Response of *Anolis sagrei* to Acoustic Calls from Predatory and Nonpredatory Birds

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ABSTRACT.—Many studies indicate that various vertebrates and invertebrates use sensory cues to recognize predators and to evaluate predation risk. Lizards and birds frequently occupy the same habitats; consequently, avian predation on lizards has been implicated as an important selective pressure on lizard behavior. However, there are few studies on how lizards respond to nonvisual cues. The response of adult male Brown Anoles (*Anolis sagrei*) to calls of birds was studied to determine whether they use auditory cues as an indicator of predation risk from birds. Anoles responded significantly more often with head tilt (increased vigilance) during playback of predatory vocalizations (Kestrel and Red-tailed Hawk calls) compared with low-risk stimuli (nonpredatory bird calls and white noise). Responses to auditory cues suggest that male Brown Anoles are able to distinguish the calls of birds known to prey upon lizards from the calls of nonpredatory birds. More important, this study demonstrates that anoles, most of which are nonvocal, are able to obtain information about predation risk through the use of auditory cues and that the role of hearing in these lizards has been underappreciated.

Predation risk selectively modifies prey behavior such as activity, reproduction, and habitat selection, thereby ultimately affecting community dynamics (Lister and Aguayo, 1992; Martín and López, 2005). Empirical evidence suggests that predation is one of many factors driving the evolution of behavioral strategies in prey organisms (Bloomberg and Shine, 2000; Stuart-Fox et al., 2003; Martín and López, 2005; Costantini et al., 2007). Selection, therefore, should favor the use of sensory mechanisms that enable organisms to detect the presence of predators and allow them to assess the associated level of predation threat. Several studies have shown that animals from diverse taxa use chemosensory, visual, or auditory cues to detect the presence of predators and assess the associated risk involved (Baxter et al., 2006; Blumstein et al., 2008; Lohrey et al., 2009; Mathot et al., 2009). Rodents (Kindermann et al., 2009), wolf spiders (Lohrey et al., 2009), marmots (Blumstein et al., 2008), bats (Baxter et al., 2006), birds (Adams et al., 2006), moths (Fullard et al., 2008), and primates (Gil-da-Costa et al., 2003) exhibit antipredator behavior in response to predatory vocalizations. The manner and intensity with which prey respond to cues depend on their ability to distinguish between nonthreatening and threatening stimuli as well as their ability to determine the level of predation risk (Adams et al., 2006). Responses to "high-risk" auditory stimuli might include fleeing, hiding, increased latency to return to exposed sites, cessation of movement or activity, and increased vigilance. Inappropriate responses during predatory encounters can be life threatening or result in the loss of time and energy associated with foraging, mating, and territory defense (Broom and Ruxton, 2005; Vanhooydonck et al., 2007); therefore it is advantageous for prey to accurately assess risk associated with nearby predators (Adams et al., 2006; Mathot et al., 2009).

Lizards often represent an important part of the diet of predatory birds (e.g., Wunderle, 1981; McLaughlin and Roughgarden, 1989; Martín and López, 1996; Poulin et al., 2001). McLaughlin and Roughgarden (1989) found that anoles make up 50–75% of the kestrel diet on the island of Anguilla, in the northern Lesser Antilles. Their results were similar to Wetmore's (1916; in McLaughlin and Roughgarden, 1989) findings that the

kestrel's diet consisted of 40.4% anoles on Puerto Rico. Furthermore, insectivorous birds may temporarily shift their diet to include lizards during times of reduced insect abundance (Wunderle, 1981). Consequently, avian predation on lizards has been implicated as an important selective pressure on lizard behavior (Martín and López, 1996; Bloomberg and Shine, 2000; Stuart-Fox et al., 2003; Costantini et al., 2007). Given that lizards commonly fall prey to birds, it is important to understand the detection mechanisms used during encounters with avian predators.

