FACTORS AFFECTING DEFENSIVE STRIKE BEHAVIOR IN BROWN TREESNAKES (*BOIGA IRREGULARIS*) PROVOKED BY HUMANS

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Abstract.—Striking is a typical antipredator defense exhibited by many species of snakes. While trapping Brown Treesnakes (*Boiga irregularis*) on Guam, we observed that snakes most frequently struck at an approaching person at a site where snakes had been trapped, marked, and handled in the past. Using a combination of between-sites and within-site comparisons, we assessed if the propensity to strike was correlated with capture histories (both recent and long-term), snake size, body condition (a proxy to nutritional stress), sex, or tail condition (broken or intact), while controlling for confounding variables. We confirmed that propensity to strike was higher at the site where we had been conducting capture-mark-recapture for several years. However, we were unable to demonstrate a correlation between striking tendencies and individual recent or long-term capture histories. The only morphological covariate that had an effect on strike propensity was sex, with females striking more often than males. After removing the site effect from our model, we found that snakes missing parts of their tails were more likely to strike than snakes with intact tails. We have yet to identify the factor(s) that cause the pronounced difference across sites in snake propensity to strike, and data from additional sites might help elucidate any geographical patterns.

Key Words.—anti-predator behavior; defensive behavior; Guam; snake trapping

INTRODUCTION

Striking is an antipredator defense exhibited by many species of snakes (Greene 1988; Herzog et al. 1992). The amount of stress an animal experiences may affect its defensive behavior (Bailey et al. 2009). One can therefore envision a direct correlation between the stress hormone corticosterone (CORT) and the degree to which a defensive behavior is expressed. Moore et al. (2005) investigated CORT levels in blood plasma of invasive Brown Treesnakes (*Boiga irregularis*, BTS) on Guam as part of a study on reproductive ecology. They found that stress may be related to body condition index (BCI), with lean (low BCI) snakes having higher levels of CORT than fat (high BCI) snakes, and that high CORT levels suppressed reproduction. Mathies et al. (2001) found that capture and confinement increased CORT levels in BTS, but it is unclear for how long such effects linger after a snake is released. These findings lead us to hypothesize that nutritionally stressed (lean) snakes may be particularly prone to strike defensively, and individuals frequently trapped in capture-mark-recapture studies might suffer from chronically elevated stress hormone levels, and might be more defensive than individuals that less often enter traps. In addition to short-term physiological effects, the past experience of a snake to stressful interactions with humans might affect their perception of, and responses to, perceived threats long after stress levels have returned to normal.

The Brown Treesnake has caused declines and extirpations of numerous vertebrate species on Guam, USA, the southernmost of the Mariana Islands (Savidge 1987; Fritts and Rodda 1998; Rodda and Savidge 2007). While studying snakes at a consistently trapped site (at least one intensive trapping bout per year during the past decade, plus efforts using hand capture) in northwest Guam, our impression was that snakes in traps struck towards an approaching person, or at a hand reaching into the trap, more often than at sites where snakes had not been previously trapped. By collecting data on propensity to strike when trapping at three different sites, we had the opportunity to assess if this defensive behavior correlates directly or indirectly to (1) the morphological and/or physiological traits of a snake (which may correlate directly to stress hormone levels); (2) recent capture histories (possibly revealing lingering stress levels); and/or (3) long-term capture histories (indicating effects of human encounters that by far exceed the time that stress levels may remain elevated). Besides BCI, the morphological/physiological traits we considered were snout-vent length (SVL), sex, and whether or not the snake had a broken tail. Susceptibility to predators may change with body size, motivating our assessment of SVL effects. Female BTS tend to have higher CORT levels than males, and in females there is a correlation between CORT and progesterone (Mathies et al. 2001); hence, a sex difference in hormone-mediated defensive behavior
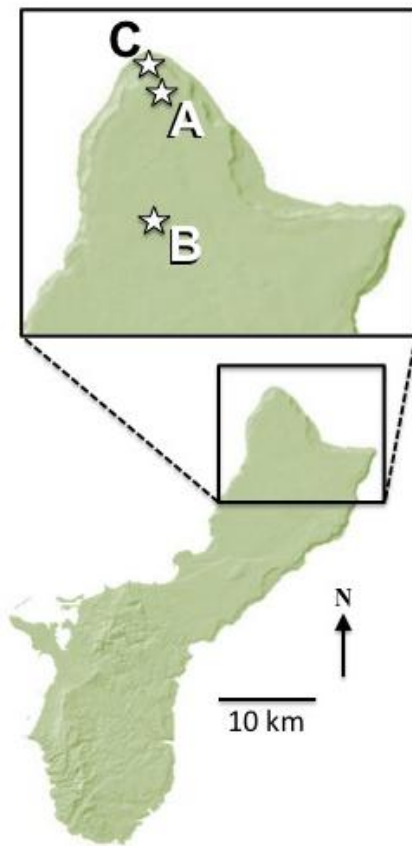
FIGURE 1. Location of the three sites trapped in 2013 for Brown Treesnakes (*Boiga irregularis*) in Guam, USA (13.5000°N, 144.8000°E). Site A is located on top of a limestone plateau and in an enclosed 5-ha area. Site B is on a forest edge. Site C is a pooled sample of three sites near the ocean.

