Not All Signals are Equal: Male Brown Anole Lizards (Anolis sagrei) Selectively Decrease Pushup Frequency Following a Simulated Predatory Attack

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Abstract

The use of conspicuous communication signals often increases a signaler's risk of predation. Many species communicate with a repertoire of signals that may differ in their conspicuousness to predators. Few studies have examined the ability of prey to selectively decrease the use of individual signals in their displays under heightened predation risk. Here, I examined the behavior of male brown anole lizards (*Anolis sagrei*) in response to a simulated predatory attack from a model kestrel. This species communicates with three major visual signal types, the head-bob, pushup, and dewlap extension, which vary in their motion and spectral characteristics. I predicted that lizards would decrease frequencies of the dewlap extension and pushup following the attack, but not the head-bob. Males modulated their use of individual signals by decreasing pushup rates, but not head-bob rates. Decreases in dewlap frequency were marginally significant. One explanation for these results is that lizards decrease frequencies of signal types based partly on their conspicuousness. The energetic cost of each signal type may be an equally important factor that determines the signaler's response to predators, particularly if a predatory attack is perceived as imminent.

Introduction

Predation risk has been implicated as a major selective force in the evolution of communication behavior (Zuk & Kolluru 1998). The tradeoff underlying the use of conspicuous communication displays often involves an opposition between sexual selection driving traits towards increased conspicuousness, and natural selection for predator avoidance favoring signals that are harder to detect (Andersson 1994). Individuals of many species modify their signaling activity according to short-term fluctuations in their predation risk (Ryan 1985; Endler 1987; Magnhagen 1991; Godin 1995; Zuk & Kolluru 1998). Several species communicate with repertoires of display components, and these components may differ in their conspicuousness to predators (Ryan et al. 1982). In visual communication systems, few studies have examined whether prey species can alter their use of individual signal types in response to varying predation risk, or whether the structure of displays is stereotyped such that individuals tend to decrease overall display rates. If prey species can modulate individual signal types, fluctuations in predation pressure may lead to variation in communication behavior by favoring the use of less conspicuous signals when predation risk is high, particularly among individuals that cannot bear the cost of conspicuous signals. This in turn may explain some of the wide variation in signaling behavior exhibited at the individual, population, and species levels in many taxa. In this study, I examine the behavior of the lizard, *Anolis sagrei*, in response to a simulated predatory attack

to examine how elevated predation risk influences signal choice.

Anolis sagrei is a territorial, polygynous lizard found in the southeastern United States, Bahamas Islands and in the Caribbean. *A. sagrei* is an ideal study species because individuals communicate to conspecifics with three major visual signals that most likely differ in their conspicuousness: the head-bob, a small up-and-down motion of the head or fore body; the pushup, an up-and-down motion of the body and tail that includes flexion of four limbs; and the dewlap extension, a pulsing of an often-colorful throatfan. In *Anolis* lizards, signal types are combined into displays that are used in territorial conflicts and courtship (Jenssen 1970; Crews 1975; Sigmund 1983), as well as species recognition (Losos 1985) and pursuit deterrence (Leal & Rodriguez-Robles 1995, 1997; Leal 1999). A few *Anolis* species perform signals in sequences that exhibit stereotypy both within and across individuals (Jenssen 1977). In *A. sagrei*, there is considerable overlap in the contexts in which different displays are used, as well as variability in the frequency with which each signal type is used across displays (Scott 1984). Rather than focus on display sequence, I instead examine only the rates of use of individual signals. I assume that the sequence of signals performed is not as important a factor in determining the lizards' visibility to predators compared to the frequency with which they perform specific signal types.

