	Grass-bush	50	4	13	23	20	20	17	18	23	17

2.4 Discussion

For visually oriented organisms, the mechanisms underlying the process of detecting visual motion can greatly influence survival and reproductive success. However, not much is known regarding the extent to which motion detection properties vary across species or the potential factors contributing to variation between species. Here, we examine such questions using *Anolis* lizards. One of the most striking results of our investigation is the increase in relative response that occurs between the 0.1 and 0.25° stimulus trials in each of the five species of anole that we considered (Figure 3). This congruence suggests a shared threshold for motion detection at an amplitude between these two values. A similar threshold around 0.25° is also present in a Central American grass anole, *A. auratus* (Fleishman 1986). Like *A. sagrei*, *A. auratus* is only distantly related to the Puerto Rican species included in this study (see Figure 1; Brandley and de Queiroz 2004, Nicholson et al. 2005), supporting the hypothesis that a specific motion detection threshold is a common characteristic of the visual system of *Anolis* lizards. This evidence strongly suggests that the motion detection systems of *Anolis* lizards are relatively conserved at a broad scale.

A shared motion detection threshold may reflect physical constraint resulting from the morphological characteristics of the anole eye. The peripheral retina mediates the visual grasp reflex and, in the typical anole with perfect optics, has an estimated minimum resolvable angle of 0.04° (Fleishman 1986). Pupil-related diffraction and lens

effects, however, could lower peripheral acuity to the motion detection threshold observed here (Fleishman 1986). If optical factors do not reduce the acuity to this extent, the threshold may result from lower-order processing that filters out non-relevant motion in visually noisy environments, such as those of the species considered in this study. Detailed ophthalmological examination of the anole eye and a comparison of the motion detection parameters of *Anolis* species inhabiting two highly distinct habitat types, such as arboreal and aquatic habitats, might help distinguish between these two possibilities.

Beyond a shared motion detection threshold, all five species in Figure 3 also appear to exhibit multiple peaks in their relative response to the stimulus trials. For example, *A. cristatellus* showed elevated responsiveness to movements of 0.25° and 1.75° , and possibly to 1.0° , while *A. evermanni* appears to have shifted its gaze more frequently to stimuli with amplitudes of 0.5° and 1.0° than to stimuli with other amplitudes. The precise locations of these peaks, being associated with higher probabilities of detecting a particular motion amplitude, can have impacts on many aspects of the behavior of individuals, such as those related to communication (Fleishman and Pallus 2010, Ord et al. 2013, Steinberg and Leal 2013, Steinberg et al. 2014) and prey and predator detection (Pallus et al. 2010). More experiments, therefore, are required to determine the extent to which interspecific differences in peak response values might affect (or be affected by) the ecology of different species.

Although the precise number of response peaks present in each species remains unclear, the multi-peak pattern exhibited by all the species supports the argument that *Anolis* may possess multiple motion detection channels (Pallus et al 2010). The neural architecture responsible for these multiple channels might arise from spatially overlapping correlation-type elementary motion detector arrays with different temporal constants, as found in other organisms (Nalbach 1989, Hammet et al. 2000) and suggested by Pallus et al. (2010). Alternatively, an individual may possess multiple correlation-type elementary motion detectors arrays with identical temporal constants, but different spatial constants. Regardless of the underlying circuitry, having multiple motion detection channels should reduce the effects of achromatic contrast on motion detection, while also allowing individuals to determine the velocity of moving objects (Pallus et al. 2010). The latter ability is crucial for decision-making processes related to prey capture and predator avoidance, and is one of the major shortcomings of correlation-type motion detectors that consist of only a single array.

Four of the five species exhibit a drop-off in response to the 2.5° amplitude stimulus (Figure 3). This reduction in sensitivity to higher amplitude movements, although counterintuitive, may provide a similar filtering function to the motion detection threshold discussed above. Because *Anolis* lizards are mainly arboreal, they tend to inhabit relatively cluttered environments and are often surrounded by branches, twigs, and leaves. Although these objects generally move in a sinusoidal fashion, any

sudden movement of vegetation near an individual would subtend a relatively large amplitude arc at that individual's eye, potentially triggering the retina's elementary motion detectors. A motion detection system with an upper limit might help avoid these false alarms. Interestingly, the sole deviation from the pattern of limited response at 2.5° is *A. gundlachi*. The microhabitat of this species is significantly less complex than those of *A. cristatellus*, *A. evermanni*, and *A. krugi* (Powell and Leal 2014) and most likely less complex than that of *A. sagrei*, which uses a microhabitat similar to *A. cristatellus* (personal observation). These findings allow for the possibility that structural habitat characteristics may, at least partially, influence motion detection parameters.

Although structural habitat complexity could slightly affect the properties of motion detection systems, ecomorphological distinctions *per se* do not appear to correlate with the spatial motion detector parameters that we examined. While our results indicate more similarities between species than differences, the differences that we did detect, namely in peak response values and the drop-off in response at 2.5°, showed no clear pattern of association with ecomorph class. There may be several explanations for these findings. First, recent studies have shown that ecomorph categories do not necessarily capture fine-scale variation in habitat complexity (Johnson et al. 2006, Powell and Leal 2014). Therefore, ecomorph classification may be too broad to identify effects of habitat structure on motion detection. Second, attributes shared across most species of anole (e.g., insectivory, susceptibility to bird predation,

arboreality) simply may have a greater effect on motion detection parameters than do attributes in which species differ, particularly structural niche. Third, as discussed earlier, physical constraints related to visual acuity might play a role in shaping traits, such as the motion detection threshold, thereby preventing any possible influence of ecomorphology. Finally, because we considered species from multiple clades, we cannot rule out the possibility that as a clade *Anolis* lacks lability in motion detection traits.

Numerous studies have shown that variation in sensory system properties can drive divergence in signaling traits (e.g., Hebets & Uetz 1999, Leal & Fleishman 2002, Seehausen et al. 2008, Tobias et al. 2010). This process has been demonstrated across sensory modalities [see Boughman (2002) and references therein], but interestingly, not for signals relying on visual motion. The similarities in response to moving stimuli presented here might help explain a conspicuous pattern in communication behavior seen across *Anolis*. Fleishman and Pallus (2010) pointed out that the presence of certain motion detection properties, if shared by most species of anole, could account for the observation that species throughout the clade use square-wave-like headbob signals. We show that square wave-like movements are effective in eliciting a behavioral response from multiple species of anole, suggesting that sensory response may indeed shape fundamental features of the movement-based displays of *Anolis* lizards. Investigating the factors, whether stochastic or selective, that might be responsible for the fine-scale

variation (e.g., number and pacing of bobs) in visual motion signals is a potentially fruitful avenue of future research

3. Sensory system properties predict signal modulation in a tropical lizard¹

3.1 Introduction

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 behavior. 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, signalers 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 signaler (Guilford & Dawkins 1991); (2) spacing of animals in a habitat is relatively fluid, leading to frequent changes in the distance between signalers 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 species.

¹ A version of this chapter was published as: Steinberg, D. S. & Leal, M. 2013. Sensory system properties predict signal modulation in a tropical lizard. *Animal Behaviour*, 85, 623–629.

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). Signaling 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, signalers 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, signaling behavior and sensory biology of *Anolis* lizards makes them an ideal model system for evaluating the potential use of signal modulation as 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 neighbors, rival males, and potential mates is fluid (Stamps 1977a, Jenssen & Nunez 1998, Jenssen et al. 2001). When signaling to these other individuals, anoles communicate using dewlap flashes and motion patterns of the head, or head bobs, 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 head bobs 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 auratus* 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* head bobs. 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 head bobs. 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 occurs and 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.

3.2 Methods

3.2.1 Study species and site

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).

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).

3.2.2 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 behavioral 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 x 16 x 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 Figure 5). 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 *Chapter 2* (Figure 1).

3.2.3 Field experiment: testing for distance-based signal modulation

3.2.3.1 Experimental design

Data were collected during 15–21 July 2011 at El Verde Field Station. To induce directed visual displays from potential signalers, we introduced tethered adult males (receivers) into the territories of other adult male *A. gundlachi* (signalers) (sensu Evans 1938; see Figure 4). First, we captured a receiver and secured it to the surface of a small, transparent box (15 x 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 behavior. 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 signaler was perched. A minimum of 20 m separated the site of receiver capture and the territory of the signaler to avoid the possibility of confounding effects of familiarity on behavior (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 signaler, we then filmed the first motion display directed towards the receiver.

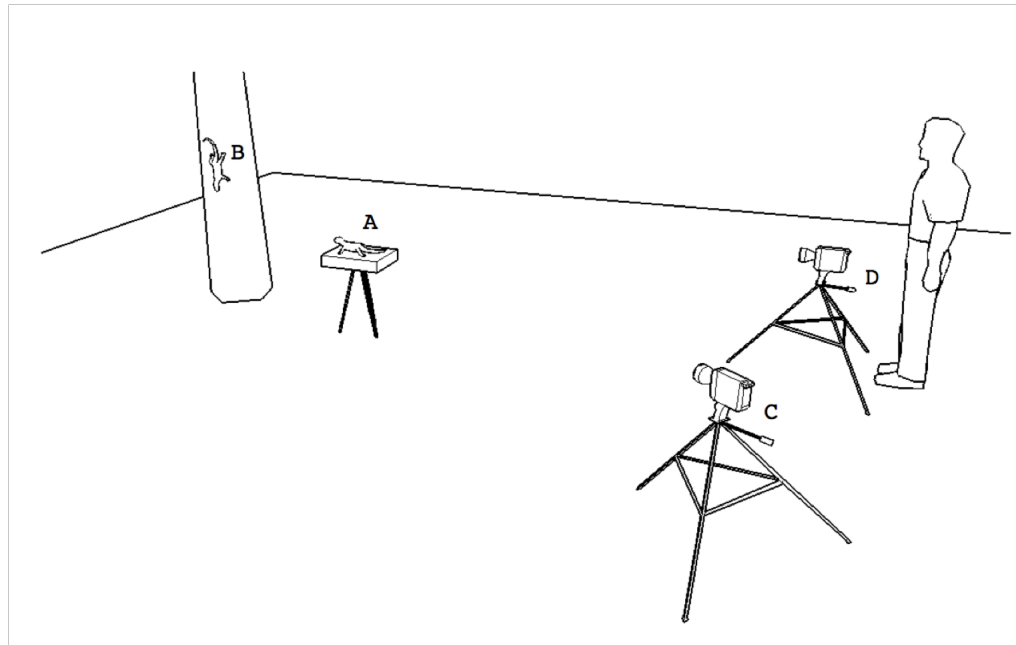


Figure 4: Schematic of the field set-up for the *Anolis gundlachi* receiver distance experiment. The 'receiver' (A) is introduced to the territory of the 'signaler' (B). One camcorder (C) films the behavior of the receiver, while another camera (D) films the headbob display of the signaler.

