

Reduced foraging in the presence of predator cues by the Black Spiny-tailed Iguana, *Ctenosaura similis* (Sauria: Iguanidae)

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Abstract

Reduced foraging in the presence of predator cues by the Black Spiny-tailed Iguana, *Ctenosaura similis* (Sauria: Iguanidae). The presence of a predator may have direct and indirect effects on the behavior of the prey. Although altered behavior may help prey avoid predators, it also can have a potential impact on critical activities such as foraging. Predator-prey interactions are routinely studied in laboratory-based experiments owing to the perceived difficulties of conducting such experiments in natural settings. We conducted an experimental study under field conditions in Palo Verde National Park in northwestern Costa Rica to assess behavioral responses of Black Spiny-tailed Iguanas (*Ctenosaura similis*) to the presence of predators and predator cues. Free-roaming iguanas were offered mango in designated areas in the presence of a predator (*Boa constrictor*), a predator cue (*B. constrictor* feces), and a control (no predator or predator cue). Results indicate that iguanas reduced their foraging efforts in the presence of both a predator and its cue.

Keywords: Squamata, Iguania, Costa Rica, foraging, predator avoidance, predator-prey interactions.

Received 28 June 2010.

Accepted 17 November 2010.

Distributed December 2010.

Resumo

Redução do forrageio do iguana-negro-de-cauda-espinhosa, *Ctenosaura similis* (Sauria: Iguanidae), na presença de estímulos do predador. A presença de um predador pode exercer efeitos diretos e indiretos sobre o comportamento da presa. Embora a alteração do comportamento possa ajudar a presa a evitar predadores, pode também ter um impacto potencial sobre atividades críticas, como o forrageio. As interações predador-presa são comumente estudadas em experimentos de laboratório devido às dificuldades em conduzir experimentos sob condições naturais. Conduzimos um estudo experimental em campo no Parque Nacional Palo Verde, no noroeste da Costa Rica, para avaliar as respostas dos iguanas-negros-de-cauda-espinhosa (*Ctenosaura similis*) à presença de predadores e de seus estímulos. Oferecemos manga a iguanas livres em áreas pré-estabelecidas na presença de um predador (*Boa constrictor*), de um estímulo do predador (fezes de *B. constrictor*) e em uma área-controle (sem predador ou estímulo). Os resultados indicam que os iguanas reduziram seus esforços de forrageio tanto na presença do predador como de seu estímulo.

Palavras-chave: Squamata, Iguania, Costa Rica, evitação do predador, forrageio, interações predador-presa.

Introduction

Interactions with predators can have a substantial impact on the time and effort that prey species allocate to behaviors such as sleeping (Revell and Hayes 2009), thermoregulation (Downes 2001), and foraging (Milinski and Heller 1978). Altering basic behaviors to minimize exposure to predators may reduce overall risk of predation (Krebs 1980, Gilliam and Fraser 1987, Lima and Dill 1990); however, it also may decrease fitness by constraining other critical, beneficial activities (Ball and Baker 1996). Therefore, animals must seek an optimal balance between avoiding predation and maximizing energy acquisition and fitness (Amo *et al.* 2007).

Chemical cues play a major role in predator detection for a wide range of vertebrate and invertebrate animal taxa (Kats and Dill 1998). The ability to detect the presence of predators, or even conspecifics (Langkilde and Shine 2005), without direct visual or physical contact is beneficial in avoiding potentially harmful predatory or competitive interactions. The organism must maintain situational awareness to avoid an attack by a predator, including those situations in which it would otherwise be vulnerable (e.g.,

while sleeping; Revell and Hayes 2009). Foraging can be time-consuming and involve activity in exposed or unfamiliar habitats, and it can reduce the organism's vigilance; therefore, foraging may increase the vulnerability of an organism to predation. If an organism can detect a predator indirectly while it forages, it may avoid an encounter with the predator.

