



# The Costs of Conspecifics: Are Social Distractions or Environmental Distractions More Salient?

Jennifer Yee, Joshua Lee, Amanda Desowitz & Daniel T. Blumstein

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

## Correspondence

Daniel T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA.  
E-mail: marmots@ucla.edu

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## Abstract

Animals have limited attention that predisposes them to distraction, but the impact of different types of distraction is relatively unknown. We first conducted a discrimination experiment to ensure brown anoles (*Anolis sagrei*) responded appropriately to model predators (a rubber snake) and model conspecifics. We found anoles responded to the snake by suppressing looking and increasing locomotion, a marked difference than their response when presented with a conspecific. Next, we designed a prime and probe experiment to test the salience of social and environmental distractions on brown anoles. The social distraction consisted of a conspecific exemplar that was presented to the focal individual. Environmental distractions were vegetation that was moved at different speeds (ambient or vigorous) near the focal individual. Following 30 seconds of distraction with one of the three treatments, we presented the model snake, which was initially moved to within 1 m of a subject, and then moved closer until the subject looked in response to the approaching threat, and then fled. There was no effect of distractor on alert distance, but anoles distracted with the conspecific tolerated a closer approach with the model predator before fleeing than they did to either of the vegetative movements. These results cannot be explained by three other models of risk assessment and suggest that social cues distracted brown anoles more than environmental cues. These results may be generalizable to other social species that must simultaneously monitor conspecifics and assess predation risk.

## Introduction

How individuals allocate attention have important implications for survivorship, especially when compromised attention influences their ability to detect predators (Chan & Blumstein 2011). Animals must divide their attention between a variety of activities (e.g., social interactions, grooming, foraging, and predator vigilance; Harcourt 1991, Cords 1995, Mooring & Hart 1995, Blumstein 1998). The inability to simultaneously allocate attention to all activities may increase predation risk for individuals engaged in certain activities that require focused attention. For instance, a foraging animal may not notice an approaching predator if it is more focused on searching for highly cryptic prey rather than conspicuous prey (Dukas 2002, 2004). An organism's ability to receive and process visual information from its

environment is restricted by its limited attention (Dukas 2004; Chan & Blumstein 2011).

To optimally perform a task, individuals must focus on one stimulus rather than attempting to process multiple stimuli (Kastner & Ungerleider 2000). However, an animal that is fully attentive to one task misses important cues from the surrounding environment because the brain is not able to simultaneously react to stimuli in different visual fields (Vandenbergh et al. 1997; Dukas 2004). For instance, blue jays (*Cyanocitta cristata*) were more attentive to prey in their peripheral visual field when the central visual field was less cryptic, demonstrating that increased focus on one portion of the visual field detracted attention from other regions (Dukas 2004). Performance of a certain task may be compromised when the rate of information input exceeds the threshold of the brain's processing capacity. This decline in

performance is especially pronounced if there is relevant information that cannot be processed due to extraneous stimuli and distractions (Clark & Dukas 2003).

Various stimuli have the potential to distract both humans and animals. Distractions can be due to environmental or social stimuli and are either natural or anthropogenic. In humans, distraction can significantly decrease task-related performance (Hagen 1967). Distractions are most effective during tasks of low perceptual load (i.e., those that require minimal cognitive engagement) but are less distracting during tasks of high perceptual load (i.e., require high cognitive engagement) (Lavie 2010). Thus, activities that differ in perceptual load may inherently differ in distraction capacity (Berti & Schröger 2003; Lavie 2010).

Furthermore, social distractions can create an attentional conflict, which lowers performance on certain tasks (Groff et al. 1983). Conspecifics can provide attractive targets for attention by providing social cues, which facilitate social reinforcement, punishment, and comparison (Baron et al. 1978; Baron 1986). Similarly, social interactions among conspecifics can distract individuals from a task. Social grooming compromises the ability of impalas (*Aepyceros melampus*) to watch for predators (Mooring & Hart 1995). Impalas must divide their attention between grooming a conspecific, individually scanning for predators, and watching their group mates for reactions to predators (among other things). Impala actively grooming a conspecific noticed a simulated predator 4 seconds later than the mean non-grooming individual and 8 seconds later than the nearest non-grooming pair. Similarly, golden marmots (*Marmota caudata aurea*) were slower to respond to playbacks of alarm calls while engaged in play behavior with conspecifics than while foraging alone (Blumstein 1998).

These studies suggest that the required focused attention associated with social interactions between conspecifics may detract from an individual's ability to assess predation risk. Furthermore, Chan et al. (2010) found that anthropogenic distractions in the form of motor boat acoustic cues distracted hermit crabs from an approaching predator. This hermit crab experiment spurred the development of the distracted prey hypothesis, which states that extraneous stimuli of any modality have the ability to divert attention from biologically significant tasks (Chan et al. 2010). However, this leaves a knowledge gap with regard to whether different types of distraction are similarly distracting. To further investigate the distracted prey hypothesis, we asked whether social or environmental cues were more distracting to brown anoles.

