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INDIVIDUAL CAPTURE HISTORY AFFECTS SITE USE AND DEFENSIVE BEHAVIOR OF  
FORAGING EASTERN COPPERHEADS AT A RECREATIONAL SITE

BY

JAMES BENJAMIN POSTAL STRATTON

THESIS APPROVED:



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Chair, Advisory Committee



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INDIVIDUAL CAPTURE HISTORY AFFECTS SITE USE AND DEFENSIVE  
BEHAVIOR OF FORAGING EASTERN COPPERHEADS AT A RECREATIONAL  
SITE

BY

JAMES BENJAMIN POSTAL STRATTON

Submitted to the Faculty of the Graduate School of  
Eastern Kentucky University  
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

2023

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## DEDICATION

I dedicate this thesis to Grandpa Jim, Grandma Marion, and Grandma Susan.  
You would have loved hearing about the snakes.

## ACKNOWLEDGEMENTS

This research would not have been possible without the kindness and support of many. I'd like to thank Dr. Stephen Richter for being both my advisor and my mentor over the last two years. During my time in your lab I've become a stronger student, scientist, and communicator, and I'm incredibly grateful I had this opportunity.

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## ABSTRACT

To maximize energy available for foraging or reproduction, optimality theory suggests individuals allocate energy toward defensive behaviors equivalent to risk of predation. In this framework, repeat encounters with humans that do not reduce individual fitness could result in a decreased defensive response toward humans in subsequent encounters. I investigated the role individual experience played in shaping the defensive behaviors and frequency of site use of foraging of eastern copperheads (*Agkistrodon contortrix*) at Koomer Ridge Campground in the Daniel Boone National Forest, Kentucky. Since 2015 this site has been used for ongoing, annual mark-recapture studies of the foraging ecology of copperheads as they predate emerging annual cicadas (*Neotibicen tibicen tibicen*). Using a standardized behavioral trial for vipers, I tested whether copperhead defensive behavior toward humans was influenced by long-term capture history, within-season site-use history, body size, sex, and soil temperature. Model averaging results indicated that intensity of copperhead behavioral response to humans increased with number of years an individual had been recaptured, but no other explanatory variables significantly influenced behavior. The frequency at which an individual foraged at Koomer during the field season was positively, significantly related to the number of years they had been recaptured. These results indicate that copperheads with longer capture histories are coming to the site to forage more frequently and are more willing to defend their foraging opportunities. My study suggests that free-ranging copperheads are able to modulate their foraging and defensive behavior based on previous experience with humans, leading to some individuals becoming more tolerant.



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## Introduction

Interactions with predators can be fatal for prey, so selection has favored the evolution of defensive behaviors (Tuttle and Ryan 1981, Endler 1986). Different defensive behaviors vary in cost, as interacting and engaging with predators may be more costly than fleeing or relying on crypsis (Ydenberg and Dill 1986, Broom and Ruxton 2005). Temporal and spatial variation in predation risk are important factors in shaping individual energy investment in anti-predator behavior (Lima and Bednekoff 1999). Optimality theory and the threat-sensitive predator avoidance hypothesis suggest that behavioral responses to predators are shaped by life history and perceived likelihood of predation (Smith 1978, Helfman 1989, Cooper and Vitt 2002), which can be influenced by various extrinsic factors such as time of day (Lima and Bednekoff 1999), seasonality (Ferreira and Faria 2021), available cover (Klug et al. 2010), and predator species (Endler 1986). Anti-predator behavior is also influenced by individual-level factors such as sex (Clutton-Brock 1991, Shine et al. 2000), body size (Whitaker et al. 2000, Roth and Johnson 2004), body temperature (Brodie III and Russell 1999), temperament (Gibert et al. 2022), or experience (Glaudas 2004). Therefore, defensive behaviors exhibited by an individual in singular encounters are the product of complex interactions between internal and external factors. However, the extent to which past experience shapes current defensive behaviors of wild vertebrates is not well understood, particularly in regard to repeated contact with humans.

