
FACTORS INFLUENCING THE DISPLAY OF MULTIPLE DEFENSIVE BEHAVIORS IN EASTERN INDIGO SNAKES (*DRYMARCHON COUPERI*)

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Abstract.—The ability to display multiple defensive behaviors may increase the chances of an individual avoiding predation. Morphological and physiological condition often influences the display of particular behaviors. Understanding the factors influencing the display of particular behaviors from a suite of potential behaviors can help understand the conditions under which displaying certain suites of defensive behaviors will confer the greatest advantage. *Drymarchon couperi* (Eastern Indigo Snake) is a large, non-venomous snake that exhibits multiple visual, auditory, olfactory, and physical defensive behaviors. We studied the responses of wild *D. couperi* to human capture and examined how the number and presence of individual behaviors were related to extrinsic and intrinsic variables using encounters from 84 snakes. Snakes were more likely to flee from the observer at warmer body temperatures and, once captured, exhibited wide variation in defensive behaviors with less costly (i.e., less aggressive) behaviors predominating. Individuals were more likely to display any type of defensive behavior earlier in the field season (i.e., November through January). However, our variables had relatively little influence on the presence of particular defensive behaviors although, for some behaviors, the probability of displaying a behavior increased as the number of other behaviors exhibited increased. Our study shows that *D. couperi* defensive behavior is quite variable and that the factors contributing variation are unclear. Environmental factors (e.g., distance to retreat site) or individual predispositions may contribute to some of this variation.

Key Words.—aggression; body temperature; death feigning; defensive response; ectotherms; hierarchical variance partitioning; predation

INTRODUCTION

The ability of an organism to avoid predation plays a critical role in influencing its fitness (Lima and Dill 1990). However, a single behavior is unlikely to effectively deter predation under all circumstances because predation threats can differ widely due to differences in predator identity, the physical environment, or individual characteristics (Abramsky et al. 1996; Honma et al. 2006; Morosinotto et al. 2010; Smolka et al. 2011; Ibanez et al. 2014). Species may therefore modify their behavior depending on the perceived level of predation risk (Lima and Dill 1990). Additionally, some species are capable of displaying multiple defensive behaviors in response to a single predatory encounter (Greene 1988). These behaviors are often perceptible by multiple sensory systems of

numerous potential predators (e.g., visual, auditory, olfactory), which may provide a more intensive response than any single behavior. Additionally, initial attempts to deter predation may fail in which case subsequent behaviors may substantially increase the chances of an individual for survival (Eilam 2005; Hopkins et al. 2011).

Previous studies have also found that individual-level characteristics influence behavioral responses to both predation threats and actual predatory encounters (e.g., Bulova 1994). These characteristics may include the morphological or physiological condition of an individual, including color pattern (Brodie 1992), body size (Roth and Johnson 2004; Herrel et al. 2009), age (Cuadrado et al. 2001; Hopkins et al. 2011), sex (Durso and Mullin 2013), or reproductive condition (Goode and Duvall 1989). Among ectotherms, body temperature has

a strong influence on defensive behaviors such as jumping performance or crawling speed (Hertz et al. 1982; Peterson et al. 1993; Gomes et al. 2002) because ectotherm physiological processes are closely coupled to body temperature (Lillywhite 1987). While the condition of an individual can have a strong influence on its behavior, certain individuals may show a disposition towards specific behavioral traits (Sih et al. 2004; Bell et al. 2009), which can be robust across a range of internal and external conditions (Brodie and Russell 1999; Citadini and Navas 2013). Differences in behavioral types may therefore have important positive or negative fitness consequences (Sih et al. 2004; Smith and Blumstein 2008). Understanding the factors influencing inter-individual variability in the expression of multiple defensive behaviors can lead to a better understanding of the relative importance of factors governing those behaviors and the conditions under which specific defensive behaviors will confer the greatest chance of avoiding predation. Yet quantitative data on variation in defensive behaviors are often lacking, particularly for non-model organisms in field conditions.

Snakes provide an excellent group in which to study the factors influencing the display of multiple defensive behaviors because they display a diversity of behaviors among and within species (Arnold and Bennet 1984; Greene 1988; Aubret et al. 2011). Many studies have described intra-specific variation in snake defensive behaviors and the factors influencing these behaviors (Mori and Burghardt 2004). However, relatively few studies have examined the factors influencing defensive behavior in non-venomous, large-bodied species. Larger species may face less predation pressure than smaller species, which could lead to relaxed pressure to maintain defensive behaviors (Bonnet et al. 2005; Aubret et al. 2011). As a result, the factors influencing the expression of those behaviors may differ from those of smaller-bodied species.