We presented brown anoles with a predator model while distracting focal individuals with either a social or environmental distraction. We used brown anoles for our experiment for a variety of reasons. First, *Anolis* lizards have been studied extensively for their dependence on vision and unique abilities to allocate visual attention. Anole vision is highly specialized for detection of peripheral visual stimuli and anoles detect predators primarily through their movements (Fleishman 1986, 1992). Fleishman (1986) found that the several *Anolis* species were able to tune out background motion that could potentially distract from more important stimuli. Any motion that was inconsistent with natural vegetation motion (i.e., changes in amplitude and frequency) elicited a greater response than natural sinusoidal vegetation movement. Second, *Anolis* lizards are highly territorial and often use visual displays as a means of attracting mates and establishing territorial dominance. Brown anoles respond differentially to conspecific neighbors than to non-neighbors (Paterson & McMann 2004), suggesting that the lizards are highly aware of their surrounding social environment. It has also been suggested that anole visual displays have evolved to easily be detected against background motion (Fleishman 1992). For instance, anoles may speed up visual displays to ensure signal reception in the presence of noisy vegetative movement (Ord et al. 2007), which demonstrates specificity of anole visual displays. For these reasons, brown anoles were an ideal species to investigate the relative importance of social versus environmental distractions during predator-prey interactions.

Due to previous studies demonstrating anoles' highly territorial nature (Paterson & McMann 2004) and ability to tune out background vegetative movement (Fleishman 1986), we predicted that a conspecific exemplar would be more distracting than either ambient or vigorous vegetation movement and therefore, by potentially capturing a subject's attention, increase predation risk. There are, however, at least two ways that distraction could influence attention and enhance risk. First, it could influence the ability to detect an approaching predator. Alert distance is typically quantified by noting the distance at which the prey looks in response to an approaching threat. Hence, a distracted prey might permit a potential predator to get closer before they prey noticed the approaching predator and looked in response. Second, distraction could influence the decision to flee from the approaching predator. Hence, a distracted prey might, because it was distracted, not be able to simultaneously monitor an approaching threat and hence tolerate closer approach. We quantified both alert

distance and flight initiation distance (FID) to study these two processes.

## Methods

### Study Site

Focal individuals were studied at Calabash Caye Field Station located on Turneffe Atoll, Belize (17°16'N, 87°48'W). Subjects were studied along 1.98 km of forest trails and beachfront from Oct. 8 to 28, 2011. From personal observation, anole density was high on the island with approx. 2 anoles/m<sup>3</sup> and trials were separated by a distance of  $\geq 5$  m to prevent resampling individuals. We focused on 2.0–7.5 cm (snout-vent length) brown anoles (average deviation for 50 length estimates =  $-0.143 \pm 0.115$  cm). Trials were conducted during the day (06:00–17:30 h). Only lizards perching within 2.5 m of the ground were tested.

### Discrimination Experiment

A discrimination experiment was initially conducted to determine whether our conspecific exemplar and snake predator elicited the appropriate reactions in the anoles. We defined two treatment categories: conspecific presentation and predator presentation. We used 5 cm (snout-vent length) toy anoles (Amscan, Elmsford, NY, USA) and painted them to resemble two male anoles, characterized by a well-defined crest stripe down the back, more pronounced dewlap, and random patterned coloration, and two female anoles, characterized by a narrow yellow/white stripe bordered by wavy triangular patterns and less pronounced dewlap (Masterson 2007). While all of our toy anoles were the same snout-vent length, this was close to the average ( $\pm$ SE) snout-vent length of the anoles we observed during our distraction experiment ( $4.58 \pm 0.123$  cm). Because exemplar size was constant, it could not explain variation in response. Sexes and exemplars were randomly assigned to treatments, and our results permit us to draw inferences about brown anoles, but not about either male or female brown anoles. For presentation, anole exemplars were mounted at the end of a collapsible fishing rod. We used a single black toy snake (1.52 m long) with its mouth open as a predator (Blockbuster Costumes, Largo, FL, USA) attached to a bamboo pole in a slightly serpentine position.

Three observers walked around the island together. Upon location of a subject, the observers oriented themselves, so the observer with the treatments approached to approx. 1.5 m while the other two

observers remained approx. 2.5 m away from the subject. The observers then froze for a 1-min habituation period with each treatment hidden under a dead palm frond. At the end of the habituation period, the closest observer unveiled one of the treatments from under the palm frond and slowly moved toward the subject. The conspecific exemplar was moved up to an average ( $\pm$ SD) distance of 0.42 m ( $\pm 0.024$  m,  $n = 39$ ) from the focal, and the predator was moved up to an average distance of 3.61 m ( $\pm 0.130$  m,  $n = 39$ ) away from the subject. A focal observation sample was dictated onto a voice recorder for each period, including the last 30 seconds of the habituation period, which served as a baseline. Based on a previous study (Huang et al. 2011), our ethogram consisted of head bob (head movement up and down), dewlap (extension and contraction of dewlap), eat (chew object in mouth), hop (movement by jumping), look (stationary with a fixed gaze, each change quantified), push up (flex two or four legs to raise body), walk (movement with all four legs with  $<30$  cm displacement), run (movement with all four legs  $>30$  cm displacement), other (any other behavior), and out of sight (subject is out of sight). In addition to this, we recorded perch height, the distance from the subject to the nearest observer, average wind speed, temperature, and number of conspecifics within a 2 m radius.