Although no studies have directly tested whether the communication displays of *Anolis* lizards are visually conspicuous to predators, evidence supports this hypothesis. Many predators of *Anolis* lizards, including birds, mammals, and some snakes, forage diurnally and use visual cues to detect prey (Fox 1969; Nellis et al. 1989; Leal & Thomas 1994; Gunturkun 2000). The movement of prey has been shown to elicit attack in several lizard predators such as the kestrel (Sarno & Gubanich 1995) and racer (Herzog & Burghardt 1974). The visual contrast of prey against the background also facilitates detection by snakes (Czaplicki & Porter 1974) and birds (Edmunds & Dewhirst 1994). In other lizard taxa, natural selection for crypsis has played a role in the evolution of color patterns found at the genus level (Stuart-Fox et al. 2004). In other lizard species, individuals with conspicuous coloration are attacked by predators more often (Stuart-Fox et al. 2003; Husak et al. 2006), or have poorer body condition, most likely as a result of the conspicuous individuals increasing vigilance or other costly anti-predator behaviors (Martin & Lopez 2001). Thus, signals involving movement and/or conspicuous colors are likely to increase a signaler's risk of predation.

The primary goal of this study was to determine whether lizards reduce the frequency with which they use individual signal types in their repertoires following a simulated predatory attack by a model kestrel. It is likely that the signals of *Anolis sagrei* vary in their conspicuousness to predators. The pushup contains 'jerky' motions of high acceleration and velocity that are effective in eliciting the attention of conspecifics (Fleishman 1986), while the dewlaps of most species contrast in color and brightness against the background vegetation of their habitats, relative to the visual systems of conspecifics (Persons et al. 1999; Fleishman 2000; Leal & Fleishman 2004). Most vertebrates detect moving stimuli primarily on the basis of the stimuli's brightness contrast against the background, with color contrast playing a smaller role (Papathomas et al. 1991; Sun & Frost 1997; Persons et al. 1999; Fleishman & Persons 2001). It is probable that the dewlap extension is more conspicuous than the pushup, because the brown body of a lizard performing a pushup may not contrast with the background to the same extent as the dewlap. Therefore, because highly conspicuous signals are riskier to perform in the presence of predators, I predicted that the dewlap extension should exhibit the greatest reductions in use following a simulated avian attack. I also predicted that pushup use should decrease moderately, while rates of the head-bob, the signal with the smallest amplitude, should change little following an attack.

Methods

Test Sites

Island size in the Bahamas is positively correlated with avifaunal richness and negatively correlated with *Anolis sagrei* survival rates (Schoener & Schoener 1978), suggesting that predation pressure increases with landmass area. I tested lizards on various landmass sizes and in different habitats to determine behavioral responses representative of a broad range of *A. sagrei* populations. Tests were conducted during the breeding season months of Jul. and Aug., 2000 and 2001, in four sites: Gun Cay forest and Calabash Cay forest sites in the Bahamas, and Key Largo Mixed and Okeechobee Open sites in Florida. The Gun Cay site encompasses a forested region of this small (0.028 km^2) island located approximately 80 km from mainland Florida. Calabash Cay is another small (0.085 km^2) island located

approximately 2.5 km east of Stafford Creek, Andros Island, Bahamas. Testing took place in an area of short forest. The Key Largo Mixed site, located in John Pennekamp State Park, Key Largo, Florida, is an orchard consisting of key lime and mango surrounded by dense forest. Lizards' territories encompassed the trees within the orchard and adjacent forest. The Okeechobee Open site is located in Pahokee, Florida within the Pahokee Campground. Subjects tested in this site inhabited a rocky boundary area separating the beach-front of Lake Okeechobee from the pines of the nearby campsites.