Male *Anolis* lizards are diurnal, social animals that use conspicuous displays during courtship (Lister and Aguayo, 1992) and territorial defense (Plavicki et al., 2004), which may increase their risk of predation (Costantini et al., 2007). Anoles also rely heavily on visual signals during social interactions and detection of potential predators (Leal and Rodriguez-Robles, 1997; Leal, 1999). However, anoles have well-developed auditory systems with enhanced directionality (Christensen-Dalsgaard and Manley, 2005, 2008) and hearing sensitivity ranging from 1000 to 7000 Hz (Brittain-Powell et al., 2010), which overlaps with the range of frequency (1000–5000 Hz) used by most birds to communicate (Dooling et al., 2000). Interestingly, most lizard species are nonvocal and therefore their auditory system may function to receive stimuli from prey (Sakaluk and Belwood, 1984) or impending danger (Wever, 1978). Many studies have been performed on the visual detection of predators by anoles (Leal and Rodriguez-Robles, 1997; Leal, 1999; Simon, 2007) but few studies have been conducted on the responses of anoles to nonvisual predatory cues.

Investigation into the use of auditory cues by lizards as a mechanism to detect the presence of predators is a relatively novel concept. However, Vitousek et al. (2007) and Ito and Mori (2010) showed that lizards eavesdrop on the alarm calls of birds and subsequently increased their vigilance (head movement) to predators. Similarly, Huang et al. (2011) found that Crested Anoles (*Anolis cristatellus*) decreased display rates following shutter sounds from a camera and playbacks of calls from predatory birds, indicating that anoles may perceive these stimuli as threatening. Our study is the first to examine whether anoles respond differently to calls from predatory birds compared with calls of nonpredatory bird species. Because of the substantial predation on anoles by birds (Wetmore, 1916;

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McLaughlin and Roughgarden, 1989), we hypothesized that anoles are capable of distinguishing predatory from nonpredatory vocalizations and would exhibit increased vigilance, characterized by visual monitoring by means of eye and head movement, in response to playbacks of the calls from predatory birds.

METHODS AND MATERIALS

Subjects.—*Anolis sagrei*, the Brown Anole, is native to Cuba and the Bahamas, and has been introduced recently into the southeastern United States and elsewhere. Thirty-two adult male wild-caught Brown Anoles were caught in Titusville, Florida during May 2009 and were housed together in two glass holding tanks (16 lizards in each) measuring $51 \times 25 \times 30$ cm (length $\times$ width $\times$ height, respectively). Holding tanks and the playback arena had coconut-fiber substrate, a wooden perch, twisting vine, and a plastic plant. A fluorescent ultraviolet B bulb and a 60-W neodymium daylight bulb maintained ambient daytime temperature between 26°C and 29°C and a basking area at 32°C. Nighttime temperatures of 21–24°C were provided by a 60-W black light bulb. Anoles were kept on a 13 : 11 h light : dark cycle, misted daily with water, and fed crickets (dusted with RepCal calcium supplement) between 1700 and 1800 h every other day. The lizards were allowed to acclimate to these conditions for 2 weeks before experimental manipulation. Lizards were donated to a high-school biology class after completion of all experimental procedures.

Audio Clips and Playback.—We obtained 48 different avian audio clips (eight exemplars from six species) from the Cornell Laboratory of Ornithology's Macaulay Library of Animal Sounds. Bird calls included possible predators of anoles (the American Kestrel, Red-tailed Hawk, and the Pearly-eyed Thrasher) and calls from nonpredators (the Song Sparrow, Northern Cardinal, and House Finch). Passerines utilize both songs and calls to communicate, each having different functions. Songs are normally complex vocalizations used by males during courtship and territory defense. Calls are typically short and simple vocalizations used by both males and females for numerous functions, including alarm calls, which are used to communicate nearby threats (Marler, 2004; Catchpole and Slater, 2008). Alarm calls, more frequently, are loud, harsh calls that carry long distances or high-pitched whistles only audible to those nearby, both of which are used in response to both aerial and ground predators (Marler, 2004). We were careful not to choose alarm calls for the nonpredatory species, as lizards may perceive these calls as threatening (indicating the presence of a shared predator) and respond similarly to the way they might respond to calls of predatory birds. Furthermore, all of the species chosen occur within the introduced North American geographic range of *A. sagrei* except the Pearly-eyed Thrasher, which is found in areas where *A. sagrei* is native.