Squamate taxa, particularly lizards of the family Iguanidae, often have been used to study predator-prey interactions because they have a variety of predators and can be observed easily, especially in laboratory settings (Burger *et al.* 1992, Bealor and Krekorian 2002, Cooper 2003, Revell and Hayes 2009). Few studies have involved experimental manipulation within a natural environment, because observing reclusive and easily disturbed animals can be difficult in an uncontrolled setting. This can be especially difficult for behavioral studies that typically require extensive control of variables and a method for observing behaviors without disturbing the subjects. Moreover, such studies rarely address effects on prey animals in the physical presence of the predator; instead, they usually rely solely on indirect proxy stimuli to examine anti-predator responses (e.g., Petranks *et al.* 1987, Wisenden 2000).

Herein we describe our observations of the foraging behavior of *Ctenosaura similis* in the presence of a predator (the boid snake *Boa constrictor*), and in the presence of predator cues but without the presence of a predator. Other iguanid species have been shown to use chemical cues for predator detection (Bealor and Krekorian 2002). *Boa constrictor* are known to prey on *C. similis* (Green 1983) and also have been shown to seek out iguana burrows actively and then to sit and wait for prey (Montgomery and Rand 1978). Although juvenile *C. similis* have a wide array of predators, including a variety of reptilian, mammalian, and avian taxa, the adults have relatively few natural predators (Fitch and Hackforth-Jones 1983). However, *Boa constrictor* is a naturally occurring predator that preys on adult *C. similis* and thus poses a threat to individuals of all ages.

This study offers insight into the behavior of squamate prey species in a natural setting, rather than in a laboratory. We predicted that a reduction in foraging effort owing to the presence of a predator and a predator cue would have a negative impact on the foraging success of the iguanas, and that the presence of a the predator would have a greater effect on their foraging than the presence of only a predator cue.

Materials and Methods

This study was conducted at Palo Verde Biological Station (PVBS; 10°21' N, 85°20' W) and MINAE Ranger Station (MRS; 10°21' N, 85°21' W), both located within Palo Verde National Park (PVNP) in Guanacaste Province of Costa Rica. The two sites are small (~800 m² and ~1000 m², respectively), isolated fragments of tropical dry forest featuring some anthropogenic alterations such as buildings and areas of mowed grass.

Both facilities feature large congregations of resident *Ctenosaura similis*. Under natural conditions, *C. similis* is highly territorial and quick to flee when approached by humans. However, at both MRS and PVBS, iguanas are relatively

habituated to human presence and take advantage of many artificial shelters such as wood piles, drainage systems, and buildings. Consequently, iguanas in these locations live in larger, denser groups than in less-disturbed areas (V. Farallo and M. Sasa, pers. obs.). Despite this unusual social context, the iguanas are exposed to the same natural predators as less-habituated conspecifics occurring in surrounding natural areas, including *B. constrictor* (routinely encountered by the authors near both stations). Given habituation of the iguanas to humans, it was easy to observe them with minimal disturbance. Owing to the latter, together with the high population density and normal exposure to natural predators, the resident populations of *C. similis* at MRS and PVBS offered an unparalleled opportunity to study anti-predator behaviors of this species under field conditions. It should be noted that “field conditions” can be extremely variable, and for our study, the term implies that the individuals were living in an unrestricted environment and were exposed to a diversity of biotic and abiotic conditions to which other iguanas also would be exposed. However, it is likely that the iguanas at our sites have uncommonly high access to food and shelter, which could affect their behavior. We anticipated that even given these optimal foraging conditions, our study would still offer insights on the potential alteration of foraging behavior in the presence of a predator or predator cues.