The recorded focal samples were later scored and analyzed in JWatcher (version 1.0; Blumstein & Daniel 2007). Behaviors were grouped into three categories: looking, displaying (head bob, push up, and dewlap), and moving (walk, hop and run). Eat was not recorded often enough to be included in our analyses. We calculated the responsiveness of the anoles to both stimuli by looking at the difference in the proportion of time of behaviors from baseline. After dividing the one-minute treatment period into four 15 s time bins, we noticed deviations in behaviors mostly occurred during the second time bin (16–30 s). Therefore, our response variables consisted of a change from baseline in time allocated to the three behavioral categories (looking, displaying, and moving) in the second time bin (16–30 s). We then used unpaired *t*-tests to explain variation in time allocation as a function of treatment. All statistics were calculated in STATVIEW 5.0 (SAS Institute Inc., Chicago, IL, USA) with  $\alpha = 0.05$ .

There was no significant difference between the  $\log_{10}$  of perch heights (ANOVA,  $F_{1,78} = 0.901$ ,  $p = 0.345$ ),  $\log_{10}$  of average wind speed (ANOVA,  $F_{1,78} = 1.200$ ,  $p = 0.277$ ),  $\log_{10}$  of temperature (ANOVA,  $F_{1,78} = 0.010$ ,  $p = 0.921$ ),  $\log_{10}$  of the size of the lizards (ANOVA,  $F_{1,78} = 0.025$ ,  $p = 0.875$ ), or the square root

of the number of conspecifics within a 2 m radius (ANOVA,  $F_{1,78} = 1.416$ ,  $p = 0.238$ ) across conspecific and predator treatments. There was a significant difference between the distance between the nearest observer and the lizard (ANOVA,  $F_{1,78} = 159.487$ ,  $p < 0.0001$ ). Thus, we added distance to observer as a covariate to our one-way ANOVAs. Neither distance to the observer ( $p > 0.440$ ) nor the interaction between distance to the observer and treatment ( $p > 0.278$ ) was significant in any model fitted. Therefore, we report results from unpaired  $t$ -tests on the effect of stimulus on time allocation.

### Distraction Experiment

A prime and probe experiment was conducted in a similar manner. Observers came upon a focal individual and oriented themselves accordingly. The person providing the distraction treatments was 2.59 m ( $\pm 0.064$  m,  $n = 101$ ) away from the focal on average, and the person with the snake model was an average of 2.77 m ( $\pm 0.092$  m,  $n = 101$ ) away. The conspecific exemplar and predator model were hidden from view of the subject before they were presented during the distraction and predatory period, respectively. Observers froze for a two-minute habituation period because the anoles took longer to habituate to the presence of the palm frond compared with the previous experiment. During the last 30 seconds of this period, a baseline focal observation was recorded. At the end of the baseline period, one of the distraction treatments was introduced for 30 s. The conspecific exemplar was presented approx. 0.5 m away from the focal and moved slightly in place to resemble a live specimen. Palm frond treatments consisted of a palm frond (*Thrinax radiata*) that was placed and remained stationary approx. 1.5 m away from the focal during the habituation period. During the distraction period, the frond was slowly moved up and down with large-amplitude motions (frequency =  $0.262 \pm 0.003$  Hz,  $n = 12$ ) for the ambient treatment or quickly with small-amplitude motions (frequency =  $6.875 \pm 0.223$  Hz,  $n = 12$ ) for the vigorous treatment. Palm fronds were obtained *in situ* every four days to avoid adding audio cues associated with dried vegetation; however, vigorous shaking did produce some leaf noise; strictly this was a multimodal stimulus.

Previous measurements of background vegetative motion quantified high and low background motion by displacement (mm) and speed (mm/s) (Fleishman 1986, 1992; Ord et al. 2007; Peters 2008; Peters et al. 2008). Our intention was to create two very different

patterns of habitat movement where the less intense movement was close to that which should not capture anole attention, and the more intense movement would represent either very strong wind or vegetative movement that would normally be associated with a large, and potentially threatening, animal.

By tracking a pixel from a video image over time, we measured the frequency of natural ambient vegetation movement at times of low (5.8 km/h) and high (27.0 km/h) wind. The average frequency of the low-velocity natural movement was  $0.22 \pm 0.010$  Hz ( $n = 12$ ), and the average frequency of the low-velocity simulated movement was  $0.26 \pm 0.003$  Hz ( $n = 12$ ); 95% confidence intervals for these values did not overlap. The average frequency of the high-velocity natural movement was  $2.99 \pm 0.360$  Hz ( $n = 12$ ), and the average frequency of the high-velocity simulated movement was  $6.88 \pm 0.223$  Hz ( $n = 12$ ); 95% confidence intervals for these values did not overlap.