Anthropogenic habitat loss and fragmentation will increase interactions between humans and non-human species (Frank and Glikman 2019). Because of human's evolutionary roles as predators, urbanization and increases in human contact exert novel

selective pressures on animal populations, possibly leading to altered behavioral patterns (Wong and Candolin 2015). Among these include shifts in foraging timing and intensity (Gaynor et al. 2018, Payne et al. 2015) and decreases in home range size (O'Donnell and delBarco-Trillo 2020). There is also evidence that increased contact with humans may affect risk assessment and defensive behaviors in vertebrate species (Bateman and Fleming 2014). The optimal risk allocation hypothesis posits that individuals experiencing and surviving frequent contact with potential predators should decrease the severity of defensive responses toward predatory stimuli; otherwise, these individuals would engage in defensive behavior so often that their own fitness would be reduced due to tradeoffs with foraging, reproductive, and other behaviors (Lima and Bednekoff 1999). Decreased energy investment in defensive behavior may occur through habituation to specific predatory stimuli (Glaudas 2004, Rodríguez-Prieto et al. 2010), or as part of generalized risk allocation strategies in predator-dense environments (Fernández-Juricic and Rodríguez-Prieto 2010). Evidence for this hypothesis has been found in urban parks, where European blackbirds (*Turdus merula*) frequently encountering humans had decreased flight initiation distances in response to both humans and novel stimuli relative to birds that rarely encounter humans (Rodríguez-Prieto et al. 2008). Similar results have been generated from studies of free-ranging ungulates, as elk (*Cervus elaphus*) wintering in areas where they were subject to frequent wolf (*Canis lupus*) exposure exhibited lower overall vigilance compared to individuals encountering wolves less often (Creel et al. 2008). Conversely, frequent interactions with potential predators, such as handling during a mark-recapture study, could create negative associations for captured individuals, leading to elevated

defensive response over time (Griffin et al. 2000). In Guam, brown tree snakes (*Boiga irregularis*) trapped at sites where sampling occurred frequently were more likely to strike at researchers relative to snakes trapped in low-intensity sampling areas (Spencer et al. 2015). Interestingly, however, the results did not support their hypothesis that strike propensity was positively associated with individual snakes' within-season or long-term capture history, which the authors proposed as the most plausible explanation for variation in behavior between sites.

Further study of human influences on defensive behavior is generally important in understanding species ecology, but particularly in cases where interactions may negatively impact one or both parties, such as contact between humans and venomous snakes. Historically, humans have often killed large or venomous snakes unnecessarily (Whitaker and Shine 2000, Godley and Moler 2013). Depending on species, venom injected via defensive strikes can be harmful, even fatal to humans. Risks of human mortality from venomous snake encounters, albeit low, coupled with typically negative depictions of serpents in western culture, have skewed public perception to the point where extermination of these species is deemed acceptable (Adams et al. 1994, Burghardt et al. 2009). Despite these misconceptions, defensive striking behavior is typically a last resort for venomous snakes because venom is energetically expensive to produce, and engaging with large predators can exact high fitness costs (McCue 2006, Adams et al. 2020). Instead, there is substantial evidence that snakes' initial response to human approach are characterized by attempts to remain undetected, often through crypsis (Herzog et al. 1989). If detected, venomous snakes exhibit a host of defensive displays and behaviors to deter or avoid predators, including musking, rattling, tail

vibrating, fleeing, or mouth gaping (Greene 1988, Whitaker et al. 2000). Additionally, these behaviors typically occur in a generalized progression; active defensive behaviors are typically preceded by avoidance attempts or passive threat displays intended to discourage predation (Duvall et al. 1985, Greene 1988). Past studies have attempted to assess impacts of human contact on members of family Viperidae (henceforth referred to as viperid) defensive behavior. A laboratory study of western cottonmouths (*Agkistrodon piscivorus*) suggested that frequency of defensive behaviors toward humans is negatively correlated with human contact, implying some form of short-term habituation (Glaudas 2004). However, testing was not conducted in the snake's natural habitat and only examined short-term habituation to one specific, repeated stimulus. Research involving western rattlesnakes (*Crotalus oreganus*) found intrapopulation differences in defensive behavior driven by anthropogenic land-use change. Snakes in more human-disturbed habitats allowed researchers to approach closer before rattling and exhibited a lower likelihood to rattle relative to individuals from low-disturbance habitats (Atkins et al. 2022). Although ecologically relevant, both of the above studies of viperid defensive responses focused on one behavior as opposed to the overall response of the snake to a predatory stimulus.