Eastern Indigo Snakes (*Drymarchon couperi*) are large (> 2 m), non-venomous colubrids native to the southeastern Coastal Plain of the USA (Enge et al. 2013). Adults have relatively few natural predators, which may include raptors, carnivorous mammals, and American Alligators (*Alligator mississippiensis*; Ernst and Ernst 2003). Although *D. couperi* are known anecdotally for their docility towards humans, they may exhibit multiple defensive behaviors, which are olfactory (musking), audible (hissing and tail rattling), visual (vertical flaring of the neck, feint striking, and death feigning), and physical (biting) in nature (Holbrook 1842; Stevenson 2003, 2010). However, the frequencies of these behaviors are quantitatively unknown as are the factors influencing the display of particular behaviors. We therefore examined data on *D. couperi* captures from ongoing monitoring studies in southern Georgia (Stevenson et al. 2009; Hyslop et al. 2011) with two

objectives in mind. Our first objective was to quantify the initial response of *D. couperi* to an observer (i.e., remain motionless or flee) and the types and frequencies of defensive behaviors exhibited following capture. Our second objective was to correlate the presence of particular behaviors with intrinsic and extrinsic variables that we expected might influence *D. couperi* defensive behaviors. Specifically, we predicted that time of year, body size, body temperature, sex, and the process of ecdysis (shedding) affected initial response to an observer and the types and total number of defensive behaviors exhibited during an encounter. We also developed a hypothesized ranking of observed behaviors from least to most costly (i.e., aggressive) and predicted that snakes would be more likely to exhibit costly behaviors if they also exhibited other defensive behaviors in that encounter.

MATERIALS AND METHODS

We collected data on *D. couperi* defensive behaviors from 31 October 2013 to 15 March 2014 at sites located throughout southern Georgia, USA. *Drymarchon couperi* may be surface active throughout the year even at low temperatures (< 10° C air temperature; Stevenson et al. 2009). Our field season also coincided with *D. couperi* breeding activity, which included male mate-searching, male-male ritualized combat, and possibly female-guarding by males (Moler 1992; Stevenson et al. 2003; Hyslop 2007). Our monitoring sites included xeric sandhill habitats supporting Gopher Tortoise (*Gopherus polyphemus*) burrows, which are required as cool-season refugia by *D. couperi* within our study region (Diemer and Speake 1983; Hyslop et al. 2009a). Xeric sandhills are open and somewhat barren environments underlain by or occurring on ridges of deep, well-drained sands, typically with a scattered canopy/subcanopy of Longleaf Pine (*Pinus palustris*) and xerophytic oaks (especially Turkey Oak, *Quercus laevis*, and Sand Post Oak, *Q. margaretta*, respectively). Ground cover is generally sparse and includes Saw Palmetto (*Serenoa repens*), Wiregrass (*Aristida stricta*), and a number of other shrubs, grasses, and forbs adapted to xeric, nutrient-limited soil. We conducted visual encounter surveys on multiple occasions at each site during daylight hours (0900–1600).

A single observer attempted to capture each snake by hand immediately upon detection and classified the behavior of the snake immediately preceding capture as motionless or moving. Most individuals were aware of our presence prior to capture although some individuals appeared unaware of the presence of the observer when captured. We assumed that the behavior of a snake prior to capture represented its initial response to a potential predator. We also assumed that capture simulated a predatory attack and would elicit relevant defensive



FIGURE 1. Examples of Eastern Indigo Snake (*Drymarchon couperi*) defensive behaviors observed during this study. A) adult male neck flaring, B) adult male neck flaring and hissing in typical pre-strike posture, C) adult male neck flaring and hissing in an aggressive pre-strike posture, D) adult female death-feigning. (Fig. 1A, 1B, and 1D photographed by Dirk Stevenson and Fig. 1C photographed by John Serrao).

