Take only pictures, leave only...fear? The effects of photography on the West Indian anole *Anolis cristatellus*

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Abstract Ecotourism encourages an environmentally friendly exploration of the world's natural habitats. Tourists often engage in wildlife photography, an activity that is generally not considered disturbing to animals. We investigated the effects of camera-related stimuli to determine whether shutter noise and/or flash affected the immediate behavior of female crested anoles *Anolis cristaellus*. Anoles decreased their display rate following stimuli that included shutter noises, but did not change their behavior in response to flash or silence treatments. To determine the relative importance of this response, we observed anole behavior following playbacks of calls from kestrels *Falco sparverius*, a predator, and bananaquits *Coereba flaveola*, a non-predator. Anoles decreased display rates following kestrel calls when compared to their response to bananaquit calls. Furthermore, anoles spent a greater proportion of time displaying following bananaquit calls compared to both kestrel calls and silence. The magnitude of response to shutter noises was about the same as that to predator calls. This demonstrates that photography may not be as benign as commonly believed, and we should consider whether restrictions on camera noises should be implemented to reduce animal disturbance [*Current Zoology* 57 (1): 77–82, 2011].

Key words Antipredator Behavior, Ecotourism, Photography, Anoles, Multimodal Risk Assessment

Ecotourism is often envisioned as a way to educate travelers and support conservation of the world's natural wildlife and habitats (Fennell, 2007; Marion and Reid, 2007). Nobody questions that ecotourism can have negative effects (Fennell, 2007), but even seemingly benign ecotourism-related activities create stimuli that may disturb animals. For instance, Karp and Root (2009) found that human conversations altered behavior and increased agitation in a hoatzin Opisthocomus hoazin. A popular activity among ecotourists is photography. The common saying, "Take only pictures, leave only footprints" encourages ecotourists to have a minimal impact on wildlife, but also suggests that taking pictures is harmless. To test the assumption that photography has no detrimental effects, we studied animals' response to photography-associated stimuli.

Humans, including ecotourists, can be perceived as predators (Frid and Dill, 2002). For instance, Klein (1993) found that approaching birds by foot was the most distracting thing done by visitors to a wildlife refuge. Photographers are allowed in almost all ecotourist locations and are more likely to approach animals for observation than regular tourists (Klein, 1993). Some photographers are attracted to pristine areas, making animals in these biodiverse locations susceptible the potential influences of photography. Changes in individual behavior can have substantial effects on individual reproductive success and population demography (Anthony and Blumstein, 2000). Therefore, even small, individual disturbances by tourists may have significant impacts on the fitness of wildlife in these destinations.

Taking a picture presents animals with a complex set of multimodal stimuli. These include a visual stimulus from the flash, and an audio stimulus from the shutter and potentially from an auto focus zoom lens. An emerging topic in contemporary animal behavior research is how and whether animals respond to multimodal stimuli differently than unimodal stimuli (e.g., Partan and Marler, 2005). Thus, to fully understand how cameras affect behavior, we must view photography in terms of a set of multimodal stimuli.

To determine whether animals perceive and/or alter their behavior in response to photography-related stimuli, we presented visual and audio stimuli from digital single lens reflex (SLR) cameras (flash and shutter noise) to crested anoles *Anolis cristatellus*. Anoles are an ideal system in which to study both multimodal assessment and subsequent antipredator behavior because they are able to perceive both visual and audio stimuli. They

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possess large eyes with very dense foveae and retinas composed entirely of cones (Crews and Greenberg, 1981). This highly developed visual system is important because anoles rely on visual cues for conspecific communication and the detection of both predators and prey (Fleishman, 1986). Less attention has been given to the importance of audition, but Rothblum et al. (1979) found that *Anolis grahami* could be trained to respond to auditory stimuli. Moreover, other iguanidae respond fearfully to heterospecific alarm calls (Vitousek et al., 2007). Due to previous studies that demonstrate that anoles are sensitive to visual and audio stimuli, we predict that they will respond to both audio and visual modalities of photography (Gallup, 1973; Vitousek et al., 2007).