Defensive behaviors exhibited by venomous snakes and their spatial overlap with humans make certain species ideal to study effects of repeated human contact on defensive behavior. The eastern copperhead (*Agkistrodon contortrix*) is one of two recognized copperhead species, and is one of the most widely distributed and commonly encountered venomous snakes in North America, with its range spanning much of the eastern United States (Ernst and Ernst 2003). In 2021, the two copperhead

species were collectively responsible for most snake envenomations in the United States (52.9%; Gummin et al. 2022). However, these envenomations are not products of copperheads striking more readily than other viperids. Instead, this trend is driven by their wide range and ability to tolerate moderate human disturbance (Novak et al. 2020). When encountering humans, copperheads initially rely on crypsis or fleeing and rarely resort to striking (Gibbons and Dorcas 2002, Glaudas et al. 2005). They also exhibit defensive behaviors, such as tail vibrations, feint strikes, and musking (Adams et al. 2020). However, it is unknown whether repeated encounters with humans over an individual snake's lifespan will alter behavioral responses toward humans. No previous studies on copperheads or other North American pit vipers have investigated the effects of human contact on defensive behaviors through the lens of risk allocation and individual experience.

The primary objective of my research was to examine possible effects of repeated captures and human encounters on defensive behaviors of free-ranging eastern copperheads. The study was conducted at Koomer Ridge Campground (KRC) on the Daniel Boone National Forest, Kentucky, which is a recreational site of relatively high copperhead activity during summer months, as the seasonal emergence of annual cicadas (*Neotibicen tibicen tibicen*) attracts many foraging individuals. A mark-recapture study was initiated at KRC in 2015, and our lab has been studying the foraging ecology of copperheads since 2017 (Hendricks 2019, Sockman 2020, Gull 2021). Most copperheads have been implanted with passive integrated transponder (PIT) tags and have known capture histories. Within this extensively studied subpopulation I aim to determine whether individual copperheads' behavioral response

to humans was influenced and explained by their capture and sampling history and the frequency at which they foraged at our study site during our sampling period. Using a four-stage behavioral trial with hierarchical scoring that simulates *in situ* encounters between humans and vipers, I tested for variation in behavioral responses among copperheads with varying levels of experience with humans. I hypothesized that individuals with longer capture histories and more frequent site use would allocate less energy into defensive behaviors toward humans and therefore respond less severely than, and score lower in behavioral trial stages relative to, snakes with few captures and low frequency of site use.

A secondary objective of this study was to investigate the relationship between copperhead capture history and frequency of site use for foraging. Decisions made by animals while foraging are informed by both direct sensory perception and the experiences of that individual while foraging previously (Shettleworth 2001, Fagan et al. 2013). It follows that individuals likely select or avoid particular patches or habitats based on past foraging success and encounters with predators (Bracis et al. 2018). For copperheads, the emergence of cicadas within a frequently used recreational site creates a unique patch that is both prey and predator dense. However, although humans may be perceived as predators, humans at KRC do not depredate copperheads. Therefore, copperheads who choose to forage at KRC could receive the benefit of foraging in a prey-dense patch without incurring the typical associated costs of predation. I hypothesized that copperheads with longer capture histories and more experience with humans will forage at KRC more frequently than individuals with shorter capture histories and less human experience.

Finally, I present general descriptive statistics of copperhead defensive behavior while foraging to compare with other studies of free-ranging snakes. Results of this study will provide important ecological information regarding the ability of wild snakes to modulate defensive and foraging behavior based on previous experience. Additionally, it will provide useful information regarding viperid behavior to recreational managers tasked with balancing conservation and public safety.

## Methods

### Study Site

Behavioral trials were conducted on eastern copperheads at Koomer Ridge Campground, a recreational site within the Cumberland Ranger District of the Daniel Boone National Forest (DBNF), in Wolfe County, Kentucky, USA. Specifically, sampling occurred at the primitive camping area, which has been used extensively over the last five years to study foraging ecology and predator-prey dynamics of eastern copperheads as they become seasonally crepuscular to forage on cicadas that emerge at the site (Hendricks 2019, Sockman 2020). The site is ca. 0.1 ha and features a mowed understory with scattered groves of trees, walking paths, a pit toilet, and several gravel pads designated for camping. Within the site, vegetation is primarily composed of red maple (*Acer rubrum*), white ash (*Fraxinus americana*), white pine (*Pinus strobus*), tulip tree (*Liriodendron tulipifera*), and shagbark hickory (*Carya ovata*). The area surrounding the site is composed of forested ridges and gorges characteristic of the central Appalachians, and is dominated by oaks (*Quercus spp.*), red maple, and pines (*Pinus spp.*). The climate was characterized as temperate continental with high humidity (Kalisz and Powell 2003).