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 behavior of the receiver throughout the trial using a tripod-mounted Canon ZR950 mini-DV video camera to control for receiver behavior (see Figure 4). 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 signaler 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 signaler 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 signalers escaped before capture) and marked them before releasing them at their original site of collection. No individual served as a signaler 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).

3.2.3.2 Video analysis

We restricted video analysis to the first 10 s of the first display given by each signaler 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 signaler) 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 analyzed the video footage of the receivers to record their behavior.

3.2.4 Statistical analysis

We used Spearman rank correlations to test for associations between the maximum amplitude of displays and distance, wind speed, and signaler body size (SVL). We used a Bonferroni correction to account for multiple comparisons, with $\alpha =$

0.0125. The sample size for the amplitude x body size correlation was smaller than the sample sizes for the other correlations because not all signalers could be captured following the trials. All statistical tests were performed in R (R Development Core Team 2009).

3.2.5 Predicting the range of amplitudes that maximize signal detection

The visual angle (θ) of a movement (i.e., apparent amplitude) varies predictably with distance according to the simple tangent function: $\theta = 2 \arctan(S/2D)$, 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 signaling individual.

3.2.6 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.

3.3 Results

3.3.1 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 ($N = 47$; Figure 5). A second increase in motion detection appeared to occur at an apparent amplitude of 2.5° (Figure 5). 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.

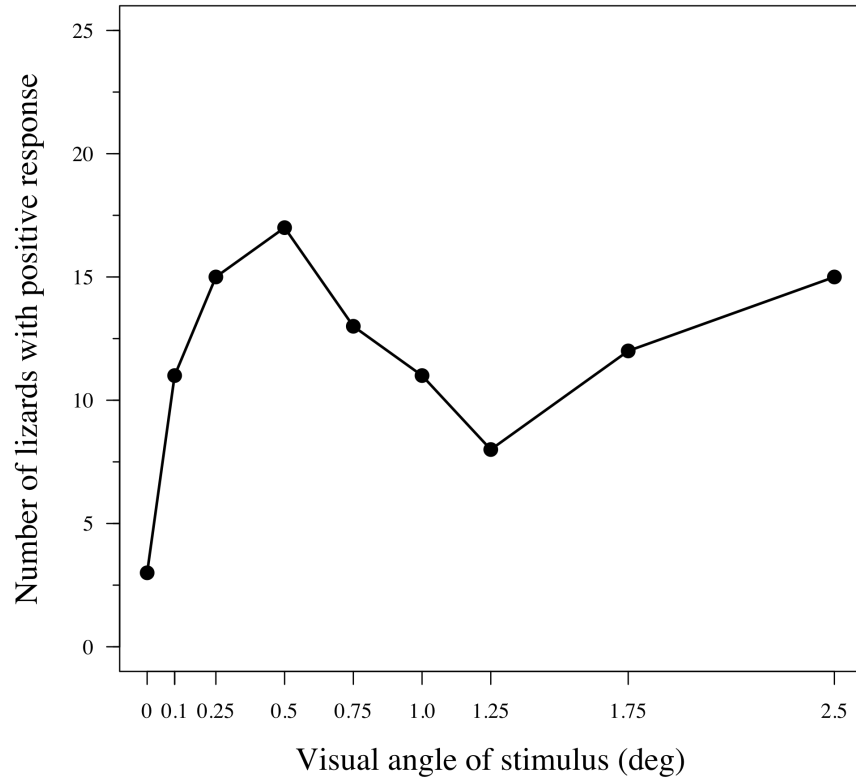


Figure 5: Total number of male *Anolis gundlachi* that positively responded to moving stimuli with different apparent amplitudes (in degrees of visual angle). Note: a visual angle of 0° indicates the control trial. Apparent amplitudes in the range of 0.25–0.75° are most frequently detected by individuals.

3.3.2 Field experiment

A typical trial consisted of four phases. (1) The signaler, likely startled by the introduction of the apparatus holding the intended receiver (see Figure 4), retreated to the side of the perch opposite the receiver. (2) After 0.5 to 5 min, the signaler 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 signaler oriented itself such that its body was presented laterally to the receiver. The signaler then produced its initial headbob display, generally a highly stereotyped square wave-like pattern resulting from combined motion of the head and body (see Figure 6). 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 signaler 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 signaler 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 behavior, such as nuchal crest extension, lateral compression and darkening of the body (Rand 1967, Jenssen 1977, Ortiz & Jenssen 1982). For the signaler, this final stage appeared to represent a transition from an initial alert display to aggressive signaling.

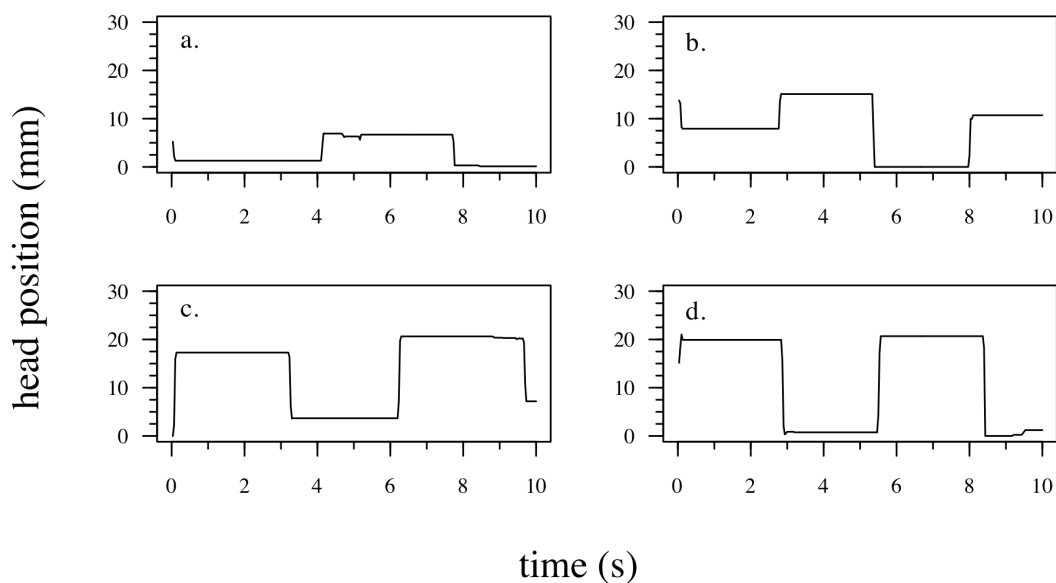


Figure 6: Representative time-motion graphs for directed headbob displays of four male *Anolis gundlachi* to receivers located (a) 66 cm, (b), 93 cm, (c) 150 cm, and (d) 202 cm away from the signaler. For each display, the trace follows the head position of the lizard along a linear axis (*y* axis, mm) 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 signalers in all trials. Therefore, the first signal given by the signaler should not have been influenced by the signaling behavior of the receiver. Wind speed also had no significant effect on the maximum amplitude of the display given by the signaler (Spearman rank correlation: $r_s = -0.078$, $N = 57$, $P = 0.563$). Similarly, body size of the signaler had no effect on display amplitude (Spearman rank correlation: $r_s = 0.189$, $N = 45$, $P = 0.213$). However, the distance between the signaler and receiver had a significant positive effect on the maximum amplitude of the display. As the distance between the

signaler and receiver increased, so did the maximum amplitude of the display given by the signaler (Spearman rank correlation: $r_s = 0.547$, $N = 57$, $P < 0.001$; Figure 7).

Furthermore, signalers 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 (Figure 7).

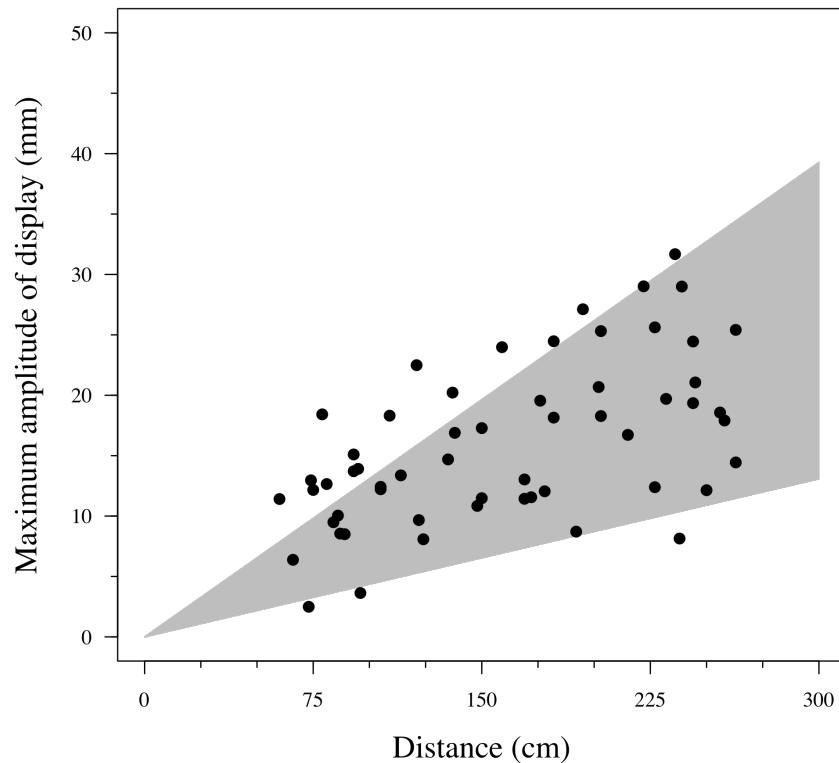


Figure 7: Correlation between receiver distance and maximum amplitude of headbob displays in *Anolis gundlachi*. As receiver distance increases, the maximum amplitude of headbob displays given by signalers also increases. The majority of headbob displays have maximum amplitudes that fall within the range of predicted values (shaded regions) for maximal stimulation of the receiver's motion detection system.

3.4 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 head bobs are those expected based on the motion detection properties of *A. gundlachi* (see Figure 7) 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 signalers 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* (Figure 3, 5) are similar to those reported for *A. sagrei* (Pallus et al. 2010).