Experimental Design

The experimental set-up consisted of a model bird of prey moving down a monofilament line into the territory of an *A. sagrei* subject. I constructed the model bird of prey to resemble an American Kestrel, given that this species is widely distributed in the Bahamas and Florida and known to consume lizards (Stevenson & Anderson 1994). The model was constructed of Styrofoam and plywood. Several characteristics of potential predators are known to mediate fright responses in lizards and other reptiles; these include large size (Fine 1999), speed (Cooper 1997; Fine 1999), presence of eyes (Gallup 1973), and direction of gaze (Burghardt & Greene 1988). These features served as a guide for my experimental design. I painted conspicuous eyes on my model and simulated a direct attack by waiting until the lizard occupied a position close to the end of the monofilament line before releasing the bird (distance between bird and lizard at end of attack path: $\bar{x} \pm SE$, 1.2 ± 0.13 m). The model raptor had a length of 36 cm and a wingspan of 57 cm, which approximates the true size of the American Kestrel and the size of models that were effective in eliciting the fear responses of lizards in Fine (1999).

At least 48 h before testing, I captured six to seven adult male *A. sagrei* by noose or hand in a given site, then measured their snout-vent length (SVL) to the nearest mm and mass with a Pesola scale with 10 g capacity (± 0.1 g). I tested a total of 26 subjects (Gun Cay, n = 7; Calabash Cay, n = 6; Okeechobee Open, n = 7; Key Largo Mixed, n = 6). Three lizards escaped before I was able to determine their mass. I then used Liquid Paper® (Sanford, Oak Brook, IL, USA) correction fluid to apply a unique combination of dots on the dorsum of each lizard for identification in the field, a technique that does not affect the survival of reptiles (Jones & Ferguson 1980). I also clipped a toe of each lizard to collect a blood sample

for a malaria test used in another study. This is a standard herpetological technique that does not compromise the animal's sprint speeds (Huey et al. 1990), nor is believed to be associated with higher mortality rates (Ferner 1979). At least 24 h before testing, I set up camouflaged 40-lb test fishing line in each territory. The far end of the line was secured to trees or other habitat features at a height of 2 m. The near end of the line was staked into the ground within the territory of each lizard, the location of which was determined based on the site of capture. The line was angled downwards from the horizontal at approximately 20°, and the length of the line averaged 7 m. In preliminary trials, the movement of the model raptor was timed at 2.5 m/s. This is slower than the cruising flight speeds of 9–14 m/s attained by birds that are lizard predators or of a similar size, such as the kestrel (*Falco tinnunculus*), common tern (*Sterna hirundo*), crow (*Corvus corone*) and grey heron (*Ardea cinerea*) (Rayner 1985), and considerably slower than raptors performing aerial dives of speeds of up to 52–58 m/s (Tucker 1998). However, rapid speeds are not necessary to elicit fear responses in lizards, as models traveling at slower speeds of 1.2–1.4 m/s are able to produce a strong fear response (Fine 1999).

Testing consisted of a 30-min 'pre-attack' observation period and a 30-min 'post-attack' observation period. Pilot trials suggested that lizards habituate to the model approximately 15 min after its movement down the line (after which it remains stationary), so I examined only the 10-min period following the release for treatment effects. During the observation periods, I recorded the behavior of the subject, including performances of each of the three major signals, the head-bob, the pushup, and dewlap extension. At times the dewlap remains extended during a pushup display; in these cases, I counted each up-and-down motion of the body with the dewlap extended as one dewlap pulse and one pushup. Persons et al. (1999) found that stimulus motions analogous to a dewlap pulsing in and out were equally effective at eliciting the attention of conspecific lizards as a dewlap moving up and down, so both motions would most likely be equally conspicuous to predators.

When the subject appeared to be signaling to conspecifics, I recorded the sex of the receiver and its distance from the subject. Identification of receivers was based upon (1) the subject's eventual movement towards the individual (occasionally resulting in a mating with a female and conflicts with males), (2) static modifiers used during male-male

interactions such as lateral compression of the body and erection of crests on the back and tail (Greenberg & Crews 1983), and (3) behaviors exhibited by the receiver in response to the subject (i.e., for subordinate males, a retreat from an approaching male; for dominant males, an approach towards the subject and/or the performance of reciprocal displays; for females, a retreat from or approach to an approaching male and/or signaling displays). Additionally, I recorded the time with a stopwatch at least every 1–2 min to determine the duration of social encounters. At times, the lizards moved to positions out of my view. In these cases, I subtracted the number of minutes that lizards were out of view from my analyses of signaling rates and rates of conspecific interactions. I recorded my observations with a microcassette recorder to allow for continual observation of the subjects.