### Experimental Design

#### *Visual Surveys for Snakes*

All sampling occurred between May and August 2022. This timeframe was chosen based on observations of copperhead emergence patterns from previous research (Hendricks 2019, Sockman 2020). Sampling was conducted between 2045 and 0100 to



account for the nocturnal nature of copperhead foraging and cicada emergence. Copperheads were located via visual surveys of the site, wherein both the perimeter and interior were searched simultaneously, allowing for documentation of new individuals entering the site, as well as those already present in the interior. The perimeter, defined as the margin between the primitive site and forest plus a 3-m buffer zone, was surveyed using a circular transect. The interior of the site was searched using a methodical zig-zag pattern of visual surveys, which ensured the entirety of the site was sampled. High-powered headlamps (Nitecore MH25, Nitecore) were used to search the ground, trees, and other foliage for snakes and cicadas while conducting transects. All sides of tree trunks and all branches up to a height of 5 m were surveyed to account for copperhead seasonal arboreal behavior. Upon location of a snake on the ground, the behavioral trial began immediately to reduce potential biasing of behavioral results. All copperheads were treated as untagged and untested for the behavioral trial until their identity could be confirmed by scanning their body for presence of a passive integrated transponder (PIT) tag using a Biomark HPR Plus Handheld PIT Tag Reader (Biomark, Boise, ID). Individuals that did not require capture due to previously being sampled were released immediately, and their PIT tag code was recorded. A minimum of three survey rounds were conducted each sampling night, and an additional round was added any time a new individual (copperhead or cicada) was identified. Between rounds, researchers turned off their lights and waited silently for a period of 5 min as to not influence any copperheads that may have been approaching the site. Date, time, and all environmental data were recorded prior to the start of each round. Ambient temperature (°C) and relative humidity were measured using a Kestrel 3000 Windmeter (Kestrel

Meters Minneapolis, MN), and soil temperature (°C) was determined using a soil probe thermometer (Agratronix 4-in-1 Soil Tester).

### *Behavioral Trial*

Upon locating a copperhead, the snake's initial body position and location was documented. Initial body position was defined as the original position of the snake's body when located and has two possible states: extended or coiled. Location was determined by the nearest numbered tree tag (Sockman 2020). These data were recorded from a distance of 3 m to reduce the likelihood of biasing behavior. To quantitatively assess copperhead defensive response, we used a four-stage trial that is common practice for categorizing and scoring the behavior of vipers (Gibbons and Dorcas 2002, Adams et al. 2020). All trials were filmed with a night-vision camera (Sony Handycam AX53, model: FDRAX3/B) for post-hoc analysis. At each stage defensive responses were recorded and scored based on the most severe behavior exhibited. The trial involved four stages (1. Location, 2. Approach, 3. Accidental contact, and 4. Intentional contact), each representing an increase in predation risk to the snake. Each stage lasted 10 sec and continued until completion or the snake fled. Two pairs of snake tongs (Gentle Giant, Midwest Tongs, [www.tongs.com](http://www.tongs.com)), each with a hiking boot or gardening glove on the end, was used to mimic a human foot or hand, respectively (Roth and Johnson. 2004, Adams et al. 2020). The shaft of the tongs was covered with a pool noodle and pant leg to provide form to the mock limbs.

In Stage 1, researchers located a copperhead and approached the anterior end to 3 m. In Stage 2, the mock leg and boot was placed adjacent to the copperhead (10-15

cm), while researchers maintained a distance of 1.5 m. Stage 3 involved gently placing the boot on top of the snake, mimicking a hiker stepping on the animal. Stage 4 represented the highest predation risk to the snake, simulated by a human attempting to pick it up. The lever-action mechanism in the tongs was used to imitate thumb movement of the mock hand, allowing a grasping motion to be achieved. The mock hand was used to pick up the snake from the central section of its body. Defensive behavior exhibited in each stage was recorded and scored according to a 0-3 scale (Table 1) (Gibbons and Dorcas 2002, Adams et al. 2020). Avoidance behavior was subset into two categories: flight and movement away from stimulus. Movement away from stimulus was defined as a change in the direction of copperhead locomotion away from the predatory stimulus that did not result in increased movement speed. Flight was classified as a change in direction of copperhead movement away from the human stimulus accompanied by a rapid increase in movement speed, which resulted in the end of the behavioral trial and represented the snake giving up on a potential foraging opportunity. In the context of this study, it is important to note that flight, while energetically taxing, represents an unwillingness to defend a potential foraging opportunity. Therefore, it is scored lower than active or passive defensive behavior.

