

Effects of Capture, Observer Presence, and Captivity on Display Behavior in a Lizard

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ABSTRACT.—Stress resulting from an investigator handling or observing subjects can affect the results of field studies. However, effects of such stressors are rarely investigated. In a series of field experiments in southern Florida we examined whether display behavior of territorial male lizards (*Anolis sagrei*) was affected by length of time between handling and observation, length of time that an observer was present and length of time that subjects were held in bags prior to release in the field. Proportion of headbob displays that were bobbing displays did not differ between periods 1–2 h after release and one day later, nor did it differ between periods 0–1 h and 1–2 h after the first appearance of an observer. Similarly, this proportion did not differ between animals previously held in bags for one night and those held for two nights. Our results contrast with other studies that have shown strong effects of several social factors on the proportion of bobbing displays. Thus, the factors we studied appear unimportant in affecting the display behavior of *A. sagrei*.

A number of studies have examined the social significance of variation in display behavior in territorial males of the lizard *Anolis sagrei*. These studies have shown that the relative frequencies of two forms of headbob displays (see descriptions below) vary markedly with residence time, the signaler's location within its home range and familiarity of potential rivals (Paterson, 1999; McMann, 2000; McMann and Paterson, 2003). However, such studies may induce stress in lizards indirectly through observer effects or directly through capture and handling effects. Although it is obviously possible to induce anthropogenic stress in almost any animal, including lizards (Moore et al., 1991), it is unclear whether such stress may have confounded effects of other factors on display behavior in previous work on *A. sagrei*.

In this study, we examined behavioral responses of male *A. sagrei* to variation in time between release and observation, as well as variation in time held in captivity. Our choice of types and levels of treatments were designed to be similar to between-treatment variation in these variables in previous work (McMann, 2000). However, the results of this study provide general information about effects of human disturbance on behavior of *A. sagrei* in the field. Sugerma (1990) found no effect of an observer on behavior of *A. sagrei* in a laboratory setting, but patterns of behavior observed in recent field studies (Paterson, 1999, 2002; McMann, 2000; McMann and Paterson, 2003) would have been impossible in the small containers in which the lizards were held. The role of observer effects is important for studies of animal behavior (Macfarlane and King, 2002) but has been often neglected in studies of lizards and other taxa.

The highly variable headbob displays that appear to mediate social interactions in *A. sagrei* can be classified as either "nodding displays" or "bobbing displays" (McMann, 2000). A nodding display is a volley of continuous rapid dorso-ventral oscillations of the front

portion of the lizard's body, whereas a bobbing display is a more prolonged volley of discontinuous oscillations of the front part of the body. Because the proportion of headbob displays that are bobbing displays appears important in communication in this species (Paterson, 1999; McMann, 2000; McMann and Paterson, 2003), we used this display characteristic as a dependent variable in the current study.

MATERIALS AND METHODS

During 1998 and 1999, we conducted two experiments at Fairchild Tropical Gardens in Miami-Dade County, Florida, while males were defending breeding territories (see Lee et al., 1989; Tokarz et al., 1998). In Experiment One, we examined the effects of time since capture and the length of time that an observer was present. In Experiment Two, we examined the effects of length of time in a bag.

We conducted Experiment One from 20 June 1998 until 7 July 1998. The study subjects were eight male *A. sagrei* that had established territories along the side of a brackish pond. The territory locations were vegetated primarily by red mangroves (*Rhizophora mangle*), Brazilian pepper (*Schinus terebinthifolius*), and coconut palms (*Cocos nucifera*), which formed a dense several-meter-wide belt of trees and shrubs between the water and mowed lawns.

We captured each subject with a noose between 0637 h and 0747 h (EST) so that it could subsequently be observed during its morning period of high activity (AVP, unpubl. data). Each lizard was marked with a number on each flank using a non-toxic paint marker. The lizard was then released within 1 m of its capture location. The entire process of capture, marking, and release took approximately 1–3 min.

After releasing a lizard, one of us (SM) observed its behavior while sitting on the lawn 5–9 m from the capture location, at a point that minimized visual obstructions between the observer and the lizard, and during the next two hours recorded the number of each type of headbob display during each half hour. The

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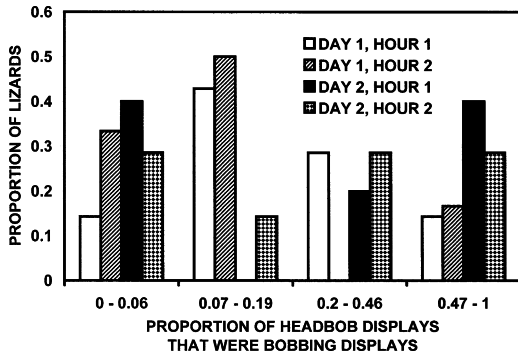


FIG. 1. Distributions of the proportions of headbob displays that were bobbing displays during four periods after capture in Experiment One.

observer moved as little as possible, but changed location if the lizard became obscured by an object such as a tree trunk. During the following day, the lizard was observed similarly, but the second set of observations was begun about 24 h after releasing the lizard (mean time difference: 5.25 ± 2.98 min earlier on the second day).

We ran trials for Experiment Two intermittently from 7 March 1999 until 8 May 1999, and one of us (SM) observed the behavior of one or two lizards on each day of trials. To reduce the possibility of confounds between treatment and between-day weather changes, the observer did not observe two lizards from the same treatment group (see below) on the same day.