After the distraction period, while the distractions were still being presented, the snake model was uncovered and moved toward the subject at a rate of 0.5 m/s until it was 1 m away from the subject (actual average distance was  $1.09 \text{ m} \pm 0.037 \text{ m}$ ,  $n = 101$ ). Behaviors were recorded for this 1-min predator period. At the end of the predator presentation, the snake was moved toward the focal at a rate of 0.5 m/s until the subject looked in response to the approaching threat (quantified by a detectable head movement) and ultimately fled. The predator model was presented within the same visual field approx.  $45^\circ$  away from the distraction. Perch height (vertical distance from the subject to the ground), alert distance (distance at which animal noticed an approaching threat), and FID (distance at which the animal moves away from the approaching threat) were recorded (Blumstein 2003).

We used unpaired  $t$ -tests to test for differences in time allocation as a function of treatment. The distraction period was split into two 15 s time bins, and the predator period was split into four 15 s time bins. To analyze alert distance, we fitted an ANOVA model where we modeled variation in alert distance as a function of treatment. To analyze FID, we fitted an ANCOVA model where we modeled FID as a function of alert distance and treatment. Both alert distance and FID were  $\log_{10}$ -transformed to normalize the distributions (which we evaluated by visually examining the distributions before and after transformation). Fisher's PLSD were performed to reveal significant differences among treatments on alert distance and FID.

There was no significant difference between the distances of the nearest observer and the lizard (ANOVA,  $F_{2,101} = 0.509$ ,  $p = 0.603$ ), in the square root of the subject's perch height (ANOVA,  $F_{2,101} = 0.718$ ,  $p = 0.491$ ), the square root of the average wind speed (ANOVA,  $F_{2,101} = 0.694$ ,  $p = 0.502$ ), the  $\log_{10}$  of temperature (ANOVA,  $F_{2,101} = 0.128$ ,  $p = 0.880$ ), lizard size (ANOVA,  $F_{2,101} = 0.472$ ,  $p = 0.625$ ), or the  $\log_{10}$  of the number of conspecifics within 2 m (ANOVA,  $F_{2,101} = 1.156$ ,  $p = 0.319$ ).

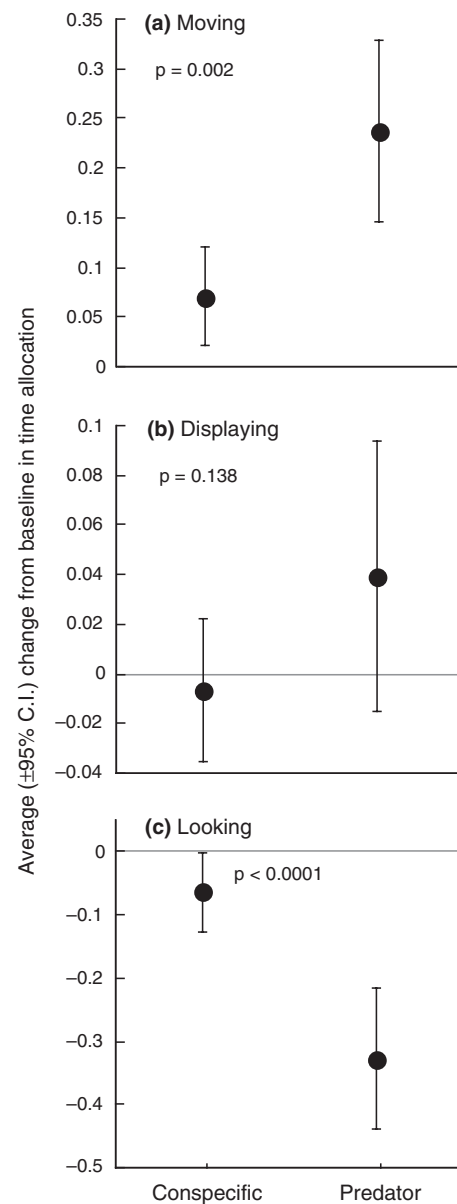
## Results

### Do Anoles Discriminate Between Predator and Conspecific Exemplars?

From observing 78 anoles (conspecific  $n = 39$ ; predator  $n = 39$ ), we found that anoles allocated significantly different amounts of time looking and moving when probed with a conspecific versus a predator exemplar (Fig. 1). Anoles spent a greater proportion of time looking in the second (16–30 s) time bin when shown a conspecific exemplar compared with a predator exemplar ( $t_{76} = 4.189$ ,  $p < 0.0001$ ). Anoles spent a greater proportion of time moving in the second time bin (16–30 s) when probed with a predator exemplar than when probed with a conspecific exemplar ( $t_{76} = -3.249$ ,  $p = 0.002$ ). Therefore, anoles mobilize more readily at the sight of a predator exemplar compared with a conspecific exemplar. Examination of 95% confidence intervals shows us that time allocated to displaying in the 16–30 s time bin was not influenced by either treatment (CI's include 0). These responses are appropriate because anoles should spend more time moving when exposed to a predator to avoid being eaten. Although we could not differentiate what exactly the anole spent more time looking at, an anole who spent more time looking at the conspecific could have viewed it as a potential competitor for its territory, forcing the subject to spend more time evaluating the conspecific rather than the predator.