To examine foraging behavior in as natural a setting as possible, we used a circular trial area 8 m in diameter with a central feeding station at which iguanas were exposed to one of three treatments: (1) no predator or cue (Control); (2) *B. constrictor* feces (Boa Cue) representing an indirect predator cue; or (3) a live *B. constrictor* (Visible Boa) acting as a direct predator cue. Although feces of *B. constrictor* have not been shown to act as a predator cue to *Ctenosaura similis*, we used them as an indirect predator cue because other squamate taxa alter their behavior in the presence of predator feces. In particular, a diurnal gecko from New Zealand, *Naultinus*

manukanus, reduces movement in the presence of fecal samples of adult tuataras, *Sphenodon punctatus*, which are a native reptilian predator on *N. manukanus* (Hoare *et al.* 2007). Moreover, during pre-experiment observations, we noted that iguanas seemed to alter their behavior in the presence of *B. constrictor* feces (V. Farallo and M. Sasa, pers. obs.).

A feeding station (39 × 28-cm white plastic tray) with 50 ± 3 g of mango was placed in an area where *Ctenosaura similis* frequently were observed foraging. Mango fruit (*Manguifera indica*) was weighed with a digital scale immediately before and after each feeding trial. We used the scale to approximate portions of mango that were about 50 g, so that we did not spend an excessive amount of time handling the fruit and include tiny pieces to adjust the accuracy of the portion; inclusion of these might have affected the time spent eating. Mango is an exotic species in the park, and was probably introduced in the late 1940s when the area was a cattle ranch. Mango was used because it was readily available and frequently is consumed by iguanas in the park (V. Farallo and M. Sasa, pers. obs.). *Ctenosaura similis* naturally eats a wide variety of food. Typically, the diet consists of green vegetation during the wet season, and flowers and fruits in the dry season (Fitch and Hackforth-Jones 1983, Savage 2002). We conducted our study during the wet season; thus, the consumption of mangos may have been slightly unusual for a wild iguana. However because these lizards are opportunistic and will eat everything from insects to small mammals (Fitch and Hackforth-Jones 1983), the type of food offered should not have a major effect on their behavior.

With the feeding station in place, a circular arena 8 m in diameter was delineated with flagging tape at eight points around the perimeter. Cue treatments were placed 0.75 m from the feeding station, in a 50 × 30 × 35-cm (l × w × h) clear-plastic enclosure with screen windows on both long sides, and with one screen side facing the station. The enclosure contained one of the three treatments during each trial (Control, Boa

Cue, or Visible Boa). Two identical enclosures were used during the course of the study. One enclosure was used only for the cue-free Control treatment, and was left empty, never coming into contact with a *B. constrictor* or its feces to avoid potential contamination. The second enclosure was used for both the Boa Cue and Visible Boa treatments. The same snake (a captive-raised *Boa constrictor* loaned by the Instituto Clodomiro Picado located in San José, Costa Rica) was used for all predator trials. We used feces of the same snake, as well as feces from other lab-raised boa constrictors from the Instituto Clodomiro Picado; all snakes were fed a diet of white mice (*Mus musculus*) and had not consumed iguanas or other reptiles.

The trial area was moved daily and new locations were arranged in clusters. Several trials were conducted in a small area of about 50 m² (a cluster), thereby allowed us to use many iguanas that routinely congregated in one area. The clusters were spaced about 1300 m apart to lessen the likelihood that iguanas were moving between them. Thus, we are reasonably sure that new iguanas were used for each trial and that we reduced the chance of pseudoreplication during the study. At the completion of each trial in areas located near one another, the iguanas were photographed. These photographs were used to ensure that the same individual was not used more than once. In five of the trials, the iguanas left the area before photos could be taken. In these cases, we recorded physical characters of the iguanas in our field notes, and relied on them to avoid using the same individuals in subsequent trials. The characters used for identification included the iguana's size, sex, defining marks, and noticeable injuries. Fifteen trials were conducted for each of the three treatments, for a total of 45 trials.

Typically, trial areas were set up either in the morning (08:00–10:00 h) or early afternoon (12:00–14:00 h), just prior to the peak foraging times used by *Ctenosaura similis* during the heat of the day (Fitch and Hackforth-Jones 1983). The observer retreated to a post at least 5 m from the trial area, depending on the level of cover

available. A trial commenced only when an iguana (1) entered the arena and (2) faced the direction of the feeding station. Trial data were discarded if outside stimuli (e.g., interference from conspecifics, humans, or other animals) noticeably affected the behavior of an iguana during the course of the trial; however, this was an uncommon occurrence.