We captured 16 focal lizards as we did in Experiment One, except that we caught them at least several hundred meters from the study site during the morning and midday hours. We then marked the lizards and placed them in individual cloth bags. We held half of them indoors for one night (short-term captives) and half for two nights (long-term captives).

During the appropriate morning, we released each focal lizard on an empty patch of artificial habitat that was similar to those used by Paterson (1999) and McMann (2000). To prevent other males from evicting focal males, we located the patch on a mowed lawn at least 10 m from dense vegetation (dense vegetation generally contained other males), and we removed any males from the patch before release. One or two females were usually on the patch, and they were allowed to remain to provide as natural a social context as possible (see Stamps, 1991). The first author then observed lizards and recorded behavior as in Experiment One.

We arcsine-transformed data to meet assumptions of parametric tests, which we used when possible (Sokal and Rohlf, 1995). Then we tested whether the proportion of headbob displays that were bobbing displays differed between the following contexts or groups of lizards. In Experiment One, we tested whether the proportion of bobbing displays differed between lizards (1) observed 1–2 h after release versus about 25–26 h after release, (2) observed during the first hour of an observer's presence versus the second hour of an observer's presence on the day of capture, and (3) observed during the first hour of an observer's presence versus the second hour of an observer's presence on the day after capture. In Experiment Two, we tested

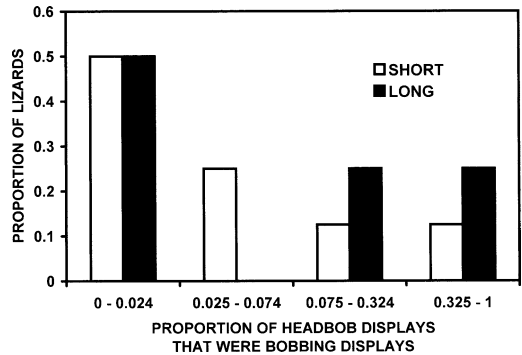


FIG. 2. Distribution of the proportion of headbob displays that were bobbing displays in Experiment Two, both for long-term captives and for short-term captives.

whether the proportion of bobbing displays differed between short-term captives and long-term captives. For the data from Experiment One, we tested the hypotheses with either paired *t*-tests or paired Wilcoxon tests, depending on whether distributions of within-animal differences deviated significantly from normal. For the data from Experiment Two, we tested the hypothesis with a two-sample Wilcoxon test because transformation did not produce normalized data. We analyzed data with SAS (SAS Institute, rele. 8.2 at University of Miami, Cary, NC, 2001). All statistical tests were two-tailed, and we treated all hypotheses as independent. Total number of headbob displays are provided as means \pm SE. Distributions of data for particular treatment groups within the experiments were often not normal; distributions are presented graphically in Figures 1 and 2.

RESULTS

The eight lizards in Experiment One produced 38.4 ± 7.0 headbob displays per hour. The relative frequencies of the two types of headbob displays were similar in all of the time intervals studied (see Fig. 1 and below). The proportion of bobbing displays was not affected by whether the lizards had been captured, handled, and released 1–2 h versus about 25–26 h before we observed them (Wilcoxon Sign-Rank Test, $N = 8$, $S = 9$, $P = 0.25$). The proportion of bobbing displays was also not affected by whether an observer first appeared 0–1 h ago or 1–2 h ago, either on the first day of observation (paired *t*-test, $N = 7$, $t = 0.2$, $P = 0.82$) or on the second day of observation (paired *t*-test, $N = 7$, $t = 0.6$, $P = 0.56$).

The 16 lizards in Experiment Two produced 24.4 ± 4.6 headbob displays per hour. The relative frequencies of display types were similar for both long-term captives and short-term captives (see Fig. 2 and below). The proportion of bobbing displays was not affected by whether the lizards had been held for one night versus two nights (Wilcoxon two-sample test, $N_1 = 8$, $N_2 = 8$, $z = 0.17$, $P = 0.87$).

DISCUSSION

We found that display behavior in *A. sagrei*, as measured by the proportion of bobbing displays, did

not differ between periods 1–2 h after release and one day later, nor did it differ between periods 0–1 h and 1–2 h after the first appearance of an observer. Similarly, this proportion did not differ between animals previously held in bags for one night and those held for two nights. However, it is important to note that a finding that the treatment differences did not cause display differences does not necessarily mean that the displays of the experimental lizards were identical to those of lizards in other contexts outside of the experiment. We did not examine the behavior of undisturbed lizards because it would have been extremely difficult to observe them without marking them in the high-density populations found in southern Florida.

The lack of differences between the treatments in the current study can be interpreted in at least two ways. Differences between levels of potential stressors studied here may not affect the proportion of bobbing displays. Alternatively, the experimental designs may have been unable to detect weak or transient effects. However, studies with roughly similar sample sizes and observation periods found that several factors strongly affected the proportion of bobbing displays (e.g. Paterson, 1999; McMann, 2000). Therefore, any undetected treatment effects in this study would be much weaker or more ephemeral than the effects of other factors studied so far.

The current study is significant in demonstrating the stability of the display behavior of *A. sagrei* in the face of human disturbance. Sugerman (1990) found similar results among captive *A. sagrei*, although other studies have found observer effects in other taxa (Macfarlane and King, 2002). Presently, we can only speculate as to why this is so. Display behavior is likely important for reproductive success in male *A. sagrei*, perhaps by facilitating territory maintenance and access to females. However, territorial males of this species may have a very limited time in which to reproduce, suggesting that mild stressors should not override display behavior.

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