behaviors. Immediately following capture, the observer firmly held the snake off the ground using both hands with one hand ca. 20–30 cm behind the head and the other hand positioned at approximately the mid-body region of the snake. Snakes were held in a manner to maximize eye contact between the observer and snake as this may influence defensive behavior in snakes (Burghardt and Greene 1989). No additional manipulation was applied to induce a defensive response and we attempted to standardize our capture and handling protocols across observers. We began timing each capture event immediately following capture, and recorded the presence or absence of defensive behaviors during the encounter which we defined as the first 3 min post-capture. We recognized the following behaviors ranked in hypothesized order from least to most costly: (1) musking; (2) tail rattling; (3) vertical flaring of the neck (neck flaring, Fig. 1A–1C); (4) hissing (Fig. 1B and 1C); (5) closed-mouthed or feint strike (striking, Fig. 1B); (6) striking with biting or chewing (biting); and (7) death-feigning (Fig. 1D). Although death-feigning is not costly per se, it is very rarely observed (Stevenson 2010) and is likely used as a final resort to deter predation. We therefore considered it an extreme behavior for *D.*

couperi. In those instances where the snake bit and actively chewed, we allowed the snake to release its grip from our person, clothing or equipment on its own accord to prevent injury to the snake.

As soon as possible following capture, we recorded the cloacal temperature of a snake approximately 5 mm into the cloaca with a quick-reading thermometer (T-6000, Miler-Weber Inc., Ridgewood, New York, USA). Based on our previous experience, we do not think these measurements affected the manner of the defensive response of the snake. We avoided any additional handling or disturbance of the snake during the encounter. Following the encounter (i.e., after the initial 3 min encounter), the observer and 1–2 additional observers began recording data on the snake and its environment. This procedure was generally completed within 15 min post-capture. We recorded the date and time of each capture and the sex, snout-vent length (SVL), and mass of each snake. We used SVL to classify each individual as an adult, subadult, or juvenile (Bauder et al. 2012). Each snake was uniquely marked using a subcutaneous passive integrated transponder (PIT) tag ca. 20 cm anterior to the vent and we recorded if a snake had been previously captured during the field

TABLE 1. Summary statistics for covariates included in an analysis of Eastern Indigo Snake (*Drymarchon couperi*) defensive behaviors. Covariate abbreviations, following those used in the text, are in parentheses. Means, standard errors (SE), ranges, and percentages are across all 84 initial encounters used in the analyses.

	Mean	SE	Range
Date (DOY)	29 Dec. 2014	NA	25 Oct. 2013 to 15 March 2014
Snout-vent length (SVL)	1.43 m	0.03 m	0.95–1.90 m
Body condition index (BC)	-0.005	0.04	-1.24–0.75
Cloacal temperature (Cloacal)	22.7° C	0.5° C	11.0–31.6° C
Sex (Sex)	62% male and 38% female		
Eyes opaque (Opaque)	86% not opaque and 14% opaque		

season. We also recorded whether or not the eyes of the snake were opaque (i.e., cloudy or blue), which was an indication that the snake was in a pre-ecdysis state. We recorded any defensive behaviors exhibited while the snake was being processed (i.e., post-encounter). We released each snake at its capture location after processing.

We selected multiple covariates that we *a priori* predicted could influence the presence of defensive behaviors. We included date (represented as day-of-year [DOY] where 1 = 25 October 2013), SVL, and cloacal temperature (Cloacal) as continuous variables and sex (Sex), whether or not the eyes were opaque (Opaque), and whether or not the snake was captured after another snake that same day (Previous) as binary categorical variables. We recorded Previous because many (57%) captures were made by the same observer(s) on days where another capture was made and lingering scent from previous captures that day could influence defensive responses of subsequent captures. We therefore included Previous in all analysis except the initial response analysis.

We predicted that body condition could influence the presence of defensive behaviors so we calculated a body condition index (BC) using the residuals of a simple linear regression of mass on SVL ($P < 0.001$, $r^2 = 0.89$). We also predicted that individuals might be more likely to exhibit costly behaviors while also exhibiting other behaviors during the encounter. For a given behavior (e.g., hissing), we therefore summed the number of all other behaviors exhibited during the encounter and included this number as a covariate (No.Others). We used a Spearman's rank correlation to test for collinearity and found low correlation among all covariates ($r_s \leq |0.31|$). We used generalized linear models (GLM) with binomial error distributions with initial response (fled or remained motionless), the presence of any defensive behavior, and the presence of individual behaviors as our response variables. We used our *a priori* covariates as predictor variables. When considering any defensive behavior, we scored an encounter as 1 if we observed any defensive behavior and 0 if we observed none. This process was repeated separately for the analysis of each individual behavior containing sufficient sample sizes (musking, tail rattling,

hissing, neck flaring, and feint striking). We also used GLM with a Poisson error distribution to examine how the total number of defensive behaviors (0–6) was influenced by our covariates. We only used data from the first encounter of an individual although a post-hoc analysis showed that including multiple encounters per individual did not strongly affect our results.