Throughout testing, I remained close to the position of model release to minimize the effects of my movement on the lizards' behavior. During the pre-release period, the model was concealed from view beneath a camouflage cloth. After the 30-min 'pre-attack' period, I waited until the lizard was in a position that was relatively close to the end of the path of the model and in an orientation that permitted the subject a clear view of the approach of the model. Typically this required only a few additional minutes, as the lizards were quite active. I then hooked the model to the line, after which it glided to the end of the line by gravity. I recorded the lizard's immediate response to the bird in the 1-min interval following the attack. Lizards in adjacent territories were tested on separate days to reduce the probability of habituation to the predator prior to testing. Because the activity of lizards is thermally-dependent, I conducted the study only on warm days with air temperatures above 24°C.

Because the lizards could be reacting to the presence of the monofilament line during the pre-attack period by decreasing signaling rates, masking the effects of the model raptor, I also conducted a 30-min observation trial of 24 subjects in the absence of the experimental set-up (the 'control' observation period). This took place on the day before testing immediately preceding the set-up of the line.

Statistical Analyses

For each subject, I calculated head-bob, pushup, and dewlap extension rates (number of signals/min observed converted to signals/h) for each of the three observation periods, and also specifically during social interactions with conspecifics. Statistical analyses were conducted with the statistical software packages SPSS version 15.0 (SPSS, Chicago, IL, USA) for parametric tests and STATXACT version 5.0 (Cytel, Inc., Cambridge, MA, USA) for nonparametric tests requiring exact p-values. I used paired t-tests for all comparisons of signaling rates between different trials. Signaling rates were square-root transformed to normalize the distributions. Means and standard errors shown in figures represent back-transformed values. Critical p-values were Bonferroni-corrected by the number of non-independent tests performed (0.05/3 signal types = 0.0167 for each set of tests). To determine whether the experimental set-up influenced the signaling behavior of lizards, I compared the rates of each signal type during the observation period without the experimental set-up (the 'control' period) versus the pre-release trial. To determine the effects of the simulated predator attack on signaling rates, I repeated the same analyses on the pre-attack versus post-attack trials. Although an Anderson–Darling normality test indicated that the distribution of pushup signaling differences between the pre-attack and post-attack trial was normal, there was an extreme outlier representing the one lizard that increased pushup rates following the simulated predatory attack. I retained this outlier to provide a more conservative test.

Lizards engaged in social interactions during the pre-attack period may be more likely to take risks in the post-release period, so I examined the counts of lizards engaged in social interactions before and after the attack with a Fisher's exact test. Only one social interaction took place in the 10-min post-attack period, so I expanded the analysis to include interactions over the entire 30-min post-attack period. Additionally, I examined whether lizards engaged in social interactions before the simulated attack had higher signal rates during the post-release period than lizards not previously engaged in social interactions. Because these data exhibited strong departures from normality even with the square root transformation, I performed a Mann–Whitney U test. All statistical tests in this analysis were two-tailed.