was deemed plausible. A broken tail might indicate past encounters with potential predators (Pleguezuelos et al. 2010), and similar to the argument for long-term capture history effects, previous experiences with predators might influence ensuing behaviors.

MATERIAL AND METHODS

We assessed snake strike propensity while trapping for BTS at three sites in northwestern Guam, USA (Fig. 1). Trapping methodology followed procedures outlined in Rodda et al. (2007) including checking all traps within four hours of sunrise. Trapping at site A took place from May to July 2013 (8,112 trap nights), trapping at site B from July to August 2013 (1,050 trap nights) and trapping at site C from July 2013 to September 2013 (1,340 trap nights). Due to differences in study designs and/or staffing logistics, traps at site A were checked daily whereas at sites B and C traps were checked three

times per week. The three transects at site C were more spread out than transects at sites A and B, but exploratory analyses indicated no difference in snake strike propensity across transects within a site and we pooled them for the analyses presented here.

As the observer approached, opened the trap, and reached for a trapped snake, (s)he scored the behavior of a snake as either striking (1) or not striking (0) before the observer was able to secure the head of the snake. We recorded morphological variables for each captured snake, including snout-vent length (SVL; estimated by stretching the snake along a measuring tape), body condition index (BCI; the residual value from a 3rd-degree polynomial describing snake weight as a function of SVL), sex (determined by probing for inverted hemipenes), and whether or not the individual had a broken tail (a relative tail length clearly below the normal, intact 0.205–0.220 tail length / total length ratio range). Our analysis of whether previous experiences of human encounters caused snakes to respond differently from "naïve" individuals was limited to data from sites A and B (at site C, all snakes were removed upon their first capture).

We used data from sites A and B when modeling the effect of how many recent (i.e., within the current study) trap-capture events a snake had experienced, possibly revealing lingering stress. This metric ranged from 1 to 14 (mean ± SD = 3.57 ± 3.17). Only at site A had snakes been subjected to previous capture-mark-recapture studies, and we therefore restricted analysis of long-term capture experience effects to snakes from that site. The number of previous captures at site A ranged from 0 to 21 (mean ± SD = 11.07 ± 4.70) if counting both trap captures and hand captures; if counting only trap captures the range is 0–9 (mean ± SD = 2.84 ± 2.91).

We investigated if several potentially confounding variables of little or no biological interest might have biased our perception of propensity to strike. A snake confined in a trap could possibly become increasingly stressed by bright daytime conditions. For two sites (A and B), we recorded the time at which traps were checked, and we used time since sunrise (Time, see Table 1) as a covariate in selected models. For sites A and B, our data included estimates of percentage cloud cover, which could potentially have affected the sense of stress of the snake from confinement in a trap during sun-lit (or if overcast, less bright) conditions. A snake that is actively moving inside a trap might be more inclined to strike as compared to a resting snake; we corrected for this potential bias by recording (at all sites) if the snake was inactive (0) or moving (1) inside the trap when the observer was within 2 m of the trap. Also, four variables relating to wind and rain (see Table 1) were available for, and evaluated with, the full data set (sites A, B, and C).