Whether this pattern of conservatism in detection parameters is a general one remains to be seen and requires direct experimental testing (see *Chapter 2* for more complete discussion of this topic). 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 head bobs 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 signaling 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 head bobs in response to the distance of potentially inattentive receivers, on a relatively fine spatial scale (Figure 7).

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 (Jensen 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-neighbor 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 signalers 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 signaler (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 Figure 7 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. gunldachi* 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-neighbor 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.

4. Predation-associated modulation of movement-based signals by a Bahamian lizard¹

4.1 Introduction

The process of communication is central to many aspects of social interaction, from attracting mates to establishing territories. The major prerequisite for communication is that an individual or its signal must effectively capture and hold the attention of intended receivers (Dusenbery 1992, Bradbury & Vehrencamp 1998). However, communication rarely occurs in a context free from the risk of predation, and thus the presence of predators is an important selective pressure on the physical designs of signals and the behaviors associated with their display (e.g., Endler 1980, Tuttle & Ryan 1981, Pocklington & Dill 1995, Zuk & Kolluru 1998, Hedrick 2000, Woods et al. 2007, Akre et al. 2011). In fact, predation pressure typically results in signals with reduced conspicuousness (i.e., the likelihood of being seen by a predator) at one or both of two timescales: (1) across generations (i.e., via evolutionary mechanisms) or (2) within the lifetime of an individual (i.e., via behavioral mechanisms). The evolution of less conspicuous signal properties in response to predation pressure has been demonstrated across signaling modalities, including acoustic, electrical, visual, and ultrasonic signals (e.g., Endler 1980, Stoddard 1999). Predation pressure also shapes the evolution of the

¹A version of this chapter was published as: Steinberg, D. S., Losos, J. B., Schoener, T. W., Spiller, D. A., Kolbe, J. J. & Leal, M. 2014. Predation-associated modulation of movement-based signal by a Bahamian lizard. *Proceedings of the National Academy of the Sciences USA*, 111, 9187–9192.

behaviors associated with the production of signals, often resulting in a shift in the amount of time spent signaling throughout the day or in the use of less vulnerable display sites (Burk 1982, Endler 1987, Lima & Dill 1990, Magnhagen 1991, Sih 1994, Brunel-Pons et al. 2011).

Behavioral changes favoring a reduction in the likelihood of communication-associated predation typically precede evolutionary changes (Lima & Dill 1990). This process most likely is driven by the plasticity of behavioral traits, which may change within the life-time of an individual. Therefore, elucidating the behavioral mechanisms by which organisms can decrease the conspicuousness of their signals in response to predation has become a major area of inquiry in behavioral and evolutionary ecology (Burk 1982, Magnhagen 1991, Zuk & Kolluru 1998).

An individual can behaviorally limit the conspicuousness of its signal to a predator via two non-mutually exclusive strategies. Commonly, individuals modulate the amount of time they spend displaying throughout the day. This response decreases the amount of time an individual is vulnerable to detection by a predator or narrows a signaler's temporal window of vulnerability (e.g., refs. Godin 1995, Koga et al. 1998, Jones et al. 2002). An alternative response is for an individual to modify the physical properties of its signal's design to decrease the ability of a predator to detect or localize the signaler (e.g., Bayly & Evans 2003). These changes often diminish the active space of a signal, which is defined as the maximum distance at which the signal can capture the

attention of a receiver. A smaller active space limits the probability of predation by shrinking the area over which a signal can be detected by a predator (i.e., narrowing the spatial window of vulnerability).

Visual signals frequently are used to study the effects of predation pressure on communication (e.g., Endler 1983, Hemmi et al. 2006, Stuart-Fox et al. 2007). Visual signals typically consist of both color and motion components, with motion often cited as the most salient feature of the display (Hailman 1977, Fleishman 1986, Clark & Uetz 1992). Nevertheless, most studies evaluating the effects of predation pressure on the conspicuousness of visual signals have focused on coloration and, in most cases, on changes on an evolutionary timescale (e.g., Cummings et al. 2003, Håstad et al. 2005, Kemp et al. 2009). Here, we evaluate the hypothesis that the movement-based visual signaling behavior of a prey species may change via behavioral mechanisms (e.g., modulation of signal properties or proportion of time spent signaling) to decrease conspicuousness and potentially limit predation risk.

We evaluate the effect of predation pressure on the physical properties of movement-based signals and on the proportion of time spent signaling by using a well-understood predator-prey system: the small semiarboreal lizard *Anolis sagrei* and one of its main predators, the much larger, mostly terrestrial curly-tailed lizard *Leiocephalus carinatus* [see Schoener et al. (1982) for photographs of this predator-prey interaction]. Previous experiments showed that curly-tailed lizards may be a major selective force on

A. sagrei, and their presence, even at low density, may greatly affect the demography and structural niche of *A. sagrei* (Schoener et al. 2002, Losos et al. 2004, Losos et al. 2006, Lopez-Darias et al. 2012). In response to the presence of curly-tailed lizards, male *A. sagrei* rarely use the ground, moving higher up in the vegetation to perches that usually are narrower and less exposed than those used by males where curly-tails are absent (Losos et al. 2004, Losos et al. 2006). Furthermore, this shift in habitat use may occur in a short period, and the magnitude of the response seems to be proportional to changes in the activity of curly-tailed lizards (Lopez-Darias et al. 2012). Finally, the perceived threat of predation is sufficiently strong that under natural conditions, if presented with a single curly-tailed lizard, individuals of *A. sagrei* will flee immediately at the mere sight of the predator (Losos et al. 2004).

In anoles, including *A. sagrei*, social interactions are mediated by visual displays, which combine abrupt movements of the head (head bobs) with expansion and retraction of a colorful throat fan, termed a “dewlap” (Greenberg & Noble 1944, Ruibal 1965, Scott 1984). These signals are given spontaneously by males to advertise their presence as they patrol their territories, as well as being directed toward other individuals during courtship and the settlement of territorial disputes (Jenssen 1977, Stamps 1977, Fleishman 1992). Theoretical predictions, supported by empirical data, have shown that the physical properties of headbob displays in *A. sagrei*, particularly the square wave-like temporal pattern generated by rapid changes in head position, are

highly conspicuous to visually oriented receivers, even when those receivers are inattentive (Fleishman & Pallus 2010, Pallus et al. 2010). The amplitude of these movements determines the maximum distance from which the sensory system of a conspecific is stimulated effectively by the signal—what is termed the “active space.” For a territorial species such as *A. sagrei*, the active space may affect an individual’s ability to repel rivals and attract mates from a distance (Fleishman 1992, How et al. 2008). Thus, in the context of social interactions, selection should favor signals that maximize active space. However, curly-tailed lizards, like anoles, are visually oriented, communicate using headbob displays that move along a vertical axis, and must detect prey that move in rapid bursts, suggesting that the visual systems of curly-tailed lizards also are likely to be sensitive to sudden linear movements (Noble & Bradley 1933, Evans 1953, Marcellini & Jenssen 1991) [also, see Pallus et al. (2010) for a discussion of visual motion detection]. As a result, male *Anolis* lizards in the presence of curly-tailed lizards may face contrasting selection pressures, because displays that maximize the conspecific active space (i.e., displays with high-amplitude head movements) should be beneficial with regard to intraspecific interactions but detrimental with regard to predator-prey interactions.

In this study, we used a replicated experimental design conducted under natural conditions to address the effects of the presence of *L. carinatus* on the signals (headbob displays) of *A. sagrei*. We predict that the amplitude of spontaneous head bobs, and thus

conspicuousness, should be lower for populations in which *L. carinatus* is present. Furthermore, we also expect to find a difference in the proportion of time spent signaling between populations, with a decreased proportion of time allocated to signaling in populations exposed to *L. carinatus*. Finally, we evaluate whether changes in signal properties might affect the efficacy of head bobs during social interactions by using an empirically derived motion detection model for *A. sagrei* to test for differences in the conspecific active space of signals.

4.2 Methods

4.2.1 Study site and experimental design

We examined lizard populations on nine small islands (mean vegetated area, $280 \pm 64 \text{ m}^2$) in the Snake Creek region of Great Abaco Island, Bahamas. These islands are characterized by a rocky substrate and dominated by relatively sparse shrubbery typically less than 2 m in height [see Schoener et al. (2002) for a general description of the vegetation on similar islands from this area]. The islands used for this study are a subset of those used for a larger experiment started in May 2008, which evaluates the impact of a top predator, *L. carinatus*, across multiple levels of the food web. In the latter experiment, 14 islands sustaining natural populations of *A. sagrei* were selected and divided into seven pairs matched by area, vegetation profile, and *A. sagrei* population size. For each pair, one island was randomly selected to introduce *L. carinatus* (experimental islands) and the other was left alone (control islands). *Leiocephalus*

carinatus occurs on nearby larger islands and is known to colonize the smaller islands (Schoener et al. 2002). Only adult *L. carinatus* were used as colonizers, and the number relocated to each island was proportional to the population size of *A. sagrei*. For this study, we sampled five experimental and four control islands chosen because of their accessibility (the remote location of some islands made them impractical for the intense monitoring of this project).

4.2.2 Data collection

Focal observations were conducted from May 18 to June 11, 2011, to characterize general aspects of the behavior of male *A. sagrei*. Observations were conducted from 0700 to 1900 hours on 240 males, for a total of 77.1 hours of observations. We visited each of the nine islands a minimum of seven times (range, 7–11 visits), walking systematically through each island until a lizard was located. The individual then was filmed with a portable mini-DV camcorder (Canon ZR-960) for ~20 min or until it moved out of sight (\bar{X} = 19.3 min; range, 5.1–22.7). Videos were analyzed later in the laboratory to extract relevant data. We calculated the mean perch height for each individual as the mean of all perches used during the observation period. These values were estimated during filming and then confirmed or amended when necessary using a tape measure immediately following the observation. Changes in perch height occurred when a lizard moved to a new perch (i.e., branch or trunk) or moved along the same perch a distance that exceeded the body length of the lizard. Proportion of time spent

signaling was calculated as the proportion of time an individual gave headbob displays and/or dewlap flashes during the observation period.

To evaluate whether the presence of curly-tailed lizards had an impact on the physical properties of the headbob displays of *A. sagrei*, we filmed spontaneous broadcast displays (i.e., nondirected displays given to advertise the presence of the signaler) of 39 adult male *A. sagrei* using a Canon GL2 mini-DV camcorder. Each individual was filmed only once, and we avoided resampling individuals by identifying each lizard with a unique mark that was applied before the study. We visited eight of the nine islands on at least four separate occasions, for a minimum of eight total hours per island (see Table S1 for detailed sampling efforts). We visited one island only twice, for 5.5 total hours, because we successfully filmed all known adult males during those trips. Spontaneous displays were recorded during the same period of dates and times of day as described above for the behavioral data. Before filming, we secured the camcorder to a tripod ~4 m from and approximately at the same height as the focal anole. For each individual, we recorded the perch height and perch diameter of the display site. Following each display, we placed a ping pong ball of known size at the site of the display to serve as a standard that could be used later to convert all movement distances to real units.