In addition to the bird calls, we generated eight different sound clips of white noise and a clip of silence as control "stimulus." Each clip was 6 sec in duration and we used Adobe Audition 3.0 to adjust their playback levels (except the silent stimulus) to the same root mean square power. The digital signals were broadcast from speakers (Zylux, 120 V, A525) driven by a Creative Sound Blaster Audigy Advanced audio card at a 44.1-kHz sampling rate. The speaker was always positioned at the same angle located at 45° above the horizontal and at a distance of 90 cm from the playback arena.

Experimental Design.—All playbacks were conducted between 1400 and 2000 h during a 2-month period. Anoles were removed from the holding tank and placed individually into the playback arena (identical in size and setup of holding tanks) that was behind a blind to eliminate the subject's view of the computer, playback equipment, and movement of the observer. The location of the playback arena was in a different room from that of the holding tanks but both were maintained under the same environmental conditions. Each anole was given 16–18 h to acclimate to the arena before playback experiment.

For the playback trials, we chose one of the eight exemplars from each bird call and noise control randomly and always used the same silent stimulus. We then randomized the order of playback for the eight stimuli (kestrel, hawk, thrasher, noise, silence, sparrow, cardinal, and finch). One 6-sec sound clip from each of the eight stimuli was played to each individual lizard and each sound clip was played three times (back to back for a total of 18 sec). No previous data could be found on the time it takes for lizards to resume a baseline level of activity following auditory cues. Therefore, sound clips for each of the eight stimuli were played at 30-min intervals, assuming that lizards would return to their normal level of activity before the next playback. Individual responses were tested for effects of playback order.

Behavioral Observations.—We visually observed, videotaped (Sony Handycam digital camcorder), and scored the behavior of the test anole during each playback. After analyzing the videos, we categorized behavioral reactions in four levels that relate to increased predation risk: no reaction, eye movement (any movement of the eyes; body and head still), head tilt (abrupt change in the angle of the head left or right or up and down, body still; Ito and Mori, 2010), and immediate flight (any movement away from the original location or to an area of refuge; Ito and Mori, 2010). If the anole exhibited more than one behavioral category then the highest category was scored for analyses. Individuals were also monitored for pursuit-deterrent signals (push-ups: up and down movement of the body produced by flexion and extension of the forelegs, and dewlap extensions: extension and contraction of the throat fan; Leal, 1999). Each subject was tested only once.

Statistical Analysis.—For statistical analysis, the four categorical behavioral responses were reclassified as either no response or antipredator response (i.e., eye movement, head tilt, immediate flight). Individuals were tested with multiple stimuli and thus responses were not independent. Therefore, we tested for behavioral differences using a generalized linear mixed model (GLMM) with binomially distributed errors using the lme4 package (Bates et al., 2011; v. 0.999375-39) in R (R Development Core Team, 2011). We started with a saturated model and used Akaike information criterion (AIC) to remove all parameters except treatment (stimulus presented) as a fixed effect and individual nested within playback order as a random effect. Nesting individual within order allowed us to account for possible effects of playback order on individual responses. A priori planned orthogonal contrasts between treatments were conducted with the multcomp package (Hothorn et al., 2011; v. 1.2–5).

RESULTS

Frequeny of Responses to Stimuli.—Anole responses (no reaction, eye movement, head tilt, and flight) to treatment stimuli were significantly different ($\chi^2 = 78.1$, df $= 7$, $P \ll 0.001$; Table 1). No

TABLE 1. Results from the generalized linear mixed model to determine if anole responses differed across acoustic stimuli. Responses were classified as no response and antipredator response. Responses to each stimulus were compared with the cardinal stimulus. Only responses to hawk and kestrel were significantly different from responses to cardinal. The overall model was highly significant ($\chi^2 = 78.1$, df = 7, $P \ll 0.001$).