### How Do Distractions Alter Predator-risk Assessment by Anoles?

From observing 101 anoles (conspecific  $n = 34$ ; ambient  $n = 34$ ; vigorous  $n = 33$ ), anole response was not significantly different from baseline for looking (ANOVA,  $F_{2,98} = 1.756$ ,  $p = 0.178$ ), moving (ANOVA,  $F_{2,98} = 0.743$ ,  $p = 0.479$ ), and displaying behaviors (ANOVA,  $F_{2,98} = 2.571$ ,  $p = 0.082$ ) in the 16–30 s time bin of the predator period

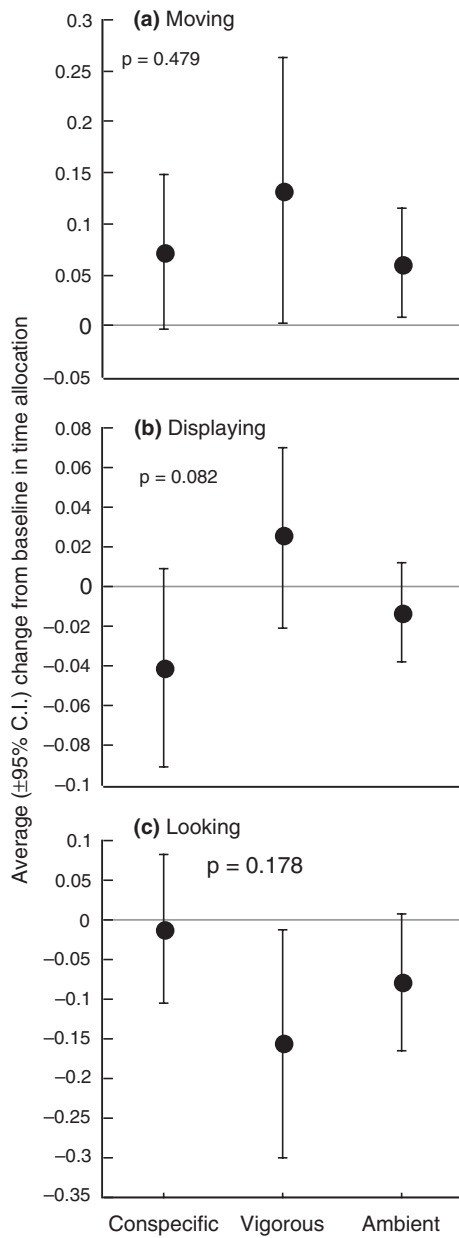


**Fig. 1:** Change in time allocated to (a) moving, (b) displaying, and (c) looking after the presentation of a conspecific or a predator model.

(Fig. 2). Visual examination of the data revealed no other obvious relationships worthy of formal analysis.

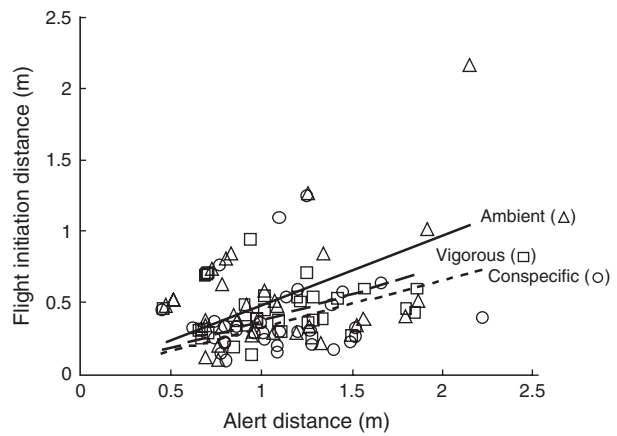
There was no significant difference in alert distance as a function of treatment (ANOVA,  $F_{2,98} = 0.249$ ,  $p = 0.780$ ), nor were any pairwise comparisons significantly different (all  $p$ -values  $> 0.514$ ).

After explaining non-significant variance in FID by alert distance (ANCOVA,  $F_{1,95} = 3.627$ ,  $p = 0.060$ ), and a non-significant interaction between alert distance and treatment (ANCOVA,  $F_{2,95} = 3.627$ ,  $p = 0.605$ ), we found that there was an effect of treatment on FID



**Fig. 2:** Change in time allocated to (a) moving, (b) displaying, and (c) looking after the presentation of a predator model while being distracted by either a model conspecific or two types of vegetative movement.