TABLE 1. Variables assessed as potential predictors of defensive strike propensity [coded binary as either striking (0) or not striking (1)] in trapped Brown Treesnakes (*Boiga irregularis*). The random effects allowed for data from repeated measures to be used (snake ID) or allowed for an incompletely crossed design of observer effects across the three field sites. Other variables were modeled as fixed effects. Not all variables were collected or available from all sites.

Variable	Notes	Coding	Sites
Random Effects			
Snake ID	Identified by scale clip or PIT tag	Categorical, random effect (a random intercept)	A, B, C
Observer	Identity of snake handler	Categorical, random effect (a random intercept)	A, B, C
Potentially Confounding			
Activity	Snake moving inside trap?	Binary (yes/no)	A, B, C
Rain Before	6 h preceding the trap check	Binary (yes/no)	A, B, C
Rain During	While traps were being checked	Binary (yes/no)	A, B, C
Wind	Beaufort scale, estimate	Integer scale, but treated as if continuous	A, B, C
Gusts	Beaufort scale, estimate	Integer scale, but treated as if continuous	A, B, C
Clouds	% cloud cover, estimate	Continuous	A, B
Time	Minutes elapsed since sunrise	Continuous	A, B
Of Inherent Interest			
Site	See Fig. 1	Categorical	A, B, C
Snout-Vent Length	Stretched along measuring tape	Continuous	A, B, C
Body Condition Index	Residual from size-weight eq.	Continuous	A, B, C
Sex	Determined by probing	Binary (M/F)	A, B, C
Tail Break	Judged from relative tail length	Binary (un-damaged/missing part of the tail)	A, B, C
Short-tern Capture History	# previous trap captures in this study	Integer scale, but treated as if continuous	A, B
Long-term Capture History	# captures in studies before this	Integer scale, but treated as if continuous	A

To ensure data used in analyses were relevant and non-biased, we removed cases where snakes were coiled up inside the hide tube (a 20-cm long, 5-cm diameter black PVC pipe) provided inside each trap. We also excluded cases where more than one snake was confined in a trap because of unknown social effects on behavior and the sequential snake extraction procedure was more time-consuming, potentially inducing more strikes. The latter practice resulted in the exclusion of the single snake at site B that struck at the observer. To avoid a non-estimable site effect, we added to the data for site B one hypothetical, striking snake with covariates equaling those of the across-site means. While this caused a mildly inflated sample size, it rendered a conservative site effect estimate because snakes from this site otherwise were less inclined to strike in comparison to snakes from sites A and C.

We used logistic regression to model if a trapped, approached, and reached-for snake struck at the observer. We specified snake individual as a random effect because all analyses included cases where focal snakes were captured repeatedly. Preliminary modeling failed to show any effect of the identity of the person extracting the snake, and because not all staff worked at all sites, we also included (as a precautionary measure) variable Observer as a random effect in all models that we estimated. All models were estimated with the R package lme4 (R Development Core Team 2010).

We used *AIC* selection criteria to remove variables without discernible impact on snake strike propensity in a stepwise model selection process. Essentially, we first assessed potentially confounding variables, and removed them if they did not improve model fit; then we addressed variables of inherent interest. Because some variables were only available for a subset of the sites, not all variables were introduced by the start of the modeling process.

RESULTS

We captured 165 individual snakes on 282 occasions across all sites that qualified for analysis of strike propensity (Table 2). Using data from all sites, we first evaluated if rain (current or within the last six hours), average wind speed, or wind gusts affected propensity to strike. This was done with a simple model that also included site, activity, and random snake and observer identity effects. None of the four weather variables had any effect on snake strike rate (for all, $P \geq 0.34$) and a model excluding them was supported over the more parameterized model (Table 3).