Although each covariate in our analysis was selected because we predicted an *a priori* relationship with the presence of defensive behaviors, we had no *a priori* reason to use any particular combination of our covariates. We therefore fit models using all possible subsets of our covariates. This also allowed us to use hierarchical variance partitioning to estimate the independent contribution of each covariate to the variance of the global model as a means of identifying the most causal factor (Chevan and Sutherland 1991; Mac Nally 2000). Because this approach does not allow interactive effects, we conducted a preliminary analysis to test for interactive effects between sex and our other covariates in each of our analyses. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham and Anderson 2002) to rank models. If models with interactive terms had stronger support than the main effects models ($\Delta\text{AIC}_c > 2$), we analyzed males and females separately and otherwise retained sex as a covariate. We used the hier.part package (v. 1.0-4, Walsh and Mac Nally 2013) to calculate the independent contributions of each covariate. We used model averaging (Burnham and Anderson 2002) with the MuMIn package (v. 1.10.0, Barton 2014) and report model-averaged parameter estimates (i.e., betas, β) and 95% confidence intervals. Means are reported ± 1 SE and we conducted all analyses in R v. 3.0.2 (R Development Core Team, Vienna, Austria).

RESULTS

We recorded 98 encounters from 85 individual *D. couperi*. Most individuals were encountered only once and the maximum number of encounters per individual was three (one individual). Of the 13 snakes for which we had more than one encounter, only two individuals showed identical responses during multiple encounters and all but two of the remaining 11 snakes displayed

TABLE 2. The frequency of defensive behaviors exhibited by Eastern Indigo Snake (*Drymarchon couperi*) during individual encounters (i.e., the first 3 min following capture, < 3 min) and post-encounter (i.e., 3 to ca. 15 min following capture, > 3 min). Individual behaviors are ranked in hypothesized order from least to most costly (i.e., aggressive). Any behavior refers to the presence of any of the seven behaviors. Percentage of encounters where each behavior was observed are in parentheses.

	Musk	Tail rattle	Neck flare	Hiss	Feint strike	Bite	Death feign	Any behavior
< 3 min	36 (43%)	50 (60%)	24 (29%)	45 (54%)	19 (23%)	4 (5%)	0 (0%)	72 (86%)
> 3 min	32 (38%)	50 (60%)	30 (36%)	47 (56%)	14 (17%)	3 (4%)	2 (2%)	73 (87%)

fewer behaviors when they were recaptured later in the field season. We used the initial encounters from 84 individuals (52 males and 32 females; Table 1) in all subsequent analyses. We recorded 62 encounters from adults (74%) and 22 encounters from subadults (26%). Most captures were made while the snake was moving (69%) as opposed to stationary (31%). At least one of our seven defensive behaviors was observed in 86% and 87% of encounters and post-encounters (i.e., post 3-min following capture), respectively. Mean total number of behaviors during encounters was 2.12 (± 0.15) and 2.14 (± 0.16) post-encounter. The coefficient of variation of the total number of defensive behaviors during encounters was 0.70 and 0.66 for post-encounter behaviors. Tail rattling and hissing were the most commonly observed defensive behaviors whereas death-feigning and biting were rarely observed (Table 2). Models with an interactive effect of sex were not better

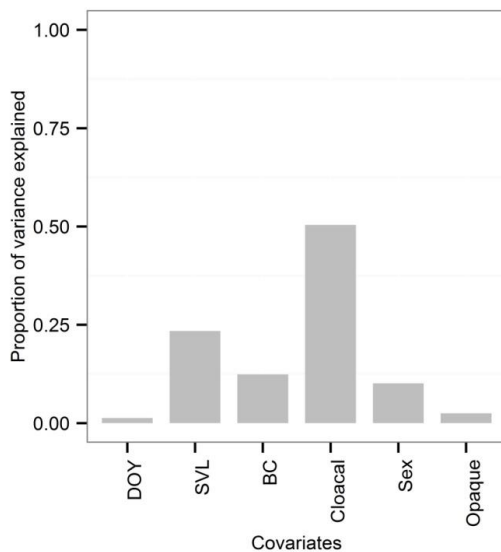


FIGURE 2. Proportion of variance in Eastern Indigo Snake (*Drymarchon couperi*) initial response explained independently by each covariate. All of the 95% CIs of the model-averaged parameter estimates overlapped zero. Covariate abbreviations are DOY = date, SVL = snout-vent length, BC = body condition, Cloacal = cloacal temperature, Sex = sex (male/female), and Opaque = eyes opaque (yes/no).

supported ($\Delta AIC_c > 2$) than their corresponding main or additive effects models for all behaviors except for hissing. We therefore analyzed the effects of our covariates on hissing separately for males and females but pooled males and females for all other analyses while including sex as a covariate.