(ANCOVA,  $F_{3,95} = 110.317$ ,  $p < 0.0001$ ). Overall, anoles tolerated closer snake approaches before fleeing when a conspecific distraction preceded the presentation of a snake model than when compared to ambient frond movement (Fisher's PLSD  $p = 0.023$ ), but there was no difference in FID when conspecific distraction was compared with vigorous frond movement (Fisher's PLSD  $p = 0.068$ ). Additionally, there was no significant



**Fig. 3:** Relationship between alert distance and flight initiation distance as a function of distraction type.

difference between ambient and vigorous frond movement (Fisher's PLSD  $p = 0.065$ ; Fig. 3). Thus, a conspecific distraction likely enhanced the likelihood of predation because anoles permitted the simulated predator to approach closer before fleeing.

### Discussion

The simultaneous presence of conspecifics and predators is a common occurrence for most social animals, yet little is known about the influence of conspecific distraction on the ability to respond to predators or on the predator-risk assessment process. We found that while there was no effect of distraction type on the distance at which lizards first looked at an approaching snake model, lizards exposed to a model conspecific tolerated a closer approach of the snake model than those exposed to simulated ambient vegetation movement. The more attention a stimulus captures, the less likely animals will be able to react to a predator (Dukas 2002, 2004). Our results are consistent with previous studies, which found that anoles tune out background vegetative movement to focus on more salient stimuli (Fleishman 1986). Therefore, anoles may be naturally predisposed to ignore distractions caused by vegetation. This is potentially beneficial to anoles because anoles would be able to allocate their attention to perform needed tasks (e.g., foraging, predator detection, searching for mates) more efficiently without the need to focus on irrelevant stimuli. Our data set includes both males and females. We expect that male anoles might be even more distracted by a conspecific intruder than females, but future studies must clarify the effect of sex on distractibility.

These results are consistent with a hypothesis that social stimuli are more distracting than environmental stimuli specifically in how they influence the decision to flee, but not the decision to initially look at the approaching threat. Thus, while it seems, anoles are able to detect predators, and risk assessment is still distracted by the presence of a conspecific. As anoles are social and territorial, they must also pay close attention to conspecifics because they are potential competitors for suitable habitat or mates (Tokarz 1985; Paterson & McMann 2004). Thus, while subjects may have noticed the predator exemplar, they elected to not flee as soon because their risk assessment was compromised by their attention being focused on the conspecific. This explanation is not entirely consistent with previous findings that demonstrated that the probability of detecting a cryptic predator was reduced when individuals focused their attention on a small area (Clark & Dukas 2003), or those studies that found that individuals were less likely to notice a predator when given difficult foraging tasks compared with more basic foraging tasks (Lawrence 1985). We know that by allocating a substantial amount of attention to focus on conspecifics, subjects have less attention available to maintain vigilance. Both Gauvin & Giraldeau (2004) and Vasquez & Kacelnik (2000) found that the presence of neighboring conspecifics, rather than heterospecifics, was associated with a decrease in feeding rate. This is potentially attributed to the need to monitor members of the same species for competition or other social cues. Supporting results from the aforementioned studies and Dukas & Kamil's (2000) experiment, the presence of conspecifics may interfere with the ongoing ability to monitor a predator in the periphery and thus, for anoles, explains the shorter FID during conspecific distraction presentations (Fig. 3). This shows that an individual's fitness might be compromised when there are conspecifics around, because it will be more focused on interacting with them than monitoring potential predatory threats.

There are at least three other hypotheses that might explain our results, but we believe that each can be refuted. First, if anoles tolerated a closer approach because of the selfish herd theory (Hamilton 1971), we would have expected individuals in a group to move toward other conspecifics or toward the center of the group to reduce their risk of predation. There was no indication that anoles moved in a way to strategically reduce predation risk; indeed, we found that anoles delayed movement altogether and did not significantly increase their movement in the presence of a conspecific during the presentation of a predator.

Second, in many species, animals in larger groups alert and flee at greater distances due to increased collective vigilance (Stankowich & Blumstein 2005). In contrast, we found that the presence of a conspecific was associated with a *decreased* FID, which is directly contradictory with this hypothesis. Third, it is also possible that the presence of other conspecifics simply diluted risk (Bertram 1978; Dehn 1990). A basic prediction of this risk dilution hypothesis would be that a single conspecific decreased risk by 50%. If so, we might expect a proportional change in risk-sensitive behaviors as a function of a change in group size when no predator was present. We did not find this when we compared conspecific and ambient treatments in the change in time allocated to looking (Fisher's PLSD  $p = 0.203$ ), or displaying (Fisher's PLSD,  $p = 0.334$ ) in the 16–30 s time bins of the distraction experiment. For these reasons, we believe that we can reject three alternative hypotheses that might be associated with predation risk driving our observed response.