1 Materials and Methods

Subjects were studied between 9-28 October 2009, on 10 km of hiking trails surrounding the Virgin Islands Environmental Resource Station, St. John, United States Virgin Islands (18°19'19.45"N 64°43'22.58"W). We focused on 2-6 cm (snout-vent length) female crested anoles, identified by their white, dorsal stripe, that were found on tree trunks at heights of 2-5 m. We chose to observe females because they were much more conspicuous and numerous; there were not enough males to collect sufficient data. We performed our experiment at ground distances of 2-5 m away from the anoles. Because of the high abundance of anoles along the trails, it was unlikely that we re-sampled any subjects. To be cautious, we performed each trial at least 3 m away from the previous subject. Experiments were only conducted during periods of limited wind (0-1 on the Beaufort scale).

1.1 Do anoles respond to camera related stimuli?

Three observers walked trails together searching for anoles. Upon locating a study subject, all observers froze standing next to each other in order to be approximately equal distance from the subject. One observer estimated the horizontal distance between ourselves and the subject and the height at which the subject was located in a tree. A second observer performed a 120 s focal observation using continuous recording on each individual, which was divided into two 60 s sections separated by the presentation of a stimulus. Our ethogram included the following behaviors: look (head fixed in position, each change quantified), push up (flex two or four legs to raise body), hop (locomote by jumping), tail wag (move tail), walk (locomote using all four legs), other (any other behavior), and out of sight (subject is out of sight).

After the initial 60 s baseline focal observation, the third observer broadcast one of four stimuli: flash only; shutter sound only; flash and shutter sound; or no stimulus (silence), which served as our control. We presented these stimuli to the subjects in a Latin Square design, alternating between treatments and shutter noises (i.e. shutter A, flash, shutter A+flash, control, shutter B...). We did this in order to eliminate any carry-over effects of previous treatments to any neighboring subjects. We continued to record the subject's behavior for another 60 s. We used an external shoe-mount camera flash to simulate the flash on a digital SLR camera, and used recordings of the shutter noises of five different digital SLR models (Canon 5D Mark 2, Canon 50D, Canon 7D, Nikon D90, Nikon D5000) to simulate the sound of a picture being taken. The recordings were played at a volume comparable to the volume of an actual DSLR shutter noise (53 dB SPL measured at 1 m using a Realistic model 33-2050 sound-level meter weighting A, fast response).

Focal samples were recorded and later scored and analyzed in JWatcher (version 1.0; Blumstein and Daniel, 2007). We grouped the behaviors into three categories: look, display (pushups and tail wags), and locomotion (walk and hop), and calculated the responsiveness of anoles to different stimuli by looking at the difference in amount and rate of behaviors from the baseline. We compared the amount and rates of all three categories to treatment as well as to baseline. We divided the last 60 s focal period into four 15 s time bins, and upon initial examination of graphs of change in behavior over time, we noticed that there was a deviation in behavior between treatments only in the last time bin (45-60 s). We therefore formally tested differences in the change from baseline in behaviors as a function of stimulus presentation by fitting one-way ANOVA models and using Fisher's PLSD tests to compare treatments in this time bin. We calculated the means and standard deviation of the response to our treatments to calculate the Cohen's d, a measure of effect size (Cohen, 1988).

There was no significant difference between the distances between the observer and the lizard (ANOVA, F_{3} , $_{153} = 0.282$, P = 0.838) across treatments, but there was a significant difference in the height in the tree across the different treatments (ANOVA, $F_{3,153} = 3.309$, P = 0.022); lizards were slightly higher in the trees during the control 'stimulus'. To be cautious, we added height in tree as a covariate to the basic ANOVA model and found that in no case was it, or the interaction between height in tree and treatment, significant. Thus, we report the results from the basic ANOVA model.