Three events were timed during each trial: (1) latency to forage (i.e., time elapsed from entering arena until feeding began); (2) latency to withdraw (i.e., time elapsed from entering arena until leaving it without having consumed all food); and (3) time foraging (i.e., time elapsed while consuming food). We recorded the number of times each iguana extruded its tongue during each trial, because there is a positive relationship between the number of tongue extrusions and detection of predators (Cooper 1990), food (Cooper and Perez-Mellado 2001), and pheromones (Bull *et al.* 2000). Moreover, *Ctenosaura similis* uses chemical cues to recognize conspecifics (Hanley *et al.* 1999); thus, tongue extrusions could be associated with detection of food, conspecifics, or predators. All of the iguanas in our study came from the same communal groups and were offered the same amount of food. Therefore, we think that differences in the number of tongue extrusions probably are linked to predator recognition rather than detection of food or conspecifics, because the presence/absence of a predator and predator cue were the only major variables that consistently differed among the treatments. We recorded the amount of food consumed to determine total foraging effort. A trial terminated in the event of any one of the following circumstances: (1) an iguana left the trial area; (2) all the food was consumed; or (3) 15 min had elapsed from the start of the trial. Additionally, because trials were different lengths of time (owing to the various endpoint criteria), the number of tongue extrusions was converted into rate of tongue extrusion (= total number of extrusions \div total trial time).

An analysis of time values was not possible because not all iguanas performed each variable

recorded and trials were terminated for one of three reasons. However, each trial was designated with a binary response of either completing or failing to complete each timed event. Specifically, iguanas had to: (1) withdraw from the trial area to complete the latency to withdraw variable; (2) reach the feeding station to complete the latency to forage variable; and (3) consume all food at the feeding station to complete the time foraging variable. Data from all iguanas were used for each statistical analysis. Nominal logistic regression analyses were performed with these data to determine if differences existed among the treatments; individual treatments then were compared visually to identify which were different. Each iguana was given a score of "1" for performing a time variable, or a "0" for failing to complete a time variable. The Wilks' Lambda test of a Multiple Analysis of Variance (MANOVA) was used to determine if there were significant differences within the behaviors measured between the iguanas exposed to the three treatments. For these analyses, treatment (Control, Boa Cue, or Visible Boa) was designated as the independent variable whereas tongue extrusions/sec and percentage of food consumed were designated as dependent variables. We examined a Mahalanobis distance plot (Mahalanobis 1936) and conducted an O'Brien's test for homogeneity of variance (O'Brien 1981), which indicated our variables met the assumptions of multivariate normality and homogeneity of variance, respectively. Once significance was determined from the MANOVA, an individual Analysis of Variance (ANOVA) was conducted for each dependent variable to determine which ones were significant. We conducted two separate tests; therefore, we reduced our alpha ($\alpha = 0.05$ to $\alpha = 0.025$) using a Bonferroni correction. Tukey's HSD tests, which correct for multiple comparisons, then were conducted on all significant dependent variables to determine which treatments were significantly different for that variable. All analyses were conducted using JMP (Ver. 7.0.1. SAS Institute Inc., Cary, NC, 1989-2007).

Results

Among treatments, a significantly different number of iguanas withdrew from the trials area (Figure 1; $\chi^2 = 20.332$, $df = 2$, $p < 0.0001$), reached the feeding station (Figure 1; $\chi^2 = 20.332$, $df = 2$, $p < 0.0001$), and consumed all food (Figure 1; $\chi^2 = 18.073$, $df = 2$, $p = 0.0001$). Two iguanas consumed food during the Visible Boa treatment (Figure 1). In contrast, 13 iguanas consumed food during the Control (Figure 1). The two iguanas that consumed food during the Visible Boa treatment finished consuming all of the food. However, of seven iguanas reaching

the food during the Boa Cue trial, only four finished all of the food (Figure 1). Only two iguanas exposed to the Control withdrew from the trial area before consuming all food or 15 min had elapsed, in contrast to the 11 and 13 iguanas withdrawing during the Boa Cue and Visible Boa trials, respectively (Figure 1).