Model support was very low for models explaining the initial response of a snake to an observer and the model-averaged 95% CI for all covariates overlapped zero (Fig. 2, Table 3). However, snakes were generally more likely to move in response to an observer at warmer temperatures ($\beta = 0.11$, 95% CI = -0.00–0.23). Model support was generally higher for our behavioral models (Table 3). Once captured, snakes were more likely to exhibit any defensive behavior ($\beta = -0.04$, 95% CI = -0.07, -0.01) and a greater number of behaviors ($\beta = -0.006$, 95% CI = -0.011, -0.002) earlier in the season (i.e., November through January). Snakes were also less likely to exhibit any behavior if opaque ($\beta = -2.15$, 95% CI = -4.12, -0.19) and more likely to exhibit any behavior if another snake had been captured earlier that day ($\beta = 2.21$, 95% CI = 0.13–4.29).

The number of other behaviors displayed during the encounter had a positive influence on the presence of individual defensive behaviors ($\beta \geq 0.27$) and the model-averaged 95% CI for this covariate overlapped zero only for hissing (Fig. 3). At least one other covariate had a relatively strong influence on all defensive behaviors except tail rattling and hissing for females. Snakes were more likely to musk earlier in the season ($\beta = -0.02$, 95% CI = -0.04, -0.00) and if they were male ($\beta = -1.78$, 95% CI = -3.13, -0.39). Snakes were less likely to neck flare if there was another snake captured earlier in the day ($\beta = -2.22$, 95% CI = -3.75, -0.69), more likely to neck flare if they were opaque ($\beta = 1.75$, 95% CI = 0.06–3.44), and more likely to neck flare later in the season ($\beta = 0.02$, 95% CI = 0.00–0.04), although these last two covariates explained a small proportion of the variation in neck flaring (Fig. 3). Snakes were more likely to feint strike if another snake had been captured earlier in the day ($\beta = 1.50$, 95% CI = 0.20–2.80). Males with longer SVL were more likely to hiss than smaller males ($\beta = 3.69$, 95% CI = 0.49–6.88).

TABLE 3. Model selection results for models examining the factors influencing Eastern Indigo Snake (*Drymarchon couperi*) initial response to capture and subsequent defensive behaviors. We used an all-subsets modeling approach and therefore report models with AIC_c model weights (w_i) ≥ 0.05 . We report the proportion of deviance explained (D^2) as an analog to r^2 for generalized linear models. Covariate abbreviations are DOY = date, SVL = snout-vent length, BC = body condition, Cloacal = cloacal temperature, Sex = sex (male/female), Opaque = eyes opaque (yes/no), Previous = another snake was captured earlier that same day (yes/no).

Model	D^2	AIC _c	Δ AIC _c	w_i
Initial response				
Cloacal + SVL	0.06	104.49	0.00	0.0870
Cloacal	0.03	104.70	0.22	0.0780
Cloacal + Sex	0.05	105.48	1.00	0.0530
Cloacal + SVL + BC	0.07	105.50	1.01	0.0520
All behaviors				
DOY + Opaque + Previous	0.34	54.18	0.00	0.2260
DOY + BC + Opaque + Previous	0.34	56.17	1.99	0.0840
DOY + SVL + Opaque + Previous	0.34	56.19	2.01	0.0830
DOY + Opaque + Sex + Previous	0.34	56.41	2.23	0.0740
DOY + Cloacal + Opaque + Previous	0.34	56.42	2.24	0.0740
Number of behaviors				
DOY	0.08	291.87	0.00	0.0710
DOY + Cloacal	0.10	291.92	0.05	0.0690
Musk				
DOY + Cloacal + Opaque + Sex + No.Others	0.24	100.03	0.00	0.2090
DOY + Opaque + Sex + No.Others	0.21	101.17	1.14	0.1180
DOY + Cloacal + Sex + No.Others	0.20	102.20	2.18	0.0700
Tail rattle				
SVL + No.Others	0.13	104.82	0.00	0.0840
Neck flare				
DOY + Opaque + No.Others + Previous	0.28	83.26	0.00	0.1920
DOY + Opaque + BC + No.Others + Previous	0.29	84.38	1.13	0.1100
DOY + Cloacal + Opaque + No.Others + Previous	0.28	85.27	2.01	0.0700
DOY + Opaque + Sex + No.Others + Previous	0.28	85.37	2.11	0.0670
DOY + Opaque + SVL + No.Others + Previous	0.28	85.43	2.17	0.0650
Hiss-Males				
Cloacal + Opaque + SVL	0.20	64.52	0.00	0.0860
Cloacal + Opaque + SVL + BC	0.23	64.52	0.00	0.0860
Cloacal + SVL + BC	0.19	64.77	0.25	0.0760
Cloacal + SVL	0.15	65.22	0.70	0.0600
Hiss-Females				
Cloacal + No.Others	0.23	40.08	0.00	0.0660
Cloacal + SVL + No.Others	0.28	40.41	0.33	0.0560
Feint strike				
DOY + BC + No.Others + Previous	0.23	79.64	0.00	0.0600
Sex + No.Others + Previous	0.21	79.78	0.14	0.0560
DOY + Sex + No.Others + Previous	0.23	79.95	0.31	0.0520
DOY + No.Others + Previous	0.20	80.01	0.37	0.0500
Cloacal + Sex + No.Others + Previous	0.23	80.02	0.38	0.0500