1.2 How do Anoles respond to the sound of natural predators?

We contrasted the responses of anoles to five different exemplars of bananaquit songs Coereba flaveola, a non-threatening stimulus, five different exemplars of kestrels calls Falco sparverius, a predator (Cruz, 1976), and silence (a control), to see if the anoles responded differently. Again, we used a Latin Square design to avoid carry-over effects to nearby anoles (i.e. bananaquit A, kestrel A, silence, bananaquit B...). Similar to the first experiment, we conducted a two-minute focal observation separated by a stimulus after the initial minute. However, we also added a one-minute acclimation period prior to the initial focal to allow the anoles to become accustomed to our presence because we suspected that delayed response to the stimuli may have been influenced by us, not the experimental treatments. We modified our ethogram for this experiment to incorporate only common behaviors and to more accurately analyze the frequency and time spent on each behavior. We excluded tail wags, and modified pushups to "up" (head and body are up with legs extended-a pushup motion), and "down" (head is slightly up but body is closer to surface with legs bent). We did this because anoles could also be "looking" while completing a pushup. The analysis for this experiment was identical to that of the previous experiment with the exception of the addition of an analysis focusing on the proportion of time anoles engaged in the different behaviors. Again, a visual scrutiny of the responses revealed that responses to the treatments deviated in the 45-60 s time bin, suggesting that anoles responses to different stimuli are indeed delayed. The fact that the response was still delayed despite the one-minute acclimation period indicates that the delay was not due to the presence of the observers, but rather to the stimulus. There was no significant difference between the distances between the observer and the lizard (ANOVA, $F_{2.85}$ = 1.342, P = 0.267), nor was there a significant difference in the height the lizard was in the tree across treatments (ANOVA, $F_{2.85} = 0.855$, P = 0.429). Moreover, the addition of either of these variables as a covariate did not significantly explain variation in the dependent variables. Thus, for this experiment, we focus on the basic ANOVA results.

We performed all statistics using Statview version 5.0. Data are expressed as mean $\pm SE$.

2 Results

2.1 Do anoles respond to camera related stimuli?

From observations of 157 anoles (shutter n = 37; shutter+flash n = 44; flash n = 36; silence n = 40), we found that anoles decreased display rates after hearing shutter sounds compared to the control (silence) (Fig. 1A). The effect of hearing shutters was moderate (shutter v. silence Fisher's PLSD P = 0.042, Cohen's d = 0.450; shutter + flash v. silence Fisher's PLSD P = 0.019, Coehn's d = 0.544). Flashes alone did not significantly change display rate compared to the control (Fisher's PLSD P = 0.560, Cohen's d = 0.122). Overall, camera-related stimuli did not significantly change baseline rates of display (ANOVA, $F_{3,153} = 2.556$, P = 0.057), locomotion (ANOVA, $F_{3,153} = 0.467$, P = 0.706, Fig. 1B) or looking (ANOVA, $F_{3,153} = 0.006$, P = 0.999, Fig. 1C).

2.2 How do anoles respond to the sound of natural predators?

From observations of 88 anoles (bananaquit n = 29; kestrel n = 31; silence n = 28), we found that anoles decreased display rates after hearing kestrel calls compared to bananaquit calls (Fig. 2A, Fisher's PLSD P =0.022, Cohen's d = 0.506). However, bananaquit (Fisher's PLSD P = 0.108, Cohen's d = 0.427) and kestrel (Fisher's PLSD P = 0.506, Cohen's d = 0.255) calls did not significantly change display rate compared to the control. Overall, natural sounds did not significantly change baseline rates of display (ANOVA, $F_{2, 85} = 2.870$, P = 0.062), locomotion (ANOVA, $F_{2, 85} = 0.085$, P =0.918) or looking (ANOVA, $F_{2,85} = 0.107$, P = 0.898) (Fig. 2A-C). Anoles spent a greater proportion of time displaying following a bananaquit playback when compared to both silence (Fisher's PLSD P = 0.047, Cohen's d = -0.416) and kestrel (Fisher's PLSD P =0.031, Cohen's d = 0.450) treatments (Fig. 2D). Kestrel calls did not significantly change (Fisher's PLSD P =0.902, Cohen's d = 0.354) the proportion of time displaying compared to the control. Overall, natural sounds did not significantly influence the proportion of time spent on display (ANOVA, $F_{2, 85} = 2.962$, P = 0.057), locomotion (ANOVA, $F_{2,85} = 0.013$, P = 0.987) or looking (ANOVA, $F_{2,85} = 0.530$, P = 0.590) (Fig. 2D–F).