There are significant differences across the dependent variables in relation to the three predator treatments (MANOVA, Wilks' Lambda = 0.409, $F_{(4,82)} = 11.540$, $p < 0.0001$). Both tongue extrusions/sec and percentage of food consumed differ significantly among treatments. Iguanas exposed to the Control consumed significantly

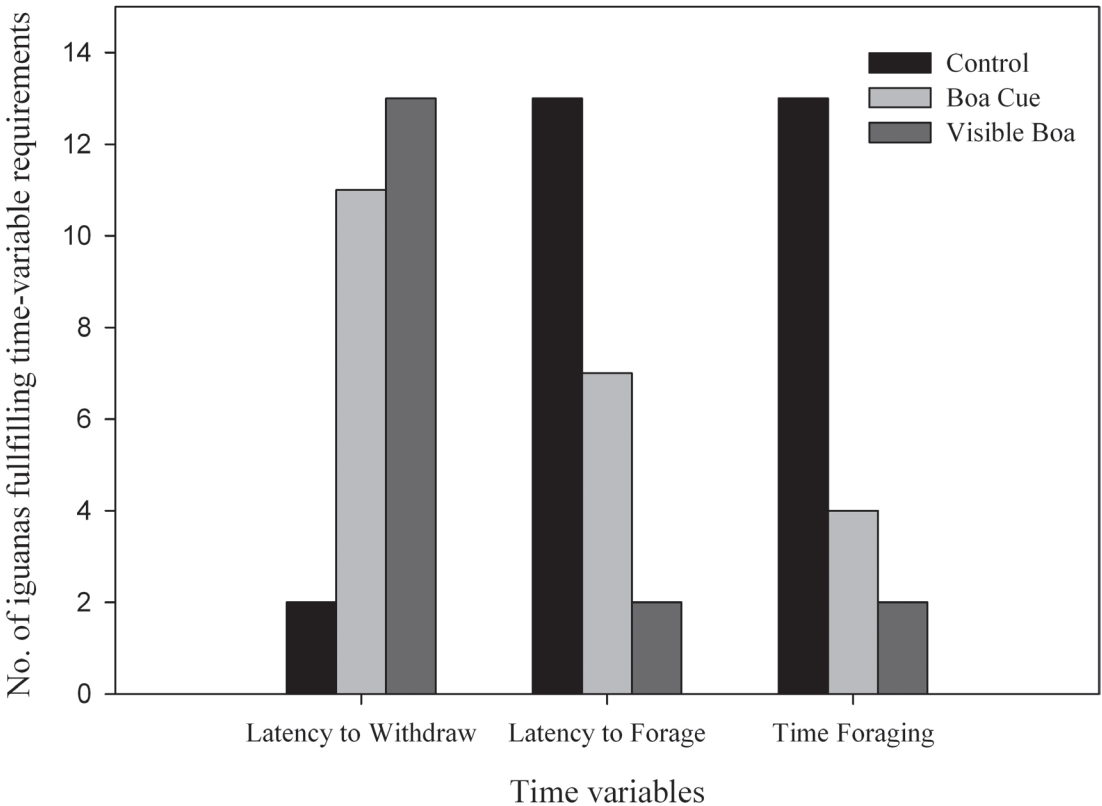


Figure 1. The total number of iguanas that fulfilled the requirements of each time variable for each treatment. See text for details. Treatments included an empty box (Control), or contained a live *Boa constrictor* (Visible Boa) or feces (Boa Cue). The maximum number of iguanas that could fulfill the requirements for a time variable for each treatment was 15.

more food than the two other treatments (Figure 2; $SS = 4.20$, $F_{(2,42)} = 13.8835$, $p < 0.0001$). Iguanas exposed to the Visible Boa treatment extruded their tongue significantly more often than did iguanas exposed to the Control treatment (Figure 3; $SS = 0.01$, $F_{(2,42)} = 9.9511$, $p = 0.0003$).