Results

Comparison of Signaling Rates During the Pre-Attack Versus Control Periods

There were no significant differences in the signaling frequencies of lizards during the pre-attack period and the control period for the head-bob (paired
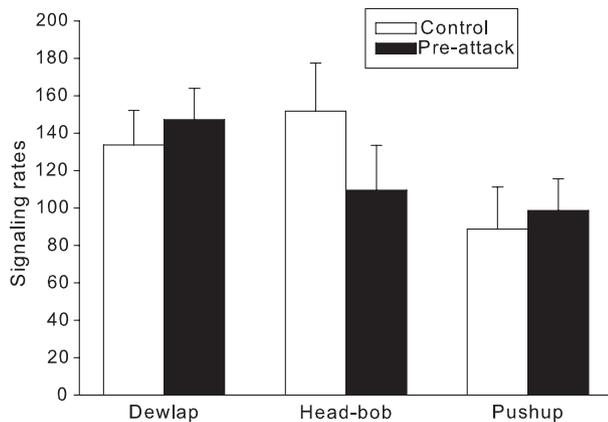
Fig. 1: Effect of fishing line set-up on signaling rates. 'Control' refers to the 30-min trial when no fishing line was present in lizards' territories; 'Pre-attack' refers to the 30-min trial when fishing line was present, before the simulated attack. Values are $\bar{x} \pm$ SE.
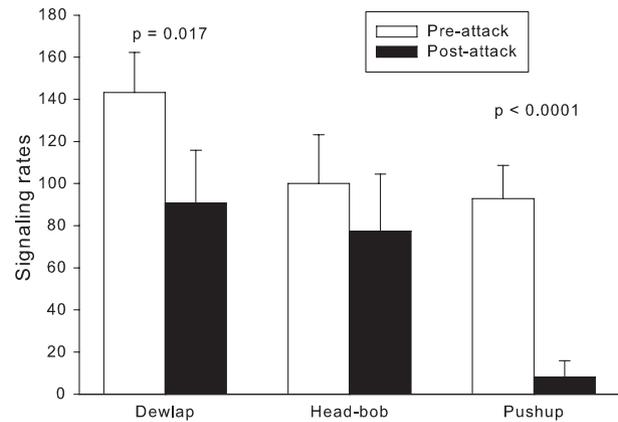

Fig. 2: Signaling rates before simulated attack and during 10 min period following the attack. N = 26 for all comparisons. Values are $\bar{x} \pm$ SE.

t-test: t = 1.4, n = 24, ns), pushup (paired t-test: t = −0.3, n = 24, ns), or dewlap extension (paired t-test: t = −0.6, n = 24, ns; Fig. 1). Therefore, the presence of fishing line in the lizards' territories during the pre-attack period did not influence their behavior, and their signaling behavior during this period was most likely an accurate representation of their baseline rates.

Effects of the Simulated Predator Attack on Escape Responses and Signaling Behavior

Individuals differed in their immediate responses to the predator (Table 1). These included hiding in refuges such as crevices and log piles, shifting to positions less easily seen by the predator (which was often accompanied with lowering their head on the substrate to reduce the conspicuousness of their silhouette), remaining stationary (tonic immobility) and running away from the bird. Ten lizards jumped a short distance away or watched the predator, then

Table 1: Immediate responses of lizards to the simulated predator attack

Response	Total	Bahamas	Florida
Hide	4	2	2
Position Shift	5	4	1
Tonic Immobility	6	2	4
Jump Away	1	1	0
Total responses without signals	16	9	7
Watch and signal	6	3	3
Jump away and signal	4	1	3
Total responses with signals	10	4	6

signaled within approximately 1 min of the attack. The Bahamas and Florida lizards did not show large differences in their immediate responses to predators (Table 1).

The effects of the simulated predator attack varied by signal type (Fig. 2). As predicted, head-bob rates did not significantly decrease (paired t-test: t = 1.0, n = 26, ns). By contrast, pushup rates decreased dramatically (rate before attack: 92.8 ± 15.9 pushups/h; after attack: 8.0 ± 7.8 pushups/h; paired t-test: t = 6.8, n = 26, p < 0.0001). Only lizards in the Okeechobee Open site performed pushups in the post-attack period, with four of seven lizards performing this signal. Contrary to my predictions, dewlap extension rates exhibited only a marginally significant decrease (paired t-test: t = 2.6, n = 26, p = 0.017).