4.2.3 Video analysis

We imported all video footage into the video editing application iMovie, in which we trimmed and converted clips of each visual display to a format appropriate for the motion analysis software VideoPoint 2.5, which allows users to superimpose a Cartesian coordinate system onto a sequence of video frames. First, we plotted the position of the snout of the lizard (i.e., a landmark) on every frame (30 frames per second). We then measured the pixel length of the standard (i.e., the ping pong ball) and converted the units of a Cartesian coordinate system overlaid onto all frames of the video clip from pixels to real units (millimeters). Next, we rotated the coordinate system such that the vertical (y) axis was aligned with the apparent axis of maximal head motion (i.e., maximum amplitude). Because this alignment is achieved “by eye,” an underestimate of maximum head amplitude might occur. To reduce the likelihood of this error, we also rotated the coordinate system 5° to the right and 5° to the 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 data obtained from the alignment that yielded the largest maximum head amplitude. We also counted the number of individual head bobs (i.e., a movement of the head up and then back down) in each display.

4.2.4 Predicting the conspecific signaling active space

Both the visual system and motion perception of anoles in general and *A. sagrei* in particular are well characterized. Behavioral experiments show that movements in a particular range of visual angles (0.2–0.8°) are more likely to capture the attention of anoles, including *A. sagrei*, than movements below or above that range; in other words, movements between 0.2° and 0.8° appear to maximally stimulate the motion detectors of receivers (Fleishman 1986, 1992; Pallus & Fleishman 2010). The visual angle (θ) of a movement is the angle at which that movement subtends the eye of a viewer and is given by $\theta = 2 \arctan(S/2D)$, where S is the amplitude of the movement and D is the distance between the moving object and the eye of the viewer (Endler 1978).

Using the above equation, we calculated the distance (D_o) at which the head movement of greatest amplitude for each display has a visual angle of 0.2°. At a distance beyond D_o , the head movement generates a suboptimal response by the motion detectors of an anoline viewer of the display. Therefore, D_o provides an estimate of the maximum distance for which the sensory system of an inattentive anoline receiver will be stimulated optimally by the head movement of a signaler and may be considered a metric for the conspecific active space of a signal (Brenowitz 1982; Fleishman 1986, 1992; Pallus & Fleishman 2010). This conspecific active space is the maximum straight-line distance from which another anole is predicted to detect a display.

4.2.5 Statistical analysis

We calculated the mean value for each island for each of the following variables: mean perch height, proportion of time spent signaling, maximum amplitude of headbob displays, and number of head bobs per display. Data for proportion of time spent signaling was arcsine square-root transformed. After confirming that all four variables were distributed normally by using the Shapiro–Wilk normality test, we compared control and experimental treatments using one-tailed, unequal variance t tests (Welch’s two-sample t tests). We used two-tailed Pearson correlations to test for associations between the maximum amplitude of headbob displays and both perch height and diameter within each of the treatments. All tests were performed using R statistical programming language V 2.15.0 (49) at $\alpha = 0.05$.

4.2.6 Ethical note

All aspects of this study were approved by the Institutional Animal Care and Use Committee of Duke University.

4.3 Results

Male *A. sagrei* perched over twice as high above the ground on islands where *L. carinatus* was present ($\bar{X} = 76.9 \pm 10.6$ cm) than on control islands ($\bar{X} = 33.8 \pm 4.2$ cm; $t = -3.76$, $P = 0.01$, $N = 9$; Figure 8). However, males from the control and experimental treatments did not differ significantly in the proportion of time spent signaling (control: $\bar{X} = 0.040 \pm 0.007$; experimental: $\bar{X} = 0.027 \pm 0.004$, $t = 1.74$, $P = 0.07$, $N = 9$; Figure 9a) or

in the number of head bobs per display (control: $\bar{X} = 6.4 \pm 0.8$ bobs/display; experimental: $\bar{X} = 6.3 \pm 0.3$ bobs/display, $t = 0.01$, $P = 0.46$, $N = 9$; Figure 9b).

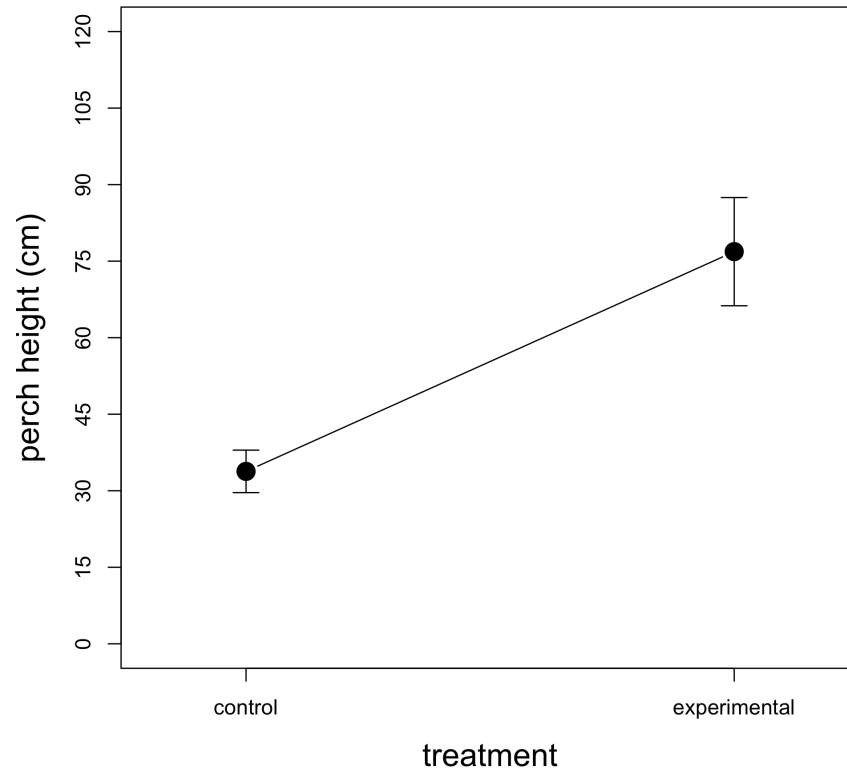


Figure 8: Mean perch height of male *Anolis sagrei* in both control (nonpredator) and experimental (predator) treatments. Values are the mean and one SEM for each treatment; $N = 9$.

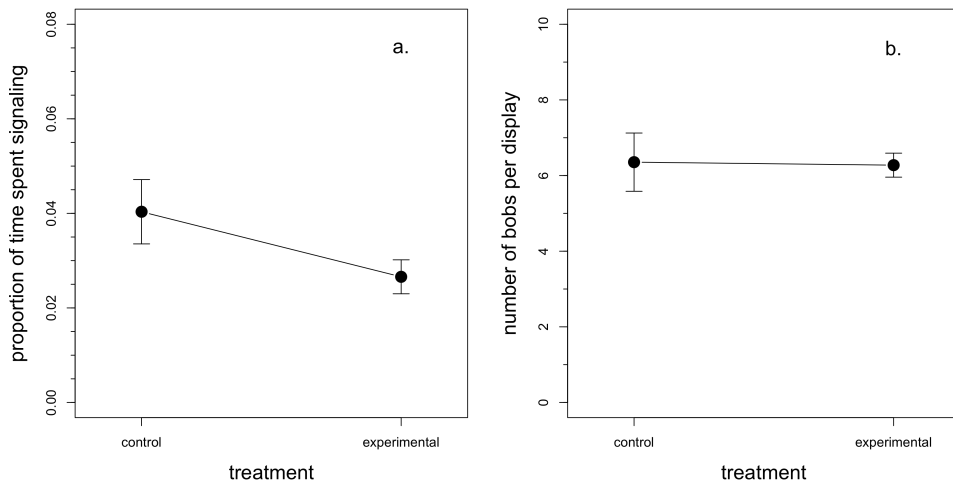


Figure 9: Behavior of male *Anolis sagrei* in both control (nonpredator) and experimental (predator) treatments. (a) Proportion of time spent signaling. (b) Number of head bobs per display. Values are the mean and one SEM for each treatment; $N = 9$.

The mean maximum amplitude of head bobs from experimental islands was 7.2 mm smaller than that of control islands (experimental: $\bar{X} = 12.9 \pm 2.2$ mm; control: $\bar{X} = 20.1 \pm 0.5$ mm; $t = 3.18$, $P = 0.01$, $N = 9$; Figure 10a). Under the relatively simple assumption that the vegetation is not obstructing the receiver's view of the signaling lizard, this difference in amplitude corresponds to a difference in active space (i.e., the maximum range of a signal) of more than 2 m between treatments ($\bar{X} = 3.7 \pm 0.6$ m vs. $\bar{X} = 5.8 \pm 0.1$ m; Figure 10b).

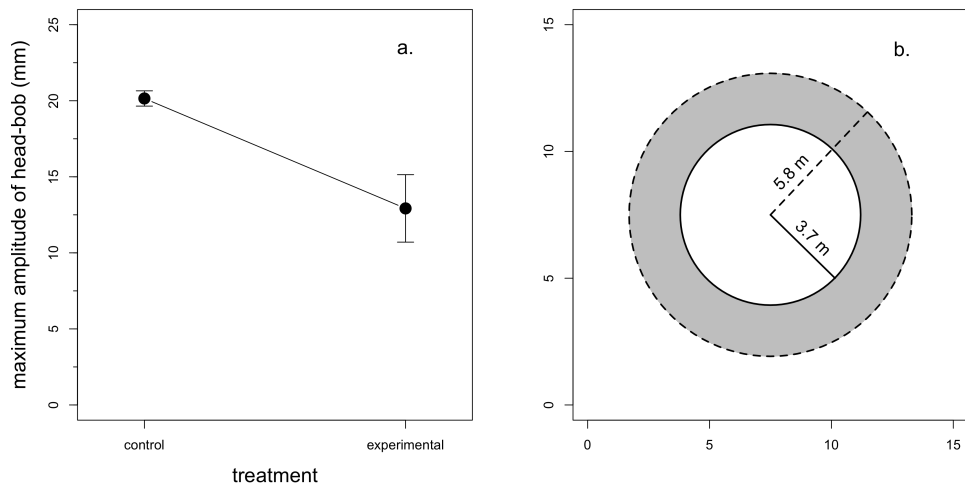


Figure 10: Change in the physical properties of head bob displays given by male *Anolis sagrei* in response to the presence of *Leiocephalus carinatus* and its effects on the signaling active space. (A) Maximum amplitude of headbob displays given in both control (nonpredator) and experimental (predator) treatments. Values are the mean and one SEM for each treatment; $N = 9$. (B) Illustration of the differences in conspecific active signaling space of *A. sagrei* on predator and nonpredator islands. The active space of a typical headbob display from a lizard on a predator island (solid line; 3.7 m) is smaller than the active space of a typical display from a lizard on a nonpredator island (dashed line; 5.8 m). Circles demarcate the area within which an anoline receiver would be maximally stimulated by a typical signal given by a lizard on a predator island (solid circle) and a typical signal given by a lizard on a nonpredator island (dashed circle), assuming that the signaling lizard is located at the center of the circle. The x- and y-axes are used simply to scale the two circles in meters.