Discussion

Our results indicate that both the actual presence of a predator and the presence of an indirect predator cue have a negative impact on the foraging behavior of *Ctenosaura similis* at feeding stations. Previous studies have indicated

that movement (Burger and Gochfeld 1990), size (Brown 1984), and even eye-size of, and eye contact with, predators (Burger *et al.* 1991, Burger *et al.* 1992) can influence the response of potential prey, including *C. similis*. Our results give additional support that olfactory cues and/or other indirect indicators of predator presence induce similar effects.

Iguanas consumed significantly less food during the Visible Boa and Boa Cue treatments than they did during the Control. Additionally, the presence of *Boa constrictor* seemed to have a stronger effect on the iguanas than did the predator cue alone. Although there was not a

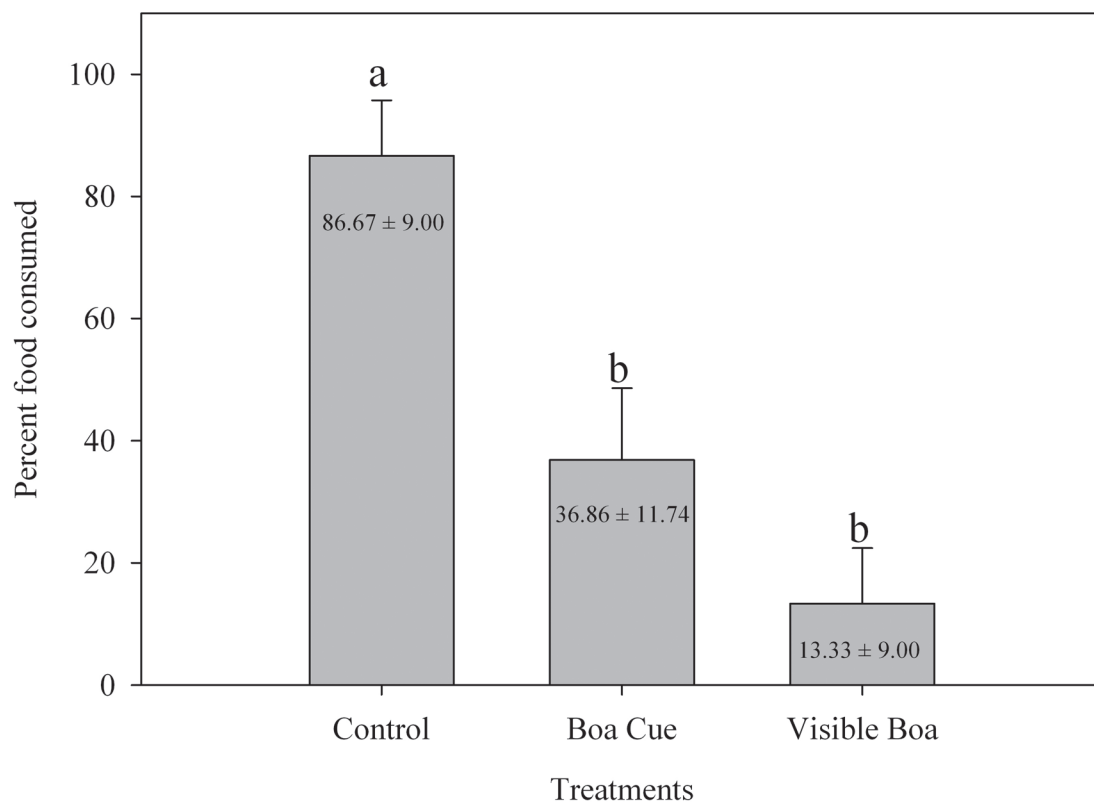


Figure 2. Mean percentage of food consumed by *Ctenosaura similis* during all 15 trials of each treatment. Values in each bar indicate the mean percent food consumed \pm SE. Dissimilar letters above bars indicate a significant difference between those treatments; identical letters indicate no significant difference.