Involvement in social interactions during the pre-attack period was positively associated with involvement in interactions during the 30-min post-attack period (Fisher's exact test, p < 0.038). Of the nine lizards engaged in social interactions during the 30-min post-attack period, seven had engaged in interactions beforehand. Lizards not engaged in social interactions before the simulated attack were much less likely to engage in post-attack interactions compared to lizards previously engaged in interactions. However a considerable proportion of the lizards that had participated in social interactions during the pre-release period ceased interacting with conspecifics in the post-attack period. Lizards that had engaged in social interactions before the attack did not display higher rates of signaling in the 10-min period after the attack compared to lizards that were not engaged in social interactions before the attack
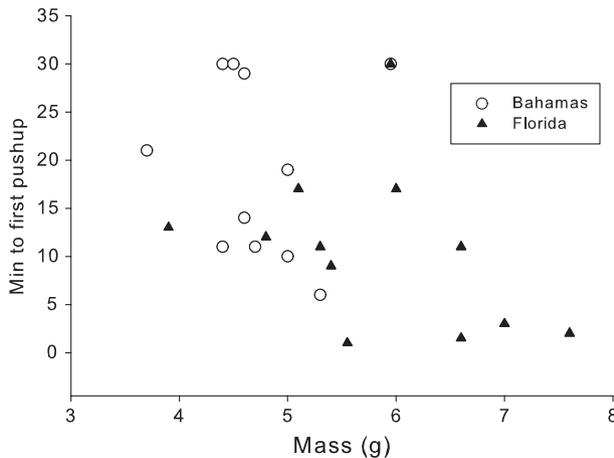
Fig. 3: Correlation between mass (g) and time to first pushup following predatory attack (min). R = −0.43; n = 23; p < 0.05.

(Mann–Whitney U tests: $U_{dewlap} = 53.5$, $n_1 = 12$, $n_2 = 14$, ns; $U_{pushup} = 87.0$, $n_1 = 12$, $n_2 = 14$, ns; $U_{head-bob} = 80$, $n_1 = 12$, $n_2 = 14$, ns).

In light of the strong decline in pushup rates, I performed a post-hoc analysis to further explore the influence of the pre-attack social interactions and another variable, body mass, on pushup use. Body size is correlated with several components of escape capacity in lizards. Thus, large lizards may be at less risk of predatory attack and able to signal with riskier signals. I examined the time (in min) from the attack to each individual's first pushup instead of pushup rates because rates were extremely low in the post-attack periods. Body size was negatively correlated with time to first pushup (Pearson: r = −0.43; N = 23; p < 0.05; Fig. 3). I then performed an ANCOVA with mass as the covariate and involvement in pre-attack social interactions as a main effect to determine whether pre-attack involvement explained a significant amount of variance in time to first pushup, independently of mass. However, only mass explained a significant amount of the variance (ANCOVA mass $F_{2,19} = 4.9$, p = 0.04; prior social interactions: $F_{2,19} = 0.4$, ns).

Discussion

These results demonstrate that lizards are able to modulate communication signal use in the presence of predators. Furthermore, subjects modulated rates of individual signals independently of one another, and dramatically decreased use of the pushup. One explanation for these findings is that signaling in the presence of predators is risky, and that predation

costs may vary across signal types. However, differences in the way in which individuals modulated signal use did not follow the pattern I had predicted. Following the simulated predatory attack, individuals decreased pushup frequencies, but not the head-bob frequencies, which is consistent with the idea that individuals selectively decrease signals associated with greater predation risk. I had predicted that pushup rates would decline more than head-bob rates based on the pushup's high velocity and acceleration, in addition to its greater amplitude of motion, which are likely to be associated with increased conspicuousness to predators. I had predicted that dewlap extensions would show the greatest decrease in post-attack use, but this decrease was only marginally significant. I consider several possible explanations for these results below.