DISCUSSION

We found that wild *D. couperi* during the late fall through early spring usually exhibited some form of

defensive response to human capture despite their reputation for docility. We observed costly behaviors (i.e., striking and biting) relatively infrequently. This trend is paralleled in many venomous snake species that

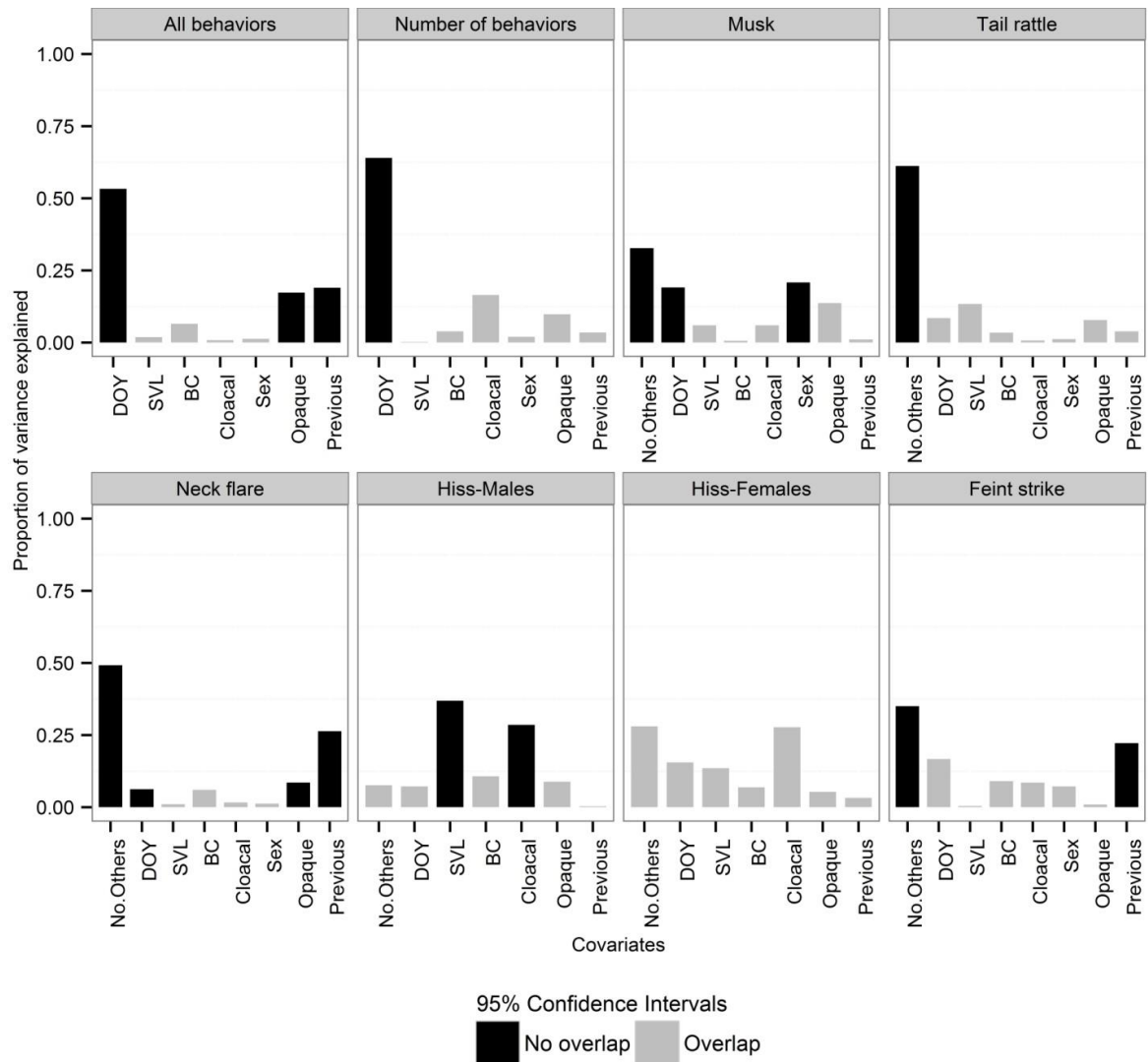


FIGURE 3. Proportion of variance explained independently by each covariate for the presence of any defensive behavior (All behaviors), the number of defensive behaviors (Number of behaviors), and individual defensive behaviors of Eastern Indigo Snakes (*Drymarchon couperi*). Dark bars represent covariates whose model-averaged 95% confidence intervals do not overlap zero. Covariate abbreviations are DOY = date, SVL = snout-vent length, BC = body condition, Cloacal = cloacal temperature, Sex = sex (male/female), Opaque = eyes opaque (yes/no), Previous = another snake was captured earlier that same day (yes/no).

display a reluctance to strike or bite when initially encountered (Whitaker et al. 2000; Gibbons and Dorcas 2002; Shine et al. 2002). Our results also confirm the anecdotal observation that *D. couperi* are reluctant to bite humans. This reluctance could reflect increased energetic expenditures or increased risk of injury or death from close contact with their predators. Reluctance to exhibit costly behaviors could also reflect relaxed selection for such behaviors (Coss 1999). Multiple studies have reported reduced defensive behaviors for snakes in areas with little or no predation pressure (Shine et al. 2002; Bonnet et al. 2005; Aubert et al. 2011). Adult *D. couperi* have relatively few natural predators, as evidenced by the relatively few

observations of natural predation and high adult survival rates (Hyslop et al. 2009b, 2011). If predation pressure on *D. couperi* is sufficiently low or individuals are otherwise able to deter predators, there may be little selective pressure for widespread exhibition of costly responses. Alternatively, *D. couperi* may simply not have perceived our captures as a threat meriting more costly responses.

We also observed substantial variation among individuals in the number of behaviors displayed and the frequency of individual behaviors. Because our capture protocol was consistent among captures and observers, this variation is not likely due to differences in the intensity of the simulated predatory encounter (Brodie et