To examine the possibility that differences in amplitude were influenced by differences in the perch height or diameter selected by the signaling individuals, we tested for a correlation between both perch height and perch diameter and maximum head amplitude. Perch height was not correlated with the maximum amplitude of headbob displays in either treatment (control: $r = 0.02$, $P = 0.94$, $N = 20$; experimental: $r =$

-0.04, $P = 0.87$, $N = 19$). Similarly, perch diameter was not correlated with display amplitude in either treatment (control: $r = -0.08$, $P = 0.73$, $N = 20$; experimental: $r = -0.17$, $P = 0.49$, $N = 19$).

Table 2: Mean \pm one SEM perch height, proportion of time spent signaling, maximum headbob amplitude, and number of bobs per display for each island. Sample sizes are given in parentheses. The number of visits to each island and number of total hours spent on each island during the filming of spontaneous headbob displays are also provided.

Treatment	Island name	Perch height (cm)	Proportion of time signaling	Maximum amplitude (mm)	Bobs per display	Visits	Hours
<i>Control</i>	Barge	27.4 \pm 2.5 (30)	0.05 \pm 0.01 (39)	21.6 \pm 5.7 (4)	5.0 \pm 1.2 (4)	4	11.5
	Buddy	30.0 \pm 3.5 (34)	0.02 \pm 0.01 (39)	19.5 \pm 1.8 (4)	8.0 \pm 1.6 (4)	8	17
	Five	46.0 \pm 6.8 (25)	0.05 \pm 0.01 (26)	19.4 \pm 1.7 (6)	7.3 \pm 0.5 (6)	4	8.5
	X3	31.8 \pm 3.4 (35)	0.04 \pm 0.01 (36)	20.0 \pm 3.2 (6)	5.1 \pm 0.6 (6)	5	12.5
<i>Experimental</i>	One	65.3 \pm 6.5 (25)	0.03 \pm 0.01 (25)	9.4 \pm 1.9 (4)	6.4 \pm 0.7 (4)	6	10.5
	One Pine	53.1 \pm 3.8 (30)	0.03 \pm 0.01 (32)	21.4 \pm 2.5 (6)	6.8 \pm 0.6 (6)	5	10.5
	Six	102.9 \pm 14.5 (8)	0.02 \pm 0.01 (8)	9.3 \pm 4.8 (2)	6.3 \pm 2.8 (2)	9	16
	X0	61.1 \pm 7.2 (12)	0.04 \pm 0.02 (12)	11.7 \pm 3.6 (4)	6.1 \pm 1.5 (4)	2	5.5
	Y5	101.9 \pm 8.4 (23)	0.02 \pm 0.01 (23)	12.8 \pm 3.5 (3)	6.0 \pm 2.0 (3)	6	13

4.4 Discussion

Animals change the physical parameters of their signals (i.e., “signal modulation”) in response to changes in environmental conditions, social interactions, or the presence of predators (Potash 1972, Cynx et al. 1998, Brumm et al. 2004, Peters et al. 2007, Anderson et al. 2008, Ord et al. 2010, Gavassa et al. 2013). Surprisingly, modulation of the physical properties of movement-based visual signals, which often are considered the most salient components of visual displays, has not been documented as a response to predation threat, despite evidence for predation-associated modulation of signals in other sensory modalities (e.g., Clark & Uetz 1992, Blumstein & Armitage 1997, Patricelli et al. 2007). For example, it was shown that *Gallus gallus* reduces the auditory frequency of its call, and potentially its vulnerability to localization by predators, in response to the presence of a potential predator (Bayly & Evans 2003).

Previous studies documented that male anoles modulate the physical properties of their head bobs to increase visibility to conspecifics under varying social and environmental conditions (e.g., Stamps & Barlow 1973, Fleishman 1988a, Ord et al. 2007, Steinberg & Leal 2013). However, in this study, modulation of headbob amplitude may serve to decrease visibility to predators. Moreover, we confirm previous reports that anoles respond to predators by altering their habitat use in demonstrating that the mean perch height of male *A. sagrei* during focal observations was more than twice as great in the presence of curly-tailed lizards than in their absence (Figure 8). These findings are

congruent with previous studies that indicate that *A. sagrei* individuals perceive the presence of *L. carinatus* as an increase in predation risk (Losos et al. 2002, Losos et al. 2006, Lopez-Darias et al 2012.).

Our results demonstrate that anoles do, indeed, modulate motion signals in response to predation pressure, probably to decrease signal conspicuousness to curly-tailed lizards. We found that male *A. sagrei* on islands with predators produced head bobs with much-reduced maximum amplitudes (up to 60%) in comparison with males on control islands (Figure 10a). This result is notable not only because it indicates that motion-signal modulation occurs in response to predators, but also because it suggests that modulation is not limited to courtship or alarm calls. The displays given by *A. sagrei* may be categorized as spontaneous broadcast signals, which often are used to advertise presence or territory ownership. Also, although it has been shown that anoles may give directed headbob displays to approaching predators as pursuit deterrent signals (Leal & Rodríguez-Robles 1997, Leal 1999), we never witnessed an individual of *L. carinatus* in the vicinity of the anoles while they displayed in this study. Thus, in our case, it is highly unlikely that the observed changes in the amplitude of the head bobs resulted from prey-predator communication or interspecific territoriality.

An important aspect of the anole-*Leiocephalus* predator-prey interaction is that curly-tailed lizards, like anoles, are visually oriented animals (Evans 1953, Marcellini & Jenssen 1991, Campano & Les 2012). Although the properties of motion detection in

Leiocephalus have not been measured explicitly, increasing the distance between a moving object and the eye of a receiver reduces the apparent size of the movement until at some point, it no longer is detectable (McIwain 1996). Consequently, a reasonable expectation is that reduction in the amplitude of *A. sagrei* head bobs would have the effect of making those displays less conspicuous to curly-tailed lizards (i.e., shortening the maximum distance of detection). In such a scenario, reducing the amplitude of head bobs likely would decrease the active space of signals to the point at which the signaler would be likely to detect (and flee or hide from) a moving predator from a much greater distance than the predator could detect the signal, thereby limiting the risk of unforeseen attacks.

One particular advantage of modulation is that it may take place immediately and, if needed, be adjusted along a relatively fine scale, because the physical properties of a signal are under control of motor neurons. The ability of individuals to modify their signaling display at such a fine temporal scale might provide an effective mechanism to balance the tradeoff between effective social communication and predation pressure. Fine-scale modulation has been documented in *Anolis gundlachi* during social interactions under natural conditions, in which males are capable of altering the amplitude of headbob displays to effectively stimulate the sensory systems of intended receivers located at varying distances (*Chapter 3*, Steinberg & Leal 2013).

The fitness impact of predation on prey species traditionally has been measured by mortality rate. However, an emerging view is that predation also may affect the individual fitness of prey indirectly through so-called risk effects that contribute to a reduction in reproductive success (reviewed in refs. Creel & Christianson 2008, Creel 2011). Based on our understanding of the natural history of anoles, including their social dynamics and the contribution of territory size to male reproductive success (Rand 1967, Andrews 1971, Trivers 1976), the observed changes in the physical properties of headbob displays in response to the presence of *L. carinatus* are likely to decrease the fitness of territorial males in multiple ways. Our signal-detection modeling approach reveals a 35% reduction in the conspecific active space of anoles in the presence of predators (Figure 10b). One obvious effect of such a reduction in active space might be a decrease in the ability of territorial males to attract distant females and successfully repel males before potentially dangerous close-range encounters, perhaps leading to smaller territory sizes and fewer females with which to mate. This influence of changes in signal active space on territory size (and possibly mate attraction) has been demonstrated in red-winged blackbirds (*Agelaius phoeniceus*) (Peek 1972, Brenowitz 1982, Patricelli et al. 2007) and spring peepers (*Hyla crucifer*) (Brenowitz et al. 1984). Such changes might then have cascading effects on sexually selected traits and mating strategies.

We predicted that male *A. sagrei* would respond to the presence of *L. carinatus* by not only decreasing display amplitude, but also by decreasing the proportion of time

spent signaling. However, we found no statistical difference in the proportion of time spent signaling (although proportion of time spent signaling is 67% higher on control islands than on islands on which *Leiocephalus* were present, a difference with a P-value of 0.07 in a one-tailed comparison; Figure 9a). Because our sample size is relatively small, it is possible that the lack of a significant difference reflects a lack of statistical power. Given that the difference in number of head bobs per display, which might serve as another means of altering an individual's temporal window of vulnerability, clearly is nonsignificant (Figure 9b) and assuming that the lack of difference we detected in proportion of time spent displaying is real, then *A. sagrei* does not follow the same trend found in other studies that find a decrease in proportion of time allocated to signaling to be one of the responses exhibited by prey species to a perceived increase in predation threat (e.g., Morris 1980, Hedrick 2000, Simon 2007, Fowler-Finn & Hebets 2011). For example, male túngara frogs reduce their calling rate, defined as the proportion of time spent calling, in response to the presence of frog-eating bats (Tuttle et al. 1982), and male Trinidadian guppies shorten the duration of courtship displays in the presence of predatory fish (Endler 1987). It should be noted that most studies reporting decreases in signaling focused on mating displays (e.g., Endler 1987, Tuttle et al. 1982); however, *A. sagrei* headbob displays not only are given as part of courtship displays, but also commonly are used for many aspects of anole social interactions.