Table 1. Scoring criteria for quantitatively assessing the defensive response of eastern copperheads (*Agkistrodon contortrix*) at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky in a four-stage trial simulating an escalating level of predation via human approach. Scores for each individual are based on the most extreme category of behavior exhibited in each stage of the trial.

Behavioral Category	No Response	Avoidance	Passive Defensive	Active Defensive
Score	0	1	2	3
Behavior Exhibited	No visible reaction	Flight, movement away from stimulus	Tail vibrations, musking, recoiling	Striking

All copperheads were scanned for PIT tags immediately following the conclusion of the trial and their ID, if tagged, was recorded. All trials were assumed to be an individual's first unless the presence of unique marking could be identified (see below). After scanning, snakes were captured with snake tongs and placed in a bucket lined with a 26.5 L snake bag and held overnight in a temperature-controlled building. Copperhead measurement and application of unique markings occurred the following morning. Latex gloves were worn during measurement and fresh gloves were used for each individual. Mass (g) was recorded while snakes were bagged, and the known mass of the bag was subtracted from that value. Individuals were then released into a large plastic tub and coaxed into a polycarbonate restraining tube (Midwest Tongs, [www.tongs.com](http://www.tongs.com)) for measurement and tagging. Snout-vent length (SVL) (cm) and total length (cm) were measured with a meter stick once the snake was immobilized and then gently extended within the tube. Sex was determined by the depth of a lubricated probe (Midwest Tongs, [www.tongs.com](http://www.tongs.com)) inserted posteriorly into the cloaca. Individuals in

which the probe penetrated less than 3-4 scale rows were documented as a female, greater depth indicated a male (Laszlo 1975). For snakes tagged in previous seasons, the total number of years they have been documented at the site was recorded. Alcohol swabs were used to sterilize the PIT tag injection site on untagged individuals. The tag was inserted beneath the skin on the lateral side of posterior section of the body using a veterinary 12-gauge N125 Injector Needle (Biomark) and MK10 Implanter (Biomark) (Gibbons and Andrew 2004). The injector was angled so the tag laid flat against the muscle wall of the body. Surgical glue was applied to the site post-injection to reduce the likelihood of tag loss and infection. Copperheads were then given a unique ultraviolet (UV) paint mark applied onto the costal scales, roughly dorsal to the cloaca. UV marks allowed researchers to visually identify previously sampled individuals with UV flashlights. Snakes were released at their capture site once paint and glued had dried.

### *Statistical Analyses*

All analyses were conducted in R (R 4.2.3). A Shapiro-Wilk test was used to assess normality of all response and predictor variables, and a chi-square test was used to check for fit of determined distributions (“pchisq”, stats package, R). A matrix using Spearman’s correlation with a cutoff of 0.7 was used to determine collinearity between model predictor variables due to the presence of non-Gaussian data. Candidate model sets were created from combinations of four *a priori* parameters: two variables known to influence squamate behavior (body size and temperature) and two prior experience variables hypothesized to be associated with copperhead behavior at our study site

(Nights Detected at Koomer in 2022, Total Number of Years Recaptured). Given that some of the nights an individual was documented foraging at KRC occurred after their first trial, I could not directly attribute defensive response to forage frequency in 2022. However, this variable may still help explain copperhead behavior in relation to human contact, so it was retained in models. Candidate model sets consisted of all variables individually and all possible combinations of two and three variables. Nights Detected and Years Recaptured variables were determined to be collinear resulting in them not being included together within individual candidate models ( $r = 0.745$ ), though both were retained in separate models due to their role in hypotheses. SVL and total length of copperheads were highly correlated with mass ( $r = 0.93, 0.93$ ) and each other ( $r = 0.96$ ). Mass was included in the models because it could be recorded more accurately. Ambient temperature and soil temperature were also found to be collinear ( $r = 0.83$ ). Soil temperature was chosen for use in models as it is likely a more accurate reflection of the thermal conditions a copperhead is experiencing than temperature taken at breast height.