al. 1991). The probability of displaying any individual behavior was positively associated with the number of other behaviors displayed during the encounter and this variable was generally the most influential out of those we considered. Most individuals (56%) displayed more than one behavior per encounter. An exploratory *post hoc* analysis found very few consistent associations among individual behaviors suggesting that the display of a particular behavior is relatively independent of any one behavior. However, we did not collect data on the sequence of behaviors and are therefore unable to infer the degree to which *D. couperi* might intensify their defensive responses over the course of a predatory encounter. Displaying multiple behaviors may lead to an overall response that is more effective at deterring predation than any single response, particularly if the cost of any single response is relatively low.

Our prediction that more costly behaviors were more strongly associated with a greater number of other behaviors was only partially supported. While the number of other behaviors was most influential for feint striking it was also very influential for tail rattling and neck flaring, behaviors we hypothesized to be less costly. However, our hypothesized rankings may oversimplify the true cost of those behaviors. Variation in the frequency of costly or aggressive responses could reflect inter-individual variation in behavioral dispositions (Sih et al. 2004; Bell et al. 2009) suggesting that some individuals are naturally more aggressive than others, a feature noted in other snake species (Arnold and Bennett 1984; Mori and Burghardt 2001; Citadini and Navas 2013). While our study was not designed to test for behavioral disposition, we found some evidence that defensive response was not consistent across multiple encounters. When we included recaptures in our analysis we found that snakes tended to exhibit fewer behaviors when recaptured than on their initial encounter ($\beta = -0.62$, 95% CI = -1.19, -0.06). However, our field experience with *D. couperi* strongly suggests that certain individuals are more aggressive than others. Additional data collected using multiple repeated encounters from multiple individuals while controlling for potentially confounding factors are needed to determine if individual *D. couperi* show consistency in defensive behaviors.