In this case, two non-mutually exclusive explanations might account for the failure of *A. sagrei* to conform to the general pattern seen in other species (Endler 1986). First, as we discussed above, the decrease in signal amplitude and its effect on the signal conspicuousness may reduce the likelihood of predation, such that altering the proportion of time spent signaling would impart little or no additional benefit. In other words, males have adopted one of two effective antipredator strategies. Second, the importance of holding a territory and attracting mates might select against a decrease in the amount of time allocated to signaling. In anoles, including *A. sagrei*, males patrol their territories while producing displays that function to advertise their position to nearby rivals and females and to repel potential intruders (Stamps 1977a, Jenssen & Nunez 1998, Jenssen et al. 2001). As we discussed above, the reduced amplitude of displays limits the active space over which the display can be detected, but within that active space, males still can attract nearby mates or repel nearby rivals by not decreasing the proportion of time spent signaling. Therefore, it is possible that a decrease in the proportion of their daily activity allocated to display might not be advantageous, even in the presence of predators, because such a strategy might hamper the ability of males to hold a territory.

Replicated large-scale manipulations, conducted under natural conditions with natural populations, have provided some of the strongest evidence that predation is a major selective force shaping the evolution of social signals [see Kemp et al. (2009) and

references therein]. We have demonstrated that these effects include modulation of headbob displays by *A. sagrei*. Because these signals are used in a variety of contexts related to social interactions, the indirect effects of such modulation might have great consequences, altering not only selection pressures, but possibly the social dynamics and population structure of prey species. Recent studies of predator-prey interactions show that elucidating the importance of risk effects on prey populations is crucial for understanding the evolutionary forces shaping predator-prey interactions (Creel & Christianson 2008, Sih et al. 2010, Creel 2011). We propose that changes in social signals also be included in these studies, because those changes have the potential to change the population dynamics of prey species.

References

- Ache, B. W. & Young, J. M. 2005. Olfaction: diverse species, conserved principles. *Neuron*, 48, 417–430.
- Akre, K. L., Farris, H. E., Lea, A. M., Page, R. A. & Ryan, M. J. 2011. Signal perception in frogs and bats and the evolution of mating signals. *Science*, 333, 751–752.
- Alberts, A. C. 1992. Constraints on the design on chemical communication systems in terrestrial vertebrates. *American Naturalist, Supplement*, 139, S62–S89.
- Anderson, R. C., Searcy, W. A., Peters, S. & Nowicki, S. 2008. Soft song in song sparrows: acoustic structure and implications for signal function. *Ethology*, 114, 662–676.
- Andrews, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology*, 52, 262–270.
- Bayly, K. L. & Evans, C. S. 2003. Dynamic changes in alarm call structure: A strategy for reducing conspicuousness to avian predators? *Behaviour*, 140, 353–369.
- Bermúdez-Cuatmatzin, E., Ríos-Chelen, A. A., Gil, D. & Macías Garcia, C. 2011. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, 7, 36–38.
- Blumstein, D. T. & Armitage, K. B. 1997. Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, 53, 143–171.
- Borst, A. & Egelhaaf, M. 1989. Principles of visual motion detection. *Trends in Neuroscience*, 12, 297–306.
- Boughman, J. W. 2001. Divergent sexual selection enhances reproduction isolation in sticklebacks. *Nature*, 411, 944–948.
- Boughman, J. W. 2002. How sensory drive can promote speciation. *Trends in Ecology & Evolution*, 17, 571–577.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Brandley, M. C. & de Queiroz, K. 2004. Phylogeny, ecomorphological evolution, and

- historical biogeography of the *Anolis cristatellus* series. *Herpetological Monographs*, 18, 90–125.
- Brenowitz, E. A. 1982. The active space of red-winged blackbird song. *Journal of Comparative Physiology*, 147, 511–522.
- Brenowitz, E. A., Wilczynski, W. & Zakon, H. H. 1984. Acoustic communication in spring peepers. *Journal of Comparative Physiology A*, 155, 585–592.
- Briscoe, A. D. & Chittka, L. 2001. The evolution of color vision in insects. *Annual review of entomology*, 46, 471–510.
- Bro-Jørgenson, J. 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology and Evolution*, 25, 292–300.
- Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior*, 35, 151–209.
- Brumm, H. & Slater, P. J. B. 2006. Animals can vary signal amplitude with receiver distance: evidence from zebra finch song. *Animal Behaviour*, 72, 699–705.
- Brumm, H., Voss, K., Kollmer, I. & Todt, D. 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. *Journal of Experimental Biology*, 207, 443–448.
- Brunel-Pons, O., Alem, S. & Greenfield, M. D. 2011. The complex auditory scene at leks: Balancing antipredator behaviour and competitive signalling in an acoustic moth. *Animal Behaviour*, 81, 231–239.
- Burk, T. 1982. Evolutionary significance of predation on sexually signalling males. *Florida Entomologist*, 65, 90–104.
- Carpenter, C. C. 1965. Comparative display behavior in the genus *Sceloporus* (Iguanidae). *Contributions to Biology and Geology from the Milwaukee Public Museum*, 16, 62–74.
- Carpenter, C. C. & Grubitz, G., III. 1961. Time-motion study of a lizard. *Ecology*, 42, 199–200.
- Campano, M. & Les, A. M. 2012. *Leiocephalus carinatus* (Northern Curly-tailed lizard). Diet. *Herpetological Review*, 43, 333–334.

- Clark, D. L. & Uetz, G. W. 1992. Morph-independent mate selection in a dimorphic jumping spider: Demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour*, 43, 247–254.
- Creel, S. 2011. Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality. *Ecology*, 92, 2190–2195.
- Creel, S. & Christianson, D. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, 23, 194–201.
- Cummings, M. E., Rosenthal, G. G. & Ryan, M. J. 2003. A private ultraviolet channel in visual communication. *Proceedings of the Royal Society of London, Series B*, 270, 897–904.
- Cynx, J., Lewis, R., Tavel, B. & Tse, H. 1998. Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Animal Behaviour*, 56, 107–113.
- Derryberry, E. P. 2007. Evolution of bird song affects signal efficacy: an experimental test using historical and current signals. *Evolution*, 61, 1938–1945.
- Doucet, S. M., Mennill, D. J. & Hill, G. E. 2007. The evolution of signal design in manakin plumage ornaments. *The American Naturalist*, 169, S62 – S80.
- Douglas, H. D. & Conner, W. E. 1999. Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. *Naturwissenschaften*, 86, 228–230.
- Dusenbery, D. B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. New York: W.H. Freeman.
- Endler, J. A. 1978. A predator's view of animal color patterns. *Evolutionary Biology*, 11, 319–364.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, 34, 76–91.
- Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, 9, 173–190.

- Endler, J. A. 1986. *Natural selection in the wild* (No. 21). Princeton University Press, Princeton, New Jersey.
- Endler, J.A. 1987. Predation, light intensity, and courtship behaviour in *Poecilia reticulata*. *Animal Behaviour*, 35, 1376–1385.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist, Supplement*, 139, S125–S153.
- Endler, J. A. & Basolo, A. L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, 13, 415–420.
- Endler, J. A. & Mielke, P. W., Jr. 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society*, 86, 405–431.
- Endler, J. A. & Thery, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *The American Naturalist*, 148, 421–452.
- Evans, L. T. 1938. Cuban field studies on territoriality of the lizard *Anolis sagrei*. *Journal of Comparative Psychology*, 25, 97–125.
- Evans, L. T. 1953. Tail display in an iguanid lizard. *Copeia*, 1953, 50–54.
- Feng, A. S., Narins, P. M., Xu, C.-H., Lin, W.-Y., Yu, Z.-L., Qiu, Q., Xu, Z.-M. & Shen, J.-X. 2006. Ultrasonic communication in frogs. *Nature*, 440, 333–336.
- Fleishman, L. J. 1986. Motion detection in the presence and absence of background motion in an *Anolis* lizard. *Journal of Comparative Physiology A*, 159, 711–720.
- Fleishman, L. J. 1988a. Sensory influences on the physical design of a visual display. *Animal Behaviour*, 36, 1420–1424.
- Fleishman, L. J. 1988b. Sensory and environmental influences on display form in *Anolis auratus*, a grass anole from Panama. *Behavioral Ecology and Sociobiology*, 22, 309–316.
- Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist, Supplement*, 139, S36–S61.

- Fleishman, L. J. & Pallus, A. C. 2010. Motion perception and visual signal design in *Anolis* lizards. *Proceedings of the Royal Society of London, Series B*, 277, 3547–3554.
- Fleishman, L. J., Leal, M. & Persons, M. H. 2009. Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *Journal of Comparative Physiology A*, 195, 1043–1060.
- Fowler-Finn, K. D. & Hebets, E. A. 2011. The degree of response to increased predation risk corresponds to male secondary sexual traits. *Behavioral Ecology*, 22, 268–275.
- Fuller, R. C. 2009. A test of the critical assumption of the sensory bias model for the evolution of female mating preference using neural networks. *Evolution*, 63, 1697–1711.
- Gavassa, S., Roach, J. P. & Stoddard, P. K. 2013. Social regulation of electric signal plasticity in male *Brachyhyopomus gauderio*. *Journal of Comparative Physiology A*, 199, 375–384.
- Godin, J.- G. J. 1995. Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecelia reticulata*). *Oecologia*, 103, 224–229.
- Greenberg, N. & Noble, G. K. 1944. Social behavior of the American chameleon (*Anolis carolinensis*). *Physiological Zoology*, 17, 392–439.
- Guilford, T. & Dawkins, M. S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*, 42, 1–14.
- Guilford, T. & M. S. Dawkins. 1993. Receiver psychology and the design of animal signals. *Trends in Neuroscience*, 16, 430–436.
- Haag, J., Denk, W. & Borst, A. 2004. Fly motion vision is based on Reichardt detectors regardless of the signal-to-noise ratio. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 16333–16338.
- Hailman, J. P. 1977. *Optical Signals* (Indiana Univ Press, Bloomington, IN).
- Hammet S. T., Thompson P. G. & Bedingham, S. 2000. The dynamics of velocity adaptation in human vision. *Current Biology*, 10, 1123–1126.