Having discarded the weather covariates, we next evaluated if any of four snake traits affected propensity to strike. Three had no effect (SVL: $P = 0.86$; BCI: $P = 0.97$; tail break: $P = 0.69$), but there was an effect of sex ($P = 0.037$); females were more inclined to strike than males. The sex effect became stronger ($P = 0.020$) in a model with sex as the only snake trait variable, and this simplified model had more support than either the model with all four snake covariates or the model with no snake covariates (Table 3).

TABLE 2. Sample size (n), range and mean (± standard deviation) of snout-vent length and body condition, proportion of females and proportion of tail breaks for 165 Brown Treesnakes (*Boiga irregularis*) from five sites in Guam, USA, captured on 282 occasions and analyzed for strike propensity. For the analysis, sites C1, C2, and C3 were pooled into one site (C).

Site	n snakes	n captures	Snout-vent Length (mm)		Body Condition Index		Proportion females	Proportion tail break
			range	mean	range	mean		
A	38	140	797–1,318	1,101 ± 107	0.85–1.52	1.16 ± 0.15	0.63 (n = 24)	0.63 (n = 24)
B	25	40	778–1,534	1,102 ± 172	0.79–1.47	1.0 5± 0.15	0.32 (n = 8)	0.00 (n = 0)
C1	45	45	808–1,214	1,014 ± 85	0.70–1.19	0.93 ± 0.10	0.51 (n = 23)	0.31 (n = 14)
C2	27	27	825–1,173	1,015 ± 75	0.77–1.41	1.00 ± 0.13	0.59 (n = 16)	0.15 (n = 4)
C3	30	30	944–1,234	1,045 ± 66	0.79–1.25	0.97 ± 0.12	0.50 (n = 15)	0.13 (n = 4)
ALL	165	282	778–1,534	1,053 ± 110	0.70–1.52	1.02 ± 0.15	0.52 (n = 86)	0.28 (n = 46)

To investigate the effect of recent trap capture experiences, we built on the above sex-effect model (2B in Table 3) and used data on the time traps were checked and cloud cover estimates from sites A and B. A model including latter two covariates was not supported (3A in Table 3) and the confidence intervals of the time and cloud effects broadly overlapped zero (for both, $P \geq$ 0.38). Snake propensity to strike was not dependent on recent trap capture history (in the model excluding time and clouds, $P = 0.39$) and a model excluding this variable was more strongly supported (Table 3). In fact, the weak trend suggested an inverse relationship between propensity to strike and number of recent trap captures. In this reduced data set the effect of sex was lost (e.g., for the simplest model with the highest support [model 3C in Table 3], $P = 0.23$).

Long-term capture histories (pooling hand and trap captures) were only available for site A. We addressed them in a simple model with the activity score and the random snake and observer identity effects. Snake propensity to strike was not dependent on long-term capture history ($P = 0.62$) and a model excluding it was more supported (Table 3). To ensure we did not overlook other possibilities, we also estimated models with only trap captures, only hand captures, and with hand versus trap captures as separate, additive effects. These three models, too, were less plausible than the null model (4B in Table 3), and the alternative capture history variables had confidence intervals broadly overlapping zero. Because we found no effect of previous capture experiences or environmental covariates, we primarily base our conclusions on the model (2B in Table 3) indicating that snakes were more inclined to strike if already active in the trap; that females struck more than males; and that snakes from our intensively studied site A were most prone to strike (Fig. 2).

We noticed that the incidence of tail breaks differed across sites (A > C > B). This partial collinearity with site may have caused a tail break effect to be obscured in analyses including the site effect. To investigate that possibility, we estimated a post-hoc model with all available data without specifying from which sites snakes originated. Because data came from all sites and sex had an effect for that data set (see above), we modeled activity, sex, and the two random effects in addition to tail break. In this model, snakes with a tail break were more inclined to strike ($P = 0.022$) and a model excluding that effect was less supported (Table 3). However, the model using site instead of tail break had overwhelming support (2B in Table 3). To illustrate the tail break effect size, we modeled the two states (broken vs. not broken) for a semi-active snake of a sex intermediate between male and female. The prediction was that a snake with a broken tail would strike on 55% of the encounters versus 32% for a snake with an intact tail.