Explanatory variable	Coefficient	SE	z	P value
Finch	0.286	0.721	0.396	0.692
Hawk	2.361	0.769	3.070	0.002
Kestrel	2.942	0.804	3.662	$\ll$0.001
Noise	0.428	0.749	0.572	0.568
Silence	−17.055	709.825	−0.024	0.981
Sparrow	0.669	0.752	0.891	0.373
Thrasher	1.016	0.770	1.320	0.187

anoles reacted to the silent stimulus (Fig. 1B). Half or less than half of the 32 anoles responded to playbacks of nonpredatory birds or white noise (cardinal: 37.5%; finch: 40.6%; sparrow: 43.8%; thrasher: 50%; white noise: 43.8%), whereas three-fourths of the anoles responded to playbacks of kestrel calls (75%) and two-thirds of the anoles responded to playbacks of Red-tailed Hawk calls (65.7%; Table 2). More often, anoles exhibited head tilts to the two predator calls (kestrel = 46.9% and Red-tailed Hawk = 37.5%; Table 2) than eye movement or flight. Flight was the least displayed reaction across all audio stimuli (combined percentages: predator = 28.2%; nonpredator = 37.5%; and control = 9.4%; Table 2).

Responses to Predatory and Nonpredatory Stimuli.—We further categorized the treatment stimuli into predatory, nonpredatory, and control groups (Table 3). Because anole responses to thrasher calls were intermediate and not significantly different from responses to nonpredator and control stimuli ($z = 1.32$; $P = 0.187$; Table 1), we used AIC to select the optimal model to determine how to categorize the stimulus. The optimal model was highly significant and categorized kestrel and Red-tailed Hawk as predatory stimuli and thrasher, sparrow, cardinal, and finch as nonpredatory stimuli ($\chi^2 = 3.88$, df = 1, $P \ll 0.001$). Because no anoles responded to the silent control, we removed that treatment from the data set and conducted the GLMM on all remaining (auditory) stimuli. Anole responses to predatory stimuli were significantly different from responses to nonpredatory ($P \ll 0.001$) and control ($P \ll 0.001$) stimuli. A priori planned orthogonal contrasts suggest that anoles discriminate between the calls of predatory and nonpredatory birds ($z = 4.35$, $P \ll 0.001$; Table 4). However, responses to nonpredator stimuli were not different from control ($z = 0.146$, $P = 0.986$; Table 4). Anoles responded with a head tilt more frequently to predatory stimuli compared with nonpredatory stimuli, suggesting increased vigilance from perceived predation risk (Fig. 1). Pursuit-deterrent signals were not exhibited by any of the anoles tested.

DISCUSSION

Our results suggest that male *A. sagrei* can distinguish among the calls of birds that they might perceive as threatening from those that they perceive as nonthreatening. Anoles exhibited significant increases in vigilance (head tilting) during playback of kestrel and Red-tailed Hawk calls compared with songs of nonpredatory species. Although there were no statistical differences between responses to kestrel and Red-tailed Hawk calls, anoles displayed a heightened sense of vigilance to kestrel calls compared with hawk calls. One explanation for this may be that Red-tailed Hawks are large raptors that feed more frequently on larger prey such as rodents, birds, and snakes (Fitch et al., 1946), in comparison with kestrels, which are small raptors that tend to feed on smaller prey such as large insects, lizards, and small mammals (Yáñez et al., 1980). However, because kestrels are also smaller in body size compared with Red-tailed Hawks they possess greater maneuverability (Templeton et al., 2005), and therefore may be perceived as a greater threat by anoles. In contrast, anole responses to predatory thrasher calls were not significant. This may be because the lizards that were tested in this study did not develop within the geographic range of thrashers and therefore may not perceive their calls as threatening. Anoles also exhibited very little response to songs of nonpredatory birds, signifying that these species are also not perceived as a threat. It is therefore likely that the use of auditory perception in assessing predation risk in anoles, and lizards in general, may be as important as visual and chemical cues in detecting and recognizing predators than previously appreciated.

The ability of anoles to discriminate the calls of predatory birds from songs of nonpredatory birds could allow them to detect the presence of danger more efficiently. Auditory cues can be detected at greater distances than visual cues, allowing anoles to locate a predator before a dangerous encounter, especially in dense vegetation or where visual detection of aerial predators may be difficult. Acquiring information through auditory cues may also allow anoles to decrease visual monitoring, thereby minimizing missed opportunity costs associated with foraging, territory defense, and courtship. Furthermore, lizards may use multiple cues in combination to detect predators (Amo et al., 2006); therefore, anoles that incorporate both auditory and visual cues during predatory encounters may obtain more accurate information on the location of predators and make more informed decisions on how to respond.