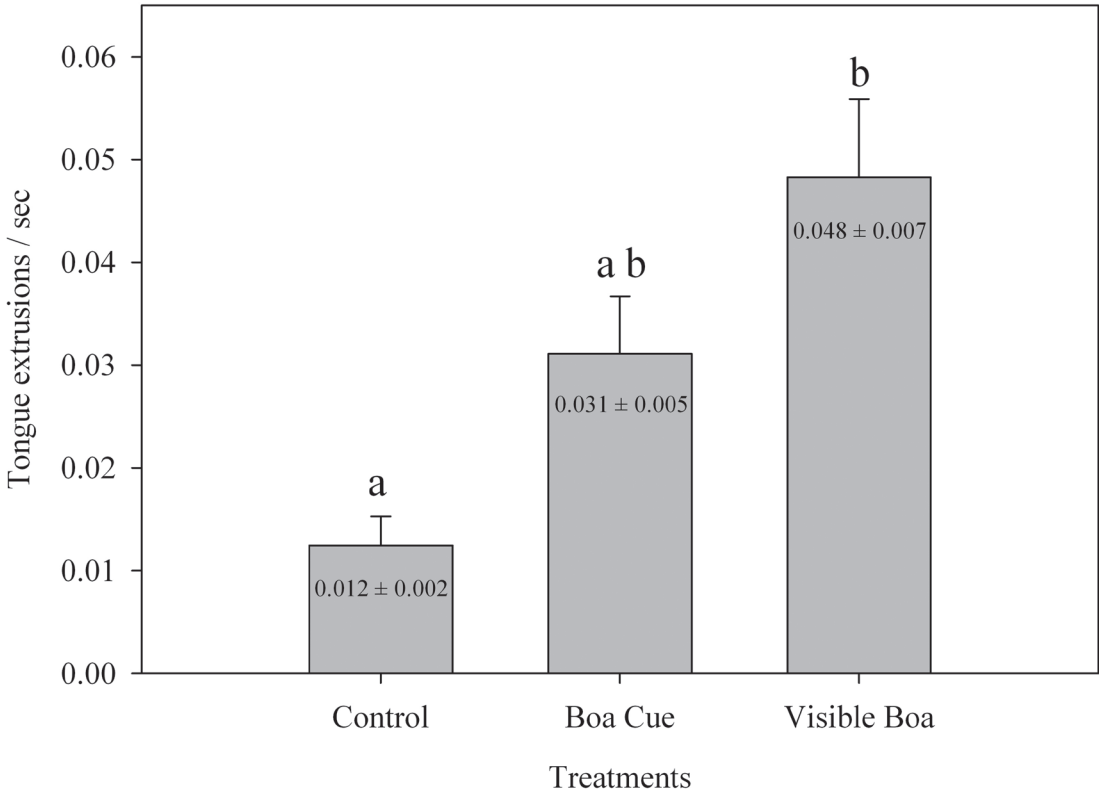


Figure 3. Mean tongue extrusions/sec by *Ctenosaura similis* during all 15 trials of each treatment. Refer to Figure 1 for description of treatments. Values in each bar are the mean tongue extrusions/sec \pm SE. Dissimilar letters above bars indicate a significant difference between those treatments; identical letters indicate no significant difference.