DISCUSSION

In this study, we evaluated a number of variables that could conceivably affect defensive strike behavior in Brown Treesnakes. Our major findings include profound differences in strike propensity between sites, evidence for a difference between sexes (though only in models using data from all three sites), and a difference in propensity to strike between active and inactive (resting) snakes in a trap. A snake that is already active in the trap may be more aware of its surroundings and more prepared to defend itself, and thus more likely to strike, than an inactive snake. The activity level of a snake in a trap is of little biological relevance, yet its inclusion in the models helped to reduce the unexplained variance and may remove bias.

Plasma levels of CORT, a steroid hormone involved in stress responses (Romero and Wikelski 2001), might be connected to snake strike propensity. Brown Treesnakes that had been in traps overnight had CORT levels 2–4 times higher than free-ranging snakes, but CORT levels in snakes that had spent three nights in a trap were intermediate between, but not significantly different from, those of free-ranging snakes and snakes that had

TABLE 3. Sequential model evaluation steps to assess which variables might affect the propensity to strike defensively by Brown Treesnakes (*Boiga irregularis*), sites from which data were available and used to estimate the focal model(s), and Akaike's Information Criterion (AIC) statistics for the estimated models. The snake individual (Snake ID) and observer effects were modeled as random intercepts in all models. For details on the variables, see the text and Table 1. For each model, fixed-effect variable coefficients with a 95% confidence interval excluding zero (i.e., significant at α = 0.05) are shown in *italics*. Asterisk (*) indicates models specified post-hoc.

Model	Random Effects	Fixed Effects	Sites	AIC	ΔAIC
1A	Snake ID, Observer	*Site*, *Activity*, Rain before, Rain during, Wind, Gust	A, B, C	246.5	6.07
1B	Snake ID, Observer	*Site*, *Activity*	A, B, C	240.2	0.00
2A	Snake ID, Observer	*Site*, *Activity*, SVL, BCI, *Sex*, Tail break	A, B, C	242.2	5.73
2B	Snake ID, Observer	*Site*, *Activity*, *Sex*	A, B, C	236.5	0.00
2C	Snake ID, Observer	*Site*, *Activity*	A, B, C	240.2	3.73
2D*	Snake ID, Observer	*Activity*, *Sex*, *Tail break*	A, B, C	244.2	7.77
2E*	Snake ID, Observer	*Activity*, *Sex*	A, B, C	247.3	10.86
3A	Snake ID, Observer	*Site*, *Activity*, Sex, Clouds, Time, Short-term Capture Hist.	A, B	172.9	4.34
3B	Snake ID, Observer	*Site*, *Activity*, Sex, Short-term capture history	A, B	169.9	1.31
3C	Snake ID, Observer	*Site*, *Activity*, Sex	A, B	168.6	0.00
4A	Snake ID, Observer	*Activity*, Long-term capture history	A	158.3	1.77
4B	Snake ID, Observer	*Activity*	A	156.5	0.00

spent only one night in a trap (Mathies et al. 2001). Some fraction of the snakes we trapped at sites B and C had spent > 1 night in a trap, and their propensity to strike might have been lower than in snakes we encountered on the morning after they entered the trap. The site effect we documented, with snakes from site A being most defensive, may therefore be partially confounded with a gradual acclimation to confinement in some of the snakes from sites B and C. However, our correction for snake activity might have counteracted that potential bias.

CORT may also be elevated in nutritionally stressed (i.e., low BCI) snakes (Moore et al. 2005) and may negatively affect reproductive ability via sex hormones

Figure 2. Model-predicted values of trapped female and male Brown Treesnakes (*Boiga irregularis*) striking at the person checking the trap at three sites on Guam (years). Snakes were categorized as active (Active) or inactive (Inact.) inside the trap when approached by the observer.

(Siegel et al. 2009). This leads to the assumption that snakes with low BCI could be more stressed and more inclined to strike than high-BCI snakes, but our results provide no support for this prediction. Snake size also had no effect on propensity to strike, but that inference is limited to the range of snake sizes studied. Very small (young) individuals face a partially different set of potential predators (e.g., Lardner et al. 2011b), and may have a different defense strategy.