3 Discussion

Auditory stimuli from both experiments caused anoles to decrease display rates, a biologically important behavior (Jenssen, 1977). Display behaviors serve as communication between conspecifics and herterospecifics and are used by females to claim territories, assert positions in social hierarchies, respond to males' courtship displays, or show fear or anxiety (Stamps, 1973). Thus, decreasing display rates could potentially interfere with mating and social structure within anole communities. The nature and magnitude of suppression in response to both shutter sounds and predator calls indicates that anoles perceived these stimuli as threatening, and are thus exhibiting antipredator behavior in response to shutter sounds. Because anoles responded to both photography and predator noises in the same manner, our findings illustrate that decreasing display rates is in fact an antipredator behavior. Though we designed our experiment as a multimodal stimulus test, we found no evidence that anoles perceived photography in a multimodal way. By comparing responses from the unimodal treatments (shutter, flash), we found that visual and audio stimuli elicit non-redundant (different) responses (Partan and Marler, 2005). Importantly, flash presentation did not significantly change anole behavior. This

was unexpected, considering that anoles are generally believed to be visually dominant (Rothblum et al., 1979).

The decrease in display rate following predator playbacks is consistent with studies showing that anoles stop displaying in the presence of a model (or actual) predator. Rather than fleeing, anoles often experience tonic immobility and freeze for a period of time (Gallup, 1973). The increase in display rates in response to bananaquit calls was unexpected. It is possible that bananaquits and anoles share common predators, in which case bananaquit calls may serve as a sign that there are no predators in the area and that it is safe for anoles to display. Alternatively, it has been proposed that anoles and bananaquits, who feed insects to nestlings, may compete for prey (Wright, 1981). If this is the case, anoles may increase display rates to signal territorial ownership or to alert bananaquits of their presence (see Waide and Regan, 1983 for a critique of Wright's hypothesis).





Fig. 1 Changes in (a) display (ANOVA $F_{3, 153} = 2.556$, P = 0.057, (b) locomotion (ANOVA, $F_{3, 153} = 0.467$, P = 0.706), and (c) looking rates (# times/s) (ANOVA, $F_{3, 153} = 0.006$, P = 0.999) from baseline to the 45-60 seconds following the multi-modal camera playback experiment

Observations from 157 anoles (shutter n = 37; shutter+flash n = 44; flash n = 36; silence n = 40).



Fig. 2 Changes in the rates of (a) display (ANOVA, $F_{2,85} = 2.870$, P = 0.062), (b) locomotion (ANOVA, $F_{2,85} = 0.085$, P = 0.918), and (c) looking (ANOVA, $F_{2,85} = 0.107$, P = 0.898), and the proportion of time allocated to (d) display (ANOVA, $F_{2,85} = 2.962$, P = 0.057), (e) locomotion (ANOVA, $F_{2,85} = 0.013$, P = 0.987), and (f) looking (ANOVA, $F_{2,85} = 0.530$, P = 0.590) Differences are calculated from the baseline to the 45-60 seconds following the playback of a non-threatening bananaquit, a predator, and a silent control. Observations of 88 anoles (bananaquit n = 29; kestrel n = 31; silence n = 28).

Differences in display rates between silence and audio stimuli in the camera experiment had approximately the same effect size as display rate changes between bananaquit and kestrel calls in the playback experiment. Thus, camera shutter sounds appear to influence anole behavior at the same degree as calls from predators.

We are unaware of any previous concern for managing shutter noises in ecotourist destinations. If shutter noises disturb anoles as much as predators, then taking pictures, even without flash, is not as benign as we believe it to be. This study suggests that photography is disturbing to animals, and additional studies should examine whether photography has similar effects in other wild species. Further, researchers should examine the fitness consequences of responding to photographyrelated stimuli, as these disturbances could perhaps be detrimental to foraging and mating success. Conversely, it is also possible that animals may habituate to these stimuli over time. While our study examined the stimuli associated with photography, we did not observe effects of the actual presence of photographers. However, wildlife managers and camera manufacturers should consider all potential ecological impacts from photography when writing tourist regulations and designing future camera technology. Educating ecotourists of the potential consequences of their activities is important to minimize ecotourism's impacts.

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