significant difference, iguanas exposed to the Visible Boa treatment consumed less food than the iguanas exposed to the Boa Cue. Only two large male iguanas consumed food during the Visible Boa treatment. During one Visible Boa trial, a large male iguana reached the feeding station but then backed away and circled around the snake enclosure when he noticed the presence of the snake. After making one complete circle, he proceeded to consume all of the food at the station. Once the iguana commenced feeding, it took him 495 sec to finish the food, which was 211 sec more than the longest time taken to finish

consuming the food by an iguana exposed to the Control. Because this iguana was clearly affected by the predator and had a very different response than other iguanas, we did not analyze times. In addition, seven iguanas reached the food during the Boa Cue treatment, but only four iguanas actually consumed all of the food. The two iguanas that consumed all of the food during the Visible Boa treatment were large males; perhaps the snake did not threaten these iguanas enough to prevent them from feeding. Our interpretation of these results is that iguanas from the Visible Boa treatment were exposed to more stimuli,

primarily visual; these stimuli caused iguanas to limit their foraging to avoid the snake. Iguanas exposed to the Boa Cue, however, were subject to fewer stimuli; therefore, not all iguanas attempted to avoid the presumed presence of a *B. constrictor*. Thus, iguanas may have detected the Boa Cue only once they reached the food; this would have accounted for the iguanas having started to consume food, and then fleeing before they finished.

The ability to detect predators without direct visual contact provides animals with a distinct advantage in avoiding ambush predators; this ability may be particularly advantageous to species such as *Ctenosaura similis*, which reside in burrows (Fitch and Hackforth-Jones 1983). Iguanas regularly return to the same burrows, which may be occupied by waiting predators lured by the scent of the resident prey item (Montgomery and Rand 1978).


Our data indicate that indirect predator cues may be of less significance to the behavior of some *Ctenosaura similis* than the presence of a live predator. This is suggested by the rate of tongue extrusion, which differed significantly between the Control and Visible Boa treatment, but not between Control and Boa Cue or between Visible Boa and Boa Cue treatments. These results indicate that sensory cues other than olfactory may stimulate the tongue-extrusion response, or that olfactory cues other than the one used in our study (predator feces) elicit that response. Therefore, olfactory cues may be useful to study the response to the specific cue tested, but they may not always be an appropriate substitute to the presence of a live predator, or the response may depend on the freshness of the cue. The chemicals being sensed from a predator cue undoubtedly breakdown making them less noticeable as time passes.

A multitude of other factors can affect the behavioral response of prey to a potential predator, such as the distance of the prey to a refuge, conspecific prey density, and the speed and directness of approach of a predator (Stankowich and Blumstein 2005). In addition, there is evidence

that individuals will alter their response to predators to maintain a healthy body condition. For example, Amo *et al.* (2007) demonstrated that the Spanish lacertid, *Iberolacerta cyreni*, with a poor body condition spent less time hiding after a predation attempt than healthier individuals, presumably to increase their time foraging. If there were pronounced differences in body condition among the iguanas in our study, then our results could be biased. These are all potential factors that were not considered in our study. Generally, all of the iguanas tested came from similar-sized congregations and similar locations, and the predator placement remained constant for all trials. We conclude that our results probably are not heavily affected by these confounding factors, but do not discount their potential influence.

This study provides an experimental examination of squamate predator-prey interactions within a natural setting. The information about the foraging behavior of *Ctenosaura similis* contributes supporting field observations to the results of laboratory studies involving iguanid species and predator-prey interactions. Our results indicate that individuals of *C. similis* are less likely to forage in the presence of both direct and indirect predator cues. Predator detection has a negative effect on foraging, but it allows the lizards to avoid confrontations with potential predators. Logically, this could extend to predator avoidance in potentially more dangerous situations, such as returning to their burrows when they cannot see an ambush predator.

Acknowledgments

We thank two anonymous reviewers who provided extensive comments on the manuscript, and the Organization for Tropical Studies (OTS) and staff at the Palo Verde Field Station and MINAE Ranger Station. Funding for this study was provided by the NSF-IRES program, Fundacion CRUSA-CSIC, and the Vicerrectoria de Investigacion (UCR 741-A9-525). All work was conducted under research permit 018-2009 ACAT and approval from OTS. 

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