When analyzing the full data set, we found evidence that females struck more often than males. CORT levels have been shown to be higher in females than in males in various handling and capture scenarios (Mathies et al. 2001), possibly supporting a correlation between CORT level and strike propensity. There is a positive correlation between progesterone and CORT plasma levels in female BTS (Mathies et al. 2001), and one may speculate about these hormones being correlated to the reproductive status of a female. In Guam, BTS may reproduce year-round (Savidge et al. 2007). We did not measure hormone levels, but of the 86 individual female snakes we captured, only seven had follicles that could be detected via manual palpation. Of these seven, only two struck. A much larger sample would be required to assess correlations between reproductive status and propensity to strike.

We used capture data collected during mark-recapture projects to assess whether prior trap- and hand capture experiences could affect strike behavior. One could argue that lingering stress could be a factor (or have an effect) for those snakes that have recently been captured. A long-term effect would rather imply some kind of imprinting from a previous experience (Lorenz 1937). However, effects of previous experience on snake behavior are highly debated (Fuenzalida et al. 1975;
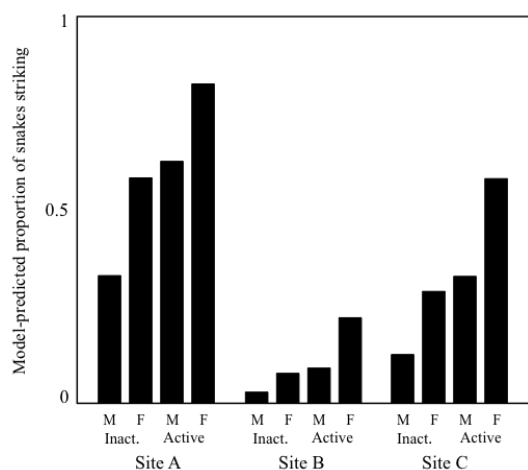
Scudder and Chiszar 1977; Herzog et al. 1989) and difficult to test. Previous experience of a perceived threat could affect defensive behavior in diametrically opposite ways. Snakes could become habituated to a threat once they realize it poses no danger (Glaudas 2004), or could conversely acquire memories of unpleasant capture and handling experiences causing them to respond more defensively over time (Griffin et al. 2000). Prior to the start of the study, we noticed the snakes most inclined to strike came from the site with long-term mark-recapture efforts, and therefore hypothesized that number of previous captures would correlate positively with propensity to strike. However, we were not able to statistically support short-term (within our focal trapping effort; sites pooled) or long-term (counting captures of snakes from site A in prior trapping efforts) capture-history effects at the individual level on the propensity of a snake to strike. Thus, our most plausible model failed to identify the proximate reason for the difference in snake strike propensity between sites.

The physical state of the tail of a snake influenced propensity to strike when omitting the site effect. Tail breaks may be indicative of a population (site) characteristic reflecting a site-specific property. The tail state in any individual snake may be a chance occurrence poorly correlated to the predator encounter rate on a per-snake basis. To evaluate if collinearity between site and a (site-specific) tail break incidence rate caused the lack of a tail break effect, future studies need to sample more sites (sites that differ in tail break incidence rate). Tail injuries in snakes can be caused by predators (small mammals: Hoyer and Stewart 2000; schools of fish: Hailey and Davies 1987; birds: Santos et al. 2011), by prey such as rats (*Rattus spp.*) retaliating during constriction and envenomation attempts by snakes, or perhaps by infections caused by fungus or other pathogens. At site A, a predation attempt by a Coconut Crab (*Birgus latro*) on an adult Brown Treesnake was observed (Lardner et al. 2011a), and other crabs are documented to prey on snakes (Voris and Jeffries 1995; Maitland 2003). Future studies could examine if near-shore sites on Guam have both a higher proportion of snakes with damaged tails and a higher propensity to strike. Data on the striking behavior of Brown Treesnakes from additional sites could offer clues on more variables and mechanisms explaining differences in defensive behavior among individual snakes at different sites, whether it involves previous experiences, hormones, genetics, or something entirely different. Understanding striking behavior may also provide insight into stress reactivity and changes in behavior induced by repeated captures for other wildlife species.

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