While we found that anoles tolerated a closer predator approach when primed with a conspecific exemplar, we failed to find significant behavioral differences from baseline across all treatments. These unexpected results may be attributed to an increase in overall vigilance during testing, which we attempted to avoid with the habituation period. It is also possible that the methods we used to analyze behavior masked the subtle behavioral differences across treatments. It may be argued that a ceiling effect from stimulus novelty blocked our ability to detect different behavioral responses. However, our results cannot be explained by novelty alone because these particular conspecific exemplars, predator exemplars, and palm fronds were all somewhat novel (even the common palm fronds suddenly appeared in a new location). Nor can results be explained by size: The palm frond was the largest stimulus, yet the anole model was more effective at capturing attention compared with slow palm frond movements.

These findings show that a purely visual conspecific distraction was more salient than a multimodal distraction (i.e., palm frond movement), but we should note that we found no significant differences between conspecific distraction and vigorous palm frond movement. The multimodality of distraction, specifically auditory and visual stimuli in the form of boat motor noise and flashing lights, has been shown to significantly decrease hiding initiation distance (HID) in hermit crabs when compared to just boat motor noise alone (Chan et al. 2010). We suggest that the attention allocated to a visual conspecific distraction

overrides the attention allocated to a multimodal vegetation distraction. Many studies have found that multimodal stimuli were more detectable than unimodal cues (Stein et al. 1989; Frassinetti et al. 2002; Roberts et al. 2006). In these studies, the bimodality of the vigorous vegetation movement might have alerted the subjects, increasing their awareness of the predator model at a farther distance. In contrast, the anoles were less vigilant toward the predator model while distracted with the unimodal conspecific exemplar.

When considering attention and distraction, it is important to consider the underlying mechanisms by which attention is controlled. How attention is allocated can depend on either top-down or bottom-up mechanisms (Buschman & Miller 2007). More specifically, top-down processes are controlled by an animal's previous experiences, expectations, and conscious attention, whereas bottom-up mechanisms are considered automatic, obligatory, and 'stimulus driven' (Miller & Bee 2012). A previous study of anole visual attention investigated stimulus properties (motion amplitude, velocity, and frequency) that capture anoles' attention (Fleishman 1986). Results of that study determined that visual attention was dependent on specific stimulus properties as well as habituation to certain motion patterns (i.e., vegetative movement), which supports bottom-up mechanisms at work. The design of our study primarily investigates bottom-up processes based on findings of previous research; however, we acknowledge the potential influence of top-down attentional control, especially in the case of socially related stimuli. In the presence of conspecifics, anoles may be more consciously allocating their attention to pick up discrete social cues, which could influence their ability to detect predators. It is possible that anoles use bottom-up processes to better detect the presence of conspecifics, and once noticed, conspecifics may capture more conscious attention. As top-down processes use information from bottom-up mechanisms (Miller & Bee 2012), it would follow that both mechanisms work in conjunction with each other. Further research into these mechanisms of attentional control may clarify these conjectures.

While conspecifics are more distracting to brown anoles than environmental stimuli, it is still unknown how these natural distractions compared with anthropogenic distractions. We speculate that it is possible that differing intensities of anthropogenic and social distractions may cause a shift in salience from one stimulus to the other. Further research on how anthropogenic visual cues relate to social and environmental visual cues in this distraction hierarchy may clarify this knowledge gap.

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## Literature Cited

- Baron, R. S. 1986: Distraction-conflict theory: progress and problems. *Adv. Exp. Soc. Psychol.* **19**, 1–36.
- Baron, R. S., Moore, D. & Sanders, G. S. 1978: Distraction as a source of drive in social facilitation research. *J. Pers. Soc. Psychol.* **36**, 816–824.
- Berti, S. & Schröger, E. 2003: Working memory controls involuntary attention switching: evidence from an auditory distraction paradigm. *Eur. J. Neurosci.* **17**, 1119–1122.
- Bertram, B. C. R. 1978: Living in groups: predators and prey. In *Behavioural Ecology: An Evolutionary Approach*. (Krebs, J. R., Davies, N. B., eds). Sinauer Associates, Sunderland, MA, pp. 64–96.
- Blumstein, D. T. 1998: Quantifying predation risk for refuging animals: a case study with golden marmots. *Ethology* **104**, 501–516.
- Blumstein, D. T. 2003: Flight initiation distance in birds is dependent on intruder starting distance. *J. Wildlife Manage.* **67**, 852–857.
- Blumstein, D. T. & Daniel, J. C. 2007: Quantifying behavior the JWatcher way. Sinauer Associates, Inc., Sunderland, MA.
- Buschman, T. J. & Miller, E. K. 2007: Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* **315**, 1860–1862.
- Chan, A. A. Y.-H. & Blumstein, D. T. 2011: Attention, noise, and implication for wildlife conservation and management. *Appl. Anim. Behav. Sci.* **131**, 1–7.
- Chan, A. A. Y.-H., Giraldo-Perez, P., Smith, S. & Blumstein, D. T. 2010: Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biol. Lett.* **6**, 458–461.
- Clark, C. W. & Dukas, R. 2003: The behavioral ecology of a cognitive constraint: limited attention. *Behav. Ecol.* **14**, 151–156.
- Cords, M. 1995: Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour* **132**, 559–569.
- Dehn, M. M. 1990: Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* **26**, 337–342.