The discrepancy between my predictions and results suggest that there may be costs associated with signals other than detectability costs. Though the dewlap extension may be a more visually conspicuous signal, the pushup may have energetic costs in addition to moderate detectability costs that together outweigh the costs associated with the dewlap. In other lizard species, pushup displays are energetically costly. Male side-blotched lizards (*Uta stansburiana*) perform a threat display to conspecific males involving lateral compression of the body. This display, which often accompanies the pushup, compromises the endurance of the signaler, most likely because it restricts aerobic metabolism (Brandt 2003). Males with greater endurance perform longer threat displays, suggesting that this display is a quality handicap that both broadcasts the signaler's endurance while simultaneously expending it. Similarly, in *Anolis cristatellus*, pushup frequency is an honest signal of the endurance capacity of the signaler during predatory encounters with model snakes (Leal 1999). These lizards are occasionally able to escape from snake attacks, which may require aerobic endurance. Therefore, in *Anolis sagrei*, the pushup is likely to be an energetically costly signal as well. In the present study, ten lizards performed signals within 1 min of the attack. It was unclear whether the lizards were signaling directly to the predator (as a pursuit-deterrent signal, e.g. Leal 1999) or were continuing to signal to conspecifics. However, only two lizards performed pushups within 2 min of the approach of the model kestrel, suggesting that the pushup is not widely used as a pursuit deterrent signal to avian predators. One explanation for this discrepancy is that avian predators are faster and more adept at catching prey, and that performing pushups does little to ward off an attack.

Supporting the idea that the pushup is a costly signal is the finding that larger lizards resumed signaling with pushups faster than smaller lizards. Several measures of escape capacity in lizards are correlated with body size, including sprint speed, both within species (Huey & Hertz 1982; Dohm et al. 1998) and across species (Losos 1990; van Damme & Vanhooydonck 2001), and aerobic endurance, both within species (Dohm et al. 1998; but see Leal 1999) and across species (Garland 1994). It is likely that lizards with greater escape capacity resumed signaling with the pushup earlier than individuals with reduced escape capacity.

The finding that lizards did not decrease dewlap frequencies to the same extent as the pushup also was unexpected. One explanation may stem from differences between the predatory encounters most often experienced by lizards and those simulated in this experiment. The direct attacks simulated in this experiment may be infrequent compared to the typical predatory encounter in which greater distances separate predator and potential prey. At greater distances, there is an increased likelihood that the lizard has not been detected by the predator. A lizard may be able to prevent an attack by reducing its use of the most conspicuous signal, which in this system, may be the dewlap. When predators are at greater distances from the signaling lizard, the energetic cost of signals may be less important until there are cues that a direct attack is imminent. To test this idea, a simulated predator could be presented to lizards at greater distances to determine whether lizards reduce dewlap frequencies. Clearly, the interpretation of these findings would be elucidated by determining which signals are most conspicuous to predators, either through the use of mathematical models of signal detection, replicas that mimic the signals, or by presenting motion stimuli to predators and measuring visual system responses.

It is likely that the responses of males to the simulated predatory attack demonstrated in this study could contribute to population-level differences in display behavior in *Anolis* lizards experiencing varying levels of exposure to predators. If individuals decrease pushup frequencies, and possibly dewlap extension frequencies in close proximity to predators, these responses could lead to significant differences in display behavior between populations that vary in predator abundance. Predation pressure could also have an indirect influence on behavior, such as through impacting population density, which is known to influence *Anolis* signaling behavior (Bloch & Irschick 2006). Few studies have explicitly explored the role of predation pressure in explaining the diversity of dewlap colors and display variation in *Anolis* lizards, yet this study suggests that predation pressure may be an important factor.

Many species communicate with signals involving body movements. These results suggest that individuals are able to alter their use of specific signal types, which, given individual and population differences in escape capacity, can lead to considerable variation in communication behavior at these levels. In addition, dynamic signals that an individual can control may allow natural selection to drive signal conspicuousness to a higher level than static signals that are more continually exposed to visual predators (for example, dorsum coloration). Finally, both the energetic and conspicuousness costs of signals may be important to consider as prey species encounter predators.

Acknowledgements

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