Adjusted Akaike's Information Criterion ( $AIC_C$ ) was used to compare models within a candidate set (Johnson and Omland 2004), and a variance inflation factor test with a cutoff of 2 was used to check for multicollinearity. The initiation (stage) and intensity (score) of snake behavioral responses in all four stages were determined to be binomial and Poisson distributed, respectively, based on the above methodology. Conditional model averaging ("MuMIn" package, R) was used as model selection did not produce a heavily weighted top model ( $\geq 0.9$   $AIC_C$  weight) (Symonds and Moussalli 2011). A total of 13 candidate models were used for the model selection

process, and those with  $\Delta AIC_c$  values  $\leq 10$  and  $AIC_C$  weights  $\geq 0.01$  were included in model averaging (Lukacs et al. 2010). Model averaging results are interpreted at the 85% confidence level, as averaging the 95% level often overlooks statistical significance due to the conservatism of selection parameters (Burnham and Anderson 2002, Arnold 2010). Hurdle models were used to assess behavior in Stages 1-3 to account for excess zeroes and to differentiate between variables affecting likelihood to respond and those affecting severity of response (“pscl” package, R) (Cragg 1971). Behavioral responses to Stage 4 did not produce any zero values and were analyzed using a generalized linear model. The total score for each snake was summed across all four stages and log transformed to fit a normal distribution, as determined by  $AIC_C$ . Total scores were analyzed using a linear model. To eliminate the potential effect of within-season habituation to researchers, only data from each snakes’ first behavioral sampling were included in models.

Several other analyses were conducted to address additional aspects of copperhead behavior. A generalized linear model with a negative binomial distribution and 95% CI was used to assess whether the frequency at which an individual foraged at the site was influenced by the number of years that individual had been recaptured and documented there. A Poisson-distributed GLM with 95% CI was used to test for copperheads’ latency to flee human approach based on the relationship between number of visible behaviors exhibited prior to fleeing and capture history. Among snakes sampled more than once, sign tests were used to determine if there was a reduction in per-stage defensive score of subsequent trials. Sign tests were only performed between first and second trial, as too few snakes were sampled three times to warrant analysis. A

Fisher's exact test was used to compare initial reactivity to human approach between experienced and inexperienced snakes. "Reactivity" was determined by the number of snakes that reacted in the trial before any physical contact. Experienced snakes are defined as those who have been captured for at least two years, whereas inexperienced individuals had not been captured previously or were only captured once. Two years captured was chosen as the cutoff point because it required individuals to return to KRC after initial capture, as some snakes were captured once but never returned in subsequent summers. A Mann-Whitney-U test was used to compare stage of flight between experienced and inexperienced snakes that fled during the trial. Krishnamoorthy and Lee's modified signed-likelihood ratio test (R package "cvequality") was used to compare coefficients of variance between inexperienced and experienced snake scores (Krishnamoorthy and Lee 2014, Marwick and Krishnamoorthy 2019). Additionally, general descriptive statistics of copperhead behavior were generated to allow comparison with previous studies.



## Results

All data were collected at KRC between May and August 2022, for a total of 30 sampling nights with at least one copperhead present. Twenty-five individual copperheads were sampled in a trial at least once, for a total of 39 trials of defensive behavior. Sampled individuals were fairly evenly split between experienced ( $n = 13$ ) and inexperienced ( $n = 12$ ) snakes. Eighty percent of sampled snakes did not exhibit any visible defensive behavior until Stage 3 of the trial. Movement away from stimulus (40%) and flight (50%) were the most frequently exhibited behaviors in Stages 3 and 4, respectively. The behaviors of flight, tail vibration, and striking were not displayed by any individuals until Stage 3. The proportion of snakes that vibrated their tails increased between Stage 3 (4%) and 4 (27%), while the frequency of strikes remained constant (4% and 4.5%, respectively) (Figure 1).