- Dukas, R. 2002: Behavioural and ecological consequences of limited attention. *Phil. Trans. R. Soc. B* **357**, 1539—1547.
- Dukas, R. 2004: Causes and consequences of limited attention. *Brain Behav. Evol.* **63**, 197—210.
- Dukas, R. & Kamil, A. C. 2000: The cost of limited attention in blue jays. *Behav. Ecol.* **11**, 502—506.
- Fleishman, L. J. 1986: Motion detection in the presence and absence of background motion in an *Anolis* lizard. *J. Comp. Physiol. A.* **159**, 711—720.
- 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. *Am. Nat.* **139**, S36—S61.
- Frassinetti, F., Bolognini, N. & Làdavas, E. 2002: Enhancement of visual perception by crossmodal visuo-auditory interaction. *Exp. Brain Res.* **147**, 332—343.
- Gauvin, S. & Giraldeau, L.-A. 2004: Nutmeg mannikins (*Lonchura punctulata*) reduce their feeding rates in response to simulated competition. *Oecologia* **139**, 150—156.
- Groff, B. D., Baron, R. S. & Moore, D. L. 1983: Distraction, attentional conflict, and driveline behavior. *J. Exp. Soc. Psychol.* **19**, 359—380.
- Hagen, J. W. 1967: The effect of distraction on selective attention. *Child Dev.* **38**, 685—694.
- Hamilton, W. D. 1971: Geometry of a selfish herd. *J. Theor. Biol.* **31**, 295—311.
- Harcourt, R. 1991: Survivorship costs of play in the South American fur seal. *Anim. Behav.* **42**, 509—511.
- Huang, B., Lubarsky, K., Teng, T. & Blumstein, D. T. 2011: Take only pictures, leave only..fear? The effects of photography on the West Indian anole *Anolis cristatellus*. *Curr. Zool.* **57**, 77—82.
- Kastner, S. & Ungerleider, L. G. 2000: Mechanisms of visual attention in the human cortex. *Annu. Rev. Neurosci.* **23**, 315—341.
- Lavie, N. 2010: Attention, distraction, and cognitive control under load. *Curr. Dir. Psychol. Sci.* **19**, 143—148.
- Lawrence, E. S. 1985: Vigilance during 'easy' and 'difficult' foraging tasks. *Anim. Behav.* **33**, 1373—1375.
- Masterson, J. 2007: *Anolis sagrei*. Smithsonian Marine Station at Fort Pierce. [http://www.sms.si.edu/irlspec/anolis\\_sagrei.htm](http://www.sms.si.edu/irlspec/anolis_sagrei.htm) (accessed 9 February 2013).
- Miller, C. T. & Bee, M. A. 2012: Receiver psychology turns 20: is it time for a broader approach? *Anim. Behav.* **83**, 331—343.
- Mooring, M. S. & Hart, B. L. 1995: Costs of allogrooming in impala: distraction from vigilance. *Anim. Behav.* **49**, 1414—1416.
- Ord, T. J., Peters, R. A., Clucas, B. & Stamps, J. A. 2007: Lizards speed up visual displays in noisy motion habitats. *Proc. Roy. Soc. B.* **274**, 1057—1062.
- Paterson, A. V. & McMann, S. 2004: Differential headbob displays toward neighbours and nonneighbours in the territorial lizard *Anolis sagrei*. *J. Herpetol.* **38**, 288—291.
- Peters, R. 2008: Environmental motion delays the detection of movement-based signals. *Biol. Lett.* **4**, 2—5.
- Peters, R., Hemmi, J. & Zeil, J. 2008: Image motion environments: background noise for movement-based animal signals. *J. Comp. Physiol.* **194**, 441—456.
- Roberts, A. J., Taylor, P. W. & Uetz, G. W. 2006: Consequences of complex signaling: predator detection of multimodal cues. *Behav. Ecol.* **18**, 236—240.
- Stankowich, T. & Blumstein, D. T. 2005: Fear in animals: a meta-analysis and review of risk assessment. *Proc. Roy. Soc. B.* **272**, 2627—2634.
- Stein, B. E., Meredith, M. A., Huneycutt, W. S. & McDade, L. 1989: Behavioral indices of multisensory integration: orientation to visual cues is affected by auditory stimuli. *J. Cogn. Neurosci.* **1**, 12—24.
- Tokarz, R. 1985: Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim. Behav.* **33**, 746—753.
- Vandenberghe, R., Duncan, J., Dupont, P., Ward, R., Poline, J.-B., Bormans, G., Michiels, J., Mortelmans, L. & Orban, G. A. 1997: Attention to one or two features in left or right visual field: a positron emission tomography study. *J. Neurosci.* **17**, 3739—3750.
- Vasquez, R. A. & Kacelnik, A. 2000: Foraging rate versus sociality in the starling *Sturnus vulgaris*. *Proc. Roy. Soc. B.* **267**, 157—164.