- Håstad, O., Victorsson, J. & Ödeen, A. 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. *Proceedings of the National Academy of Sciences, U.S.A.*, 102, 6391–6394.
- Hebets, E. A. & Uetz, G. W. 1999. Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus *Schizocosa* (Araneae: Lycosidae). *Animal Behaviour*, 57, 865–872.
- Hedrick, A. V. 2000. Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proceedings of the Royal Society of London, Series B*, 267, 671–675.
- Hemmi, J. M., Marshall, J., Pix, W., Vorobyev, M. & Zeil, J. 2006. The variable colours of the fiddler crab *Uca vomeris* and their relation to background and predation. *Journal of Experimental Biology*, 209, 4140–4153.
- How, M. J., Hemmi, J. M., Zeil, J. & Peters, R. 2008. Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. *Animal Behaviour*, 75, 1015–1022.
- Ingle, D. J. 1982. Organization of visuomotor behaviors in vertebrates. In: *Analysis of Visual Behavior* (Ed. by D. J. Ingle, M. A. Goodale & R. J. W. Mansfield), pp. 67–109. Cambridge, Massachusetts: MIT Press.
- Jenssen, T. A. 1977. Evolution of anoline display behavior. *American Zoologist*, 17, 203–215.
- Jenssen, T. A. & Feely, P. C. 1991. Social behavior of the male anoline lizard *Chamaelinorops barbouri*, with a comparison to *Anolis*. *Journal of Herpetology*, 25, 454–462.
- Jenssen, T. A. & Nunez, S. C. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. *Behaviour*, 135, 981–1003.
- Jenssen, T. A., Lovern, M. B. & Congdon, J. D. 2001. Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model? *Behavioral Ecology and Sociobiology*, 50, 162–172.
- Johnson, M. A., Revell, L. J. & Losos, J. B. 2010. Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution*, 64, 1151–1159.

- Jones G., Barabas, A., Elliott, W. & Parsons, S. 2002. Female greater wax moths reduce sexual display behavior in relation to the potential risk of predation by echolocating bats. *Behavioral Ecology*, 13, 375–380.
- Kemp, D. J., Reznick, D. N., Grether, G. F. & Endler, J. A. 2009. Predicting the direction of ornament evolution in Trinidadian guppies (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B*, 276, 4335–4343.
- Koga T., Backwell, P. R. Y., Jennions, M. D. & Christy, J. H, 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proceedings of the Royal Society of London, Series B*, 265, 1385–1390.
- Krams, I. 2001. Communication in crested tits and the risk of predation. *Animal Behaviour*, 61, 1065–1068.
- Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In: *Behavioral ecology: an evolutionary approach* (Ed. by J.R. Krebs and N.B. Davies), pp. 380–402. Oxford: Blackwell.
- Land, M. F. & Nilsson, D.-E. 2002. *Animal Eyes*. New York: Oxford University Press.
- Layne, J. E. 1998. Retinal location is the key to identifying predators in fiddler crabs (*Uca pugilator*). *The Journal of experimental biology*, 201, 2253–2261.
- Leal, M. 1999. Honest signalling during prey–predator interactions in the lizard *Anolis cristatellus*. *Animal Behaviour*, 58, 521–526.
- Leal, M. & Fleishman, L. J. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proceedings of the Royal Society of London, Series B*, 269, 351–359.
- Leal, M. & Fleishman, L. J. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *American Naturalist*, 163, 26–39.
- Leal, M. & Rodríguez-Robles, J. A. 1997. Signalling displays during predator–prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Animal Behaviour*, 54, 1147–1154.
- Leal, M., Rodríguez-Robles, J. A. & Losos, J. B. 1998. An experimental study of

- interspecific interactions between two Puerto Rican *Anolis* lizards. *Oecologia*, 117, 273–278.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- Lopez-Darias, M., Schoener, T. W., Spiller, D. A. & Losos, J. B. 2012. Predators determine how weather affects the spatial niche of lizard prey: Exploring niche dynamics at a fine scale. *Ecology*, 93, 2512–2518.
- Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs*, 1990, 369–388.
- Losos, J. B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, California: University of California Press.
- Losos, J. B., Schoener, T. W., Langerhans, R. B. & Spiller, D. A. 2006. Rapid temporal reversal in predator-driven natural selection. *Science*, 314, 1111.
- Losos, J. B., Schoener, T. W. & Spiller, D. A. 2004. Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature*, 432, 505–508.
- Lucas, P. W., Dominy, N. J., Riba-Hernandez, P., Stoner, K. E., Yamashita, N., Calderön, E. L., Peterson-Pereira, W., Rojas-Durán, Y., Salas-Pena, R., Solis-Madrigal, Osorio, D. & Darvell, B. W. (2003). Evolution and function of routine trichromatic vision in primates. *Evolution*, 57, 2636–2643.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology and Evolution*, 6, 183–186.
- Marcellini, D. L. & Jenssen, T. A. 1991. Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersi*: Implications for anti-predator behavior. *Journal of Herpetology*, 25, 238–241.
- Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature*, 362, 149–152.
- Martel, G. & Dill, L. M. 1995. Influence of movement by coho salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). *Ethology*, 99, 139–149.

- Martins, E. P., Ord, T. J. & Davenport, S. W. 2005. Combining motions into complex displays: playbacks with a robotic lizard. *Behavioral Ecology and Sociobiology*, 58, 351–360.
- McIlwain, J. T. 1996. *An Introduction to the Biology of Vision*. New York: Cambridge University Press.
- McNett, G. D., Luan, L. H. & Cocroft, R. B. 2010. Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behavioral Ecology and Sociobiology*, 64, 2043–2051.
- Mizutani, A., Chahl, J. S. & Srinivasan, M. V. 2003. Motion camouflage in dragonflies. *Nature*, 423, 604.
- Morris, G. K. 1980. Calling display and mating behaviour of *Copiphora rhinoceros* Pictet (Orthoptera: Tettigoniidae). *Animal Behaviour*, 28, 42–51.
- Nalbach, H.-O. 1989. Three temporal frequency channels constitute the dynamics of the optokinetic system of the crab, *Carcinus maenas* (L.). *Biological Cybernetics*, 61, 59–70.
- Neuhofer, D., Wohlgemuth, S., Stumpner, A. & Ronacher, B. 2008. Evolutionarily conserved coding properties of auditory neurons across grasshopper species. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1965–1974.
- Nicholson, K. E., Glor, R. E., Kolbe, J. J., Larson, A., Hedges, S. B. & Losos, J. B. 2005. Mainland colonization by island lizards. *Journal of Biogeography*, 32, 929–938.
- Noble, G. K. & Bradley, H. T. 1933 The mating behavior of lizards; its bearing on the theory of sexual selection. *Annals of the New York Academy of Sciences*, 35, 25–100.
- Ord, T. J. 2012. Receiver perception predicts species divergence in long-range communication. *Animal Behaviour*, 83, 3–10.
- Ord, T. J. & Stamps, J. A. 2008. Alert signals enhance animal communication in ‘noisy’ environments. *Proceedings of the National Academy of Sciences, U.S.A.*, 105, 18830–18835.
- Ord, T. J., Peters, R. A., Clucas, B. & Stamps, J. A. 2007. Lizards speed up visual displays

- in noisy motion habitats. *Proceedings of the Royal Society of London, Series B*, 274, 1057–1062.
- Ord, T. J., Stamps, J. A. & Losos, J. B. 2010. Adaptation and plasticity of animal communication in fluctuating environments. *Evolution*, 64, 3134–3148.
- Ortiz, P. R. & Jenssen, T. A. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Zeitschrift für Tierpsychologie*, 60, 227–238.
- Osorio, D. & Vorobyev, M. 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proceedings of the Royal Society B: Biological Sciences*, 272, 1745–1752.
- Ott, M., Schaeffel, F. & Kirmse, W. 1998. Binocular vision and accommodation in prey-catching chameleons. *Journal of Comparative Physiology A*, 182, 319–330.
- Ott, M., Ostheim, J. & Sherbrooke, W. C. 2004. Prey snapping and visual distance estimation in Texas horned lizards, *Phrynosoma cornutum*. *Journal of Experimental Biology*, 207, 3067–3072.
- Pallus, A. C., Fleishman, L. J. & Castonguay, P. M. 2010. Modeling and measuring the visual detection of ecologically relevant motion by an *Anolis* lizard. *Journal of Comparative Physiology A*, 196, 1–13.
- Palombit, R. A. 1992. A preliminary study of vocal communication in wild long-tailed macaques (*Macaca fascicularis*). II. Potential of calls to regulate intragroup spacing. *International Journal of Primatology*, 13, 183–207.
- Partan, S. R. & Marler, P. 2005. Issues in the classification of multimodal communication signals. *The American Naturalist*, 166, 231–245.
- Paterson, A. V. & McMann, S. 2004. Differential headbob displays toward neighbors and nonneighbors in the territorial lizard *Anolis sagrei*. *Journal of Herpetology*, 38, 288–291.
- Patricelli, G. L., Dantzker, M. S. & Bradbury, J. W. 2007. Differences in acoustic directionality among vocalizations of the male red-winged blackbird (*Agelaius phoeniceus*) are related to function in communication. *Behavioral Ecology and Sociobiology*, 61, 1099–1110.

- Peek, F. W. 1972. An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoeniceus*). *Animal Behaviour*, 20, 112–118.
- Peters, R. A. 2010. Movement-based signalling and the physical world: modelling the changing perceptual task for receivers. In: *Modelling Perception with Artificial Neural Networks* (Ed. by C. R. Tosh & G. D. Ruxton), pp. 269–292. New York: Cambridge University Press.
- Peters, R. A. & Allen, S. J. 2009. Movement signal choreography unaffected by receiver distance in the Australian Jacky lizard, *Amphibolurus muricatus*. *Behavioral Ecology and Sociobiology*, 63, 1593–1602.
- Peters, R. A. & Evans, C. S. 2003. Design of the Jacky dragon visual display: signal and noise characteristics in a complex moving environment. *Journal of Comparative Physiology A*, 189, 447–459.
- Peters, R. A., Hemmi, J. M. & Zeil, J. 2007. Signaling against the wind: modifying motion-signal structure in response to increased noise. *Current Biology*, 17, 1231–1234.
- Phelps, S. M. & Ryan, M. J. 2000. History influences signal recognition: neural network models of tungara frogs. *Proceedings of the Royal Society of London, Series B*, 267, 1633–1639.
- Philibosian, R. 1975. Territorial behavior and population regulation in the lizards, *Anolis acutus* and *A. cristatellus*. *Copeia*, 1975, 428–444.
- Pocklington R. & Dill, L. M. 1995. Predation on females or males: Who pays for bright male traits? *Animal Behaviour*, 49, 1122–1124.
- Potash, L.M. 1972. Noise-induced changes in calls of the Japanese quail. *Psychonomic Science*, 26, 252–254.
- Pough, F. H. 1991. *Recommendations for the Care of Amphibians and Reptiles in Academic Institutions*. Washington, D.C.: National Academic Press.
- Powell, B. J. & Leal, M. 2014. Brain organization and habitat complexity in *Anolis* lizards. *Brain, behavior and evolution*, 84, 8–18.