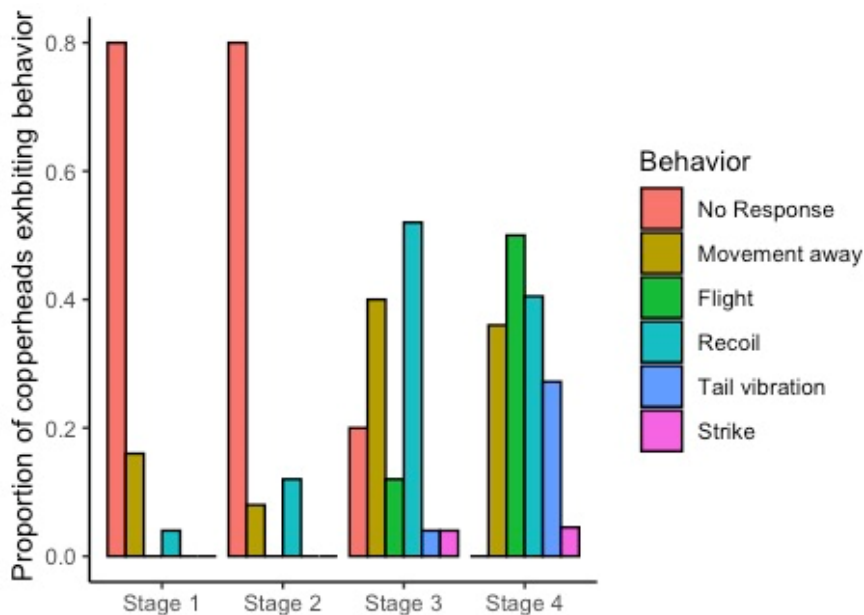


Figure 1. Proportion of sampled eastern copperheads (*Agkistrodon contortrix*) exhibiting each defensive behavior across a four-stage trial ( $n_{1,2,3} = 25$ ,  $n_4 = 22$ ). Copperheads are capable of exhibiting multiple behaviors per stage. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

## Experienced vs. Inexperienced Copperheads

Inexperienced snakes responded with visible behavior before physical contact with the predatory stimulus more frequently (6/12) than experienced snakes (3/13) (Figure 2), although, this difference was not statistically significant ( $p = 0.2262$ , odds ratio = 3.168, 95% CI = 0.46006 – 27.51499)

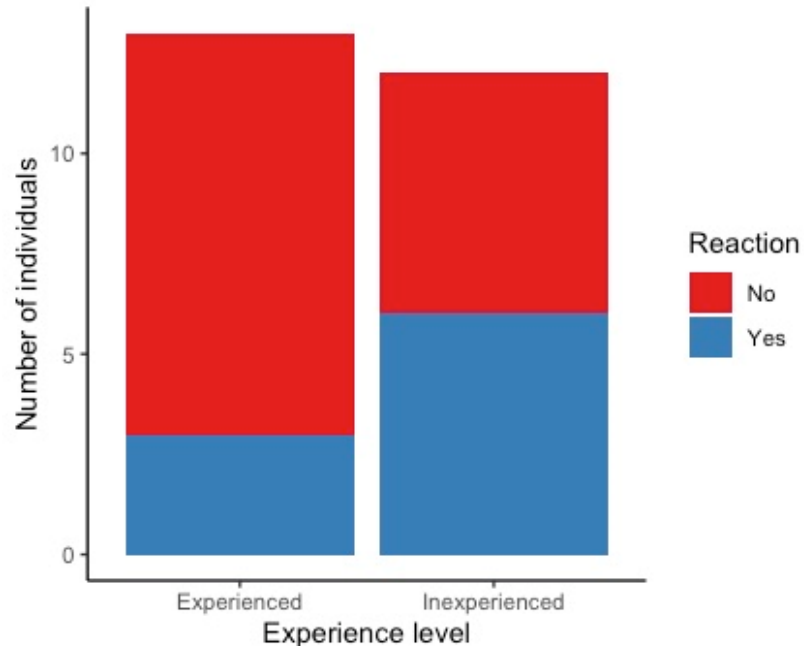


Figure 2. Number of experienced ( $n = 13$ ) and inexperienced ( $n = 12$ ) eastern copperheads (*Agkistrodon contortrix*) exhibiting visible defensive behavior before physical contact with the predatory stimulus in Stage 3 of the behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

A total of 14 individuals fled from the predatory stimulus during the trial. Mean rank of flight stage did not differ significantly between experienced (3.875) and inexperienced snakes (3.667) ( $W = 29$ ,  $p = 0.2074$ ) (Figure 3). Experienced snakes were no more uniform in their flight response than inexperienced snakes ( $CV_{\text{Experienced}} = 9.12$ ,  $CV_{\text{Inexperienced}} = 14.08$ ,  $MSLRT = 0.9063$ ,  $p = 0.341$ ) (Figure 3).