Many studies have examined the effects of temperature on the degree of aggressiveness or intensity in snake defensive behaviors and have reported conflicting results. Some studies have reported increased aggression at low temperatures and a tendency towards flight at warmer temperatures (Passek and Gillingham 1997; Mori and Burghardt 2001; Llewelyn et al. 2010) while other studies have reported increased aggression at high temperatures (Schieffelin and de Quieroz 1991; Keogh and DeSerto 1994; Shine et al. 2002) or relatively little influence of temperature on the

type of defensive behavior (Citidani and Navas 2013). This variation may be due to methodological differences (e.g., experimental design, behavioral terminology) as well as biologically relevant inter-specific differences (Mori and Burghardt 2004; Llewelyn et al. 2010). In a review of studies on snake defensive behavior, Mori and Burghardt (2004) concluded that previous studies showed a trend for more active responses at high temperature with escape generally preceding threatening responses. The data from our study are partially consistent with this trend. We did find that *D. couperi* were more likely to flee rather than remain motionless at warmer temperatures. However, once captured, the defensive behavior(s) displayed was generally independent of temperature. We observed all defensive behaviors (except death-feigning) at body temperatures $< 18^{\circ}\text{C}$. Although data on *D. couperi* thermal performance is lacking, it is possible that the defensive behaviors we observed have relatively low thermal dependencies (Bennett 1980), particularly because *D. couperi* remains surface-active during the winter. We only recorded one individual with a body temperature $< 15^{\circ}\text{C}$ (11°C) so the range of body temperatures in our study also may not have extended low enough to allow us to detect an effect of temperature.

Of our remaining covariates, date exhibited the greatest influence on the presence of any defensive behavior but its influence on the presence of each individual behavior was comparatively weak. Snakes were more likely to display at least one defensive behavior and display more behaviors November through January compared to February and March. These months generally include the peak of *D. couperi* breeding activity and cool-season surface activity (Stevenson et al. 2009). These activities may increase their risk of predation and therefore lead to more vigorous defensive displays. Body condition is generally lower later in the winter (Stevenson et al. 2009), which could also influence defensive response, although we found little effect of body condition in our analysis. Alternatively, this trend could reflect heightened aggression associated with breeding activities (e.g., male-male combat). Seasonal increases in aggression during the breeding season have been noted in other taxa as individuals defend territories or nest sites or compete for mates (Sandell and Smith 1997; Garcia and Arroyo 2002; Shepard 2004). We found no support for an interactive effect of sex and DOY although our small sample size would have reduced our ability to detect such an effect. We found relatively little influence of body size although size-specific variation in defensive behaviors has been documented in many snake species (but see Mori and Burghardt 2001) both between juveniles and adults (Shine et al. 2002; Gregory 2008) and among adults (Roth and Johnson 2004). We only examined adult and subadult *D. couperi* in our study, the

smallest of which was 0.95 m SVL. At these relatively large sizes, there may be relatively little advantage to exhibiting size-specific defensive behaviors.

Our study shows that *D. couperi* can exhibit wide variation in defensive behaviors during the late fall through early spring. Our study also found that *D. couperi* primarily exhibited relatively unaggressive responses and that aggressive (i.e., costly) responses were infrequent. However, the covariates we included in this study explained a low to moderate amount of the variation in the presence of particular defensive behaviors. It is therefore unclear which factor(s) are primarily influencing *D. couperi* defensive responses. In an observational field study such as ours, it is difficult to control for potentially confounding effects particularly with relatively small sample sizes. A wide range of factors may influence the defensive response of an animal, including many factors we did not consider in this study such as microhabitat (Main 1987; Cuadrado et al. 2001; Shine et al. 2002) and distance to retreat site (Bulova 1994). In addition, although we found no support for interactive effects among the covariates we considered, small sample sizes may have prevented us from detecting such effects. Finally, our study was not designed to test for an effect of individual predisposition. Nevertheless, our study illustrates the potential value of observational, field-based studies for quantifying the frequency and variability of defensive behaviors in a natural setting and providing a first step towards more controlled studies designed to explicitly test the effects of specific factors on individual defensive behaviors.

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FRANKIE SNOW has studied the natural world of south-central Georgia for nearly 45 y and has worked at South Georgia State College for over 34 y. His biological training was at Georgia Southern University. He has participated in the monitoring of Eastern Indigo Snake populations in south-central Georgia for over two decades. In addition to his ecological research, he has made significant contributions to the regional archaeology and recently was honored with the Don Crabtree Award from the Society for American Archaeology. (Photographed by Dirk Stevenson).



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