Anoles exhibited increased vigilance during playbacks of calls from predatory birds rather than fleeing. Raptors, and predators in general, do not vocalize while hunting; therefore the perceived level of threat may not have been great enough to elicit flight behavior in these lizards. In addition, louder calls, suggestive of a nearby predator, may be perceived as a greater risk. Also, lizards exposed to a greater frequency of calls from predatory birds on a daily basis may perceive their environment as more risky compared with a lizard that rarely hears calls from predatory birds; therefore threat assessment may be context dependent over spatial and temporal scales depending on their environmental surroundings. However, it may be that in the absence of visual cues to establish the exact location of the predator, anoles lacked enough information to accurately assess risk level or determine direction of escape.

Anoles also did not exhibit pursuit-deterrent signals to calls of predatory birds, as they might with visual predators. This is consistent with Simon's (2007) findings, that male Brown Anoles, in the presence of a model kestrel, decreased push-up and dewlap frequencies, suggesting that these displays are not commonly used as pursuit-deterrent signals with kestrels. One explanation may be that avian predators attack from above by swooping down; consequently, performing pursuit-deterrent signals may attract attention and therefore do little to discourage an attack. In addition, escape responses and pursuit-deterrent signals are energetically costly compared with vigilance behavior (Ydenberg and Dill, 1986) and may be less
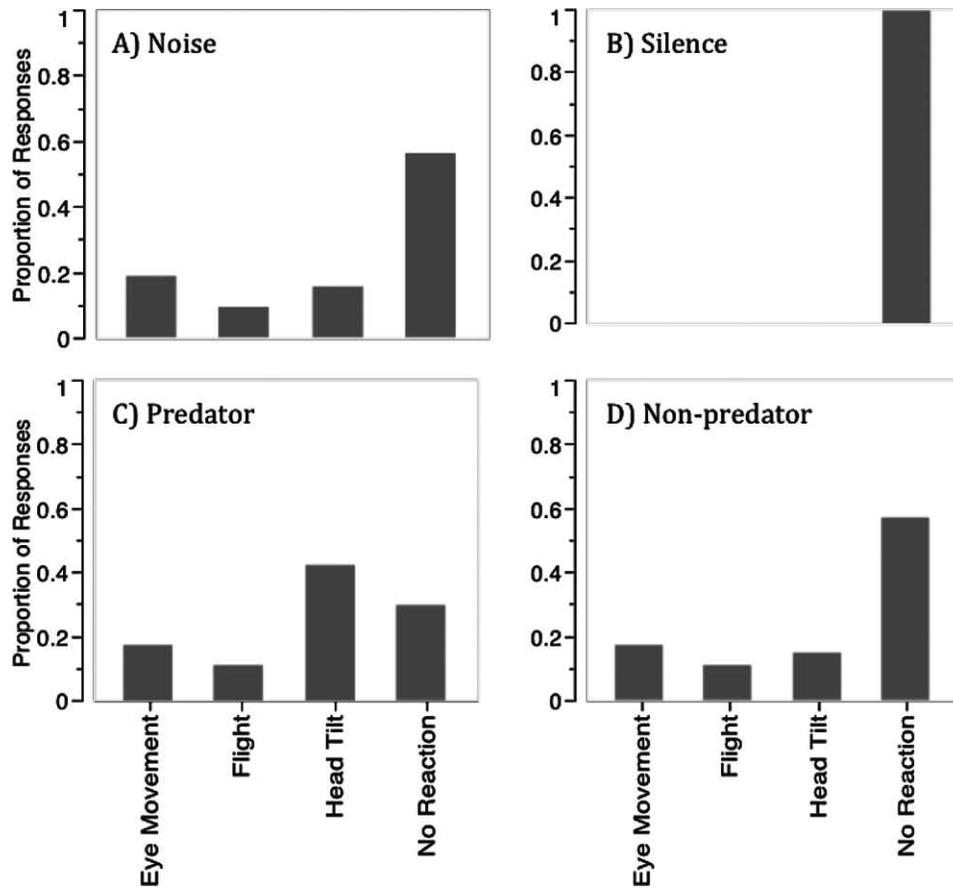
FIG. 1. Proportion of responses displayed by anoles ($N = 32$) for each category of playback stimulus (A: noise, B: silence, C: predator, and D: nonpredator). Responses differed significantly across stimuli ($\chi^2 = 78.12$, df = 7, $P \ll 0.001$). Anole responses to predator calls (kestrel and Red-tailed Hawk) were highly significant ($P \ll 0.001$) compared with controls and nonpredator stimuli with more responses in the head tilt category. Responses to noise and nonpredator (sparrow, cardinal, finch, and thrasher) categories did not differ.