- Proppe, D. S., Sturdy, C. B. & Cassady St. Clair, C. 2011. Flexibility in animal signals facilitates adaptation to rapidly changing environments. *PLOS One*, 6, 1–4.
- Qualls, C. P. & Jaeger, R. G. 1991. Dear enemy recognition in *Anolis carolinensis*. *Journal of Herpetology*, 25, 361–363.
- R Development Core Team 2009. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rand, A. S. 1964. Ecological distributions of anoline lizards of Puerto Rico. *Ecology*, 45, 745–752.
- Rand, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proceedings of the United States National Museum*, 122, 1–79.
- Rand, A. S. & Williams, E. E. 1970. An estimation of redundancy and information content of anole dewlaps. *The American Naturalist*, 104, 99–103.
- Ratcliffe, J. M. & Nydam, M. L. 2008. Multimodal warning signals for a multiple predator world. *Nature*, 455, 96–99.
- Reagan, D. P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain-forest. *Biotropica*, 23, 468–474.
- Reichardt, W. 1961. Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In: *Principles of Sensory Communication* (Ed. by W. A. Rosenblith), pp. 303–317. New York, New York: Wiley Press.
- Rivero, J. A. 1978. *Los Anfibios y Reptiles de Puerto Rico*. San Juan, Puerto Rico: Editorial Universitaria, Universidad de Puerto Rico.
- Rodríguez-Robles, J. A., Leal, M. & Losos, J. B. 2005. Habitat selection by the Puerto Rican yellow-chinned anole, *Anolis gundlachi*. *Canadian Journal of Zoology*, 83, 983–988.
- Rosenthal, G. G. 2007. Spatiotemporal dimensions of visual signals in animal communication. *Annual Review of Ecology, Evolution, and Systematics*, 38, 155–178.
- Ruibal, R. 1965. Evolution and behavior of West Indian *Anolis*. In: *Lizard Ecology: a Symposium* (Ed. by W. W. Milstead), pp. 116–140. Columbia, Missouri:

University of Missouri Press.

- Ryan, M. J. 1998. Sexual selection, receiver biases, and the evolution of sex differences. *Science*, 281, 1999–2003.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a neotropical anuran. *The American Naturalist*, 119, 136–139.
- Schleidt, W. M. 1961. Reaktionen von Truthuhern auf fliegende Raubvögel und Versuche zur Analyse ihrer AAM's. *Zeitschrift für Tierzucht und Züchtungsbiologie*, 18, 534–560.
- Schoener, T. W., Slade, J. B. & Stinson, C. H. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. *Oecologia* 53, 160–169.
- Schoener, T. W., Spiller, D. A. & Losos, J. B. 2002. Predation on a common *Anolis* lizard: Can the food-web effects of a devastating predator be reversed? *Ecological Monographs*, 72, 383–407.
- Schwartz, A. & Henderson, R. W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. Gainesville: University of Florida Press.
- Scott, M.P. 1984. Agonistic and courtship displays of male *Anolis sagrei*. *Breviora*, 479, 1–22.
- Seehausen, O., Terai, Y., Magalhaes, I. S., Carleton, K. L., Mrosso, H. D., Miyagi, R., van der Sluijs, I., Schneider, M. V., Maan, M. E., Tachida, H., Imai, H. & Okada, N. 2008. Speciation through sensory drive in cichlid fish. *Nature*, 455, 620–626.
- Siddiqi A., Cronin, T. W., Loew, E. R., Vorobyev, M. & Summers, K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology*, 207, 2471–2485.
- Sih, A. 1994. Predation risk and the evolutionary ecology of reproductive behaviour. *Journal of Fish Biology*, 45 (Suppl. A), 111–130.
- Sih, A., Bolnick, D. I., Luttbeg, B. Orrock, J. L., Peacor, S. D., Pintor, L. M., Preisser, E., Rehage, J. S. & Vonesh, J. R. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, 119, 610–621.

- Simon, V. B. 2007. Not all signals are equal: male brown anole lizards (*Anolis sagrei*) selectively decrease pushup frequency following a simulated predatory attack. *Ethology*, 113, 793–801.
- Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature*, 424, 267.
- Stamps, J. A. 1977a. The function of the survey posture in *Anolis* lizards. *Copeia*, 1977, 756–758.
- Stamps, J. A. 1977b. Social behavior and spacing patterns in lizards. In: *Biology of the Reptilia: Ecology and Behavior* (Ed. by C. Gans & D. W. Winkle), pp. 265–334. New York: Academic Press.
- Stamps, J. A. & Barlow, G. W. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). *Behaviour*, 47, 67–94.
- Steinberg, D. S. & Leal, M. .2013. Sensory system properties predict signal modulation in a tropical lizard. *Animal Behaviour*, 85, 623–629.
- Steinberg, D. S., Losos, J. B., Schoener, T. W., Spiller, D. A., Kolbe, J. J. & Leal, M. 2014. Predation-associated modulation of movement-based signal by a Bahamian lizard. *Proceedings of the National Academy of the Sciences USA*, 111, 9187–9192.
- Stoddard, P. K. 1999. Predation enhances complexity in the evolution of electric fish signals. *Nature*, 400, 254–256.
- Stoddard, P. K. 2002. Electric signals: predation, sex, and environmental constraints. In: *Advances in the Study of Behavior*. Vol. 31 (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon & T. J. Roper), pp. 201–242. San Diego, California: Academic Press.
- Stuart-Fox, D., Moussalli, A. & Whiting, M. J. 2007. Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *American Naturalist*, 170, 916–930.
- Sullivan-Beckers, L. & Hebets, E. A. 2011. Modality-specific experience with female feedback increases the efficacy of courtship signalling in male wolf spiders. *Animal Behaviour*, 82, 1051–1057.
- Titus, R. C. 1998. Short-range and long-range songs: use of two acoustically distinct song

- classes by dark-eyed juncos. *Auk*, 115, 386–393.
- Tobias, J. A., Aben, J., Brumfield, R. T., Derryberry, E. P., Halfwerk, W., Slabbekoorn, H., & Seddon, N. 2010. Song divergence by sensory drive in Amazonian birds. *Evolution*, 64, 2820–2839.
- de la Torre, S. & Snowdon, C. T. 2002. Environmental correlates of vocal communication of wild pygmy marmosets, *Cebuella pygmaea*. *Animal Behaviour*, 63, 847–856.
- Trivers, R. L. 1976. Sexual selection and resource-accurring abilities in *Anolis garmani*. *Evolution*, 30, 253–269.
- Tuttle, M. D. & Ryan, M. J. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science*, 214, 677–678.
- Tuttle, M. D., Taft, L. K. & Ryan, M. J. 1982. Evasive behaviour of a frog in response to bat predation. *Animal Behaviour*, 30, 393–397.
- Underwood, G. 1970. The eye. In: *Biology of the Reptilia, Volume 2* (Ed. by C. Gans), pp. 1–97. New York, New York: Academic Press.
- Uy, J. A. C. & Stein, A. C. 2007. Variable visual habitats may influence the spread of colourful plumage across an avian hybrid zone. *Journal of Evolutionary Biology*, 20, 1847–1858.
- Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P. & Slabbekoorn, H. 2010. Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. *Journal of Experimental Biology*, 213, 2575–2581.
- Wiley, R. H. 1983. The evolution of communication: information and manipulation. In: *Animal Behaviour. Vol. 2: Communication* (Ed. by R. Halliday & P. J. B. Slater), pp. 156–189. New York: W.H. Freeman.
- Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, 3, 69–94.
- Wilgers, D. J. & Hebets, E. A. 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. *Current Zoology*, 57, 175–186.

- Williams, E. E. 1972. The origins of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evolutionary Biology*, 6, 47–89.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of Anolis. In: *Lizard ecology: studies of a model organism* (Ed. by R. B. Huey, E. R. Pianka, and T.W. Schoener), pp. 326–370. Cambridge, Massachusetts: Harvard University Press.
- Wisenden, B. D. & Harter, K. R. 2001. Motion, not shape, facilitates association of predation risk with novel objects by fathead minnows (*Pimephales promelas*). *Ethology*, 107, 357–364.
- Woods W. A, Jr., Hendrickson, H., Mason, J. & Lewis, S. M. 2007. Energy and predation costs of firefly courtship signals. *The American Naturalist*, 170, 702–708.
- Zanker, J. M. & Zeil, J. 2001. *Motion vision*. Springer.
- Zaret, T. M. 1980. The effect of prey motion on planktivore choice. In: *Evolution and Ecology of Zooplankton Communities* (Ed. by W. C. Kerfoot), pp. 594–603. Hanover, New Hampshire: The University Press of New England.
- Zeil, J. M. & Zanker, J. 1997. A glimpse into crabworld. *Vision Research*, 37, 3417–3426.
- Zelick, R. & Narins, P. M. 1985. Characterization of the advertisement call oscillator in the frog *Eleutherodactylus coqui*. *Journal of Comparative Physiology A*, 156, 223–229.
- Zuk, M. & Kolluru, G. R. 1998. Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology*, 73, 415–438.

Biography

David Scott Steinberg was born in Philadelphia, Pennsylvania, USA, on 16 June 1985. He graduated from Vanderbilt University in 2008, with a Bachelor's of Science degree in Ecology, Evolution, and Organismal Biology. While at Vanderbilt, Dave published "Population densities, water loss rates, and diets of *Sphaerodactylus vincenti* on St. Vincent, West Indies" in *Journal of Herpetology*, along with descriptive reviews of *Sphaerodactylus vincenti* and *S. kirbyi* in *Catalogue of American Amphibians and Reptiles*.

In 2008 Dave joined the laboratory of Dr. Manuel Leal in the Department of Biology at Duke University. He received his Doctor of Philosophy in Biology and a Certificate in College Teaching in 2015. While at Duke, Dave published "Predation-associated modulation of movement-based signals by a Bahamian lizard" in the *Proceedings of the National Academy of Sciences USA* and "Sensory system properties predict signal modulation in a tropical lizard" in *Animal Behaviour*, both with M. Leal. His work was supported by a Graduate Research Fellowship from the National Science Foundation, James B. Duke Fellowship from Duke's Graduate School, and Tyson Fellowship from the Organization for Tropical Studies. He also received research grants from Duke's Department of Biology, Graduate School, and Center for Latin American and Caribbean Studies, along with Duke Sigma Xi, the North Carolina Academy of Science, and The Herpetologists' League. In 2015 Dave received a Bass Instructor-of-Record Fellowship, which allowed him to design and teach a course on herpetology.