likely to be exhibited in response to stimuli perceived as being at lower threat levels. However, the lizards in our experiment were not exposed to visual stimuli of predators and therefore pursuit-deterrent signals may not have been warranted.

Studies have shown that predator detection (Martín and López, 2005; Cooper, 2006a,b) and the ability to locate sound sources (Christensen-Dalsgaard and Manley, 2008) are impor-

tant elements for evaluating threat. Christensen-Dalsgaard and Manley (2005, 2008) found that the lizard ear is highly directional and should assist in localizing sound sources. We found that responses to the kestrel and Red-tailed Hawk calls consisted mostly of head tilt, suggesting that lizards may have been trying to determine the position or location of the bird.

Our results reveal that *A. sagrei*, a nonvocal species, can distinguish between the calls of known predatory and non-predatory bird species. Although Brown Anoles are nonvocal, they possess a highly sensitive auditory system (Manley, 2000; Brittain-Powell et al., 2010). The prime function of this system may be to receive ecologically relevant auditory stimuli, including those that signal danger. Anoles, and lizards in

TABLE 2. Frequency of behavioral responses (1 = no reaction, 2 = eye movement, 3 = head tilt, 4 = flight) exhibited by male Brown Anoles ($N = 32$) to playbacks of the calls of predatory and nonpredatory birds, and control stimuli.

Stimulus type	Behavioral Responses			
	1	2	3	4
Predators				
Kestrel	0.250	0.125	0.469	0.156
Hawk	0.344	0.219	0.375	0.063
Thrasher	0.500	0.250	0.187	0.063
Nonpredators				
Sparrow	0.562	0.125	0.219	0.094
Cardinal	0.625	0.156	0.094	0.125
Finch	0.593	0.156	0.094	0.156
Controls				
White noise	0.563	0.188	0.156	0.094
Silence	1	0	0	0

TABLE 3. Total number of binomial responses used for the generalized linear mixed model (GLMM) exhibited by anoles to each of the recategorized stimulus types (predator: kestrel and hawk; nonpredator: thrasher, cardinal, sparrow, and finch; and control: white noise). Anole responses to predatory stimuli were significantly different from responses to nonpredatory ($z = 4.35$; $P \ll 0.001$) and control ($z = 3.312$; $P \ll 0.001$) stimuli. Responses to nonpredator stimuli did not differ from control ($z = 0.146$; $P = 0.986$).

Stimulus type	No response	Antipredator response
Predator	19	45
Nonpredator	73	55
Control	18	14

TABLE 4. Results from a priori planned orthogonal contrasts following a generalized linear mixed model. Anole responses to the calls of predatory birds differ significantly from responses to the calls of nonpredatory birds. However, responses to the calls of nonpredatory birds did not differ from responses to control stimuli. The optimal model was highly significant ($\chi^2 = 32.5$, df = 1, $P \ll 0.001$).

Comparison	Coefficient	SE	z	P value
Predator–nonpredator	2.14	0.493	4.35	$\ll 0.001$
Nonpredator–control	0.0852	0.586	0.146	0.986

general, may use a multimodal system to obtain the most accurate information to assess predation risk, allowing them to make optimal behavioral decisions under risky conditions. Evidence from our study along with those conducted on Galapagos Marine Iguanas (*Amblyrhynchus cristatus*; Vitousek et al., 2007) and Madagascan Spiny-tailed Iguanas (*Oplurus c. cuvieri*; Ito and Mori, 2010) suggests that lizards are capable of deriving information about predation risk through the use of differential auditory signals. It is therefore likely that the use of auditory stimuli to assess predation risk in Brown Anoles, and lizards in general, has been underappreciated and may be more common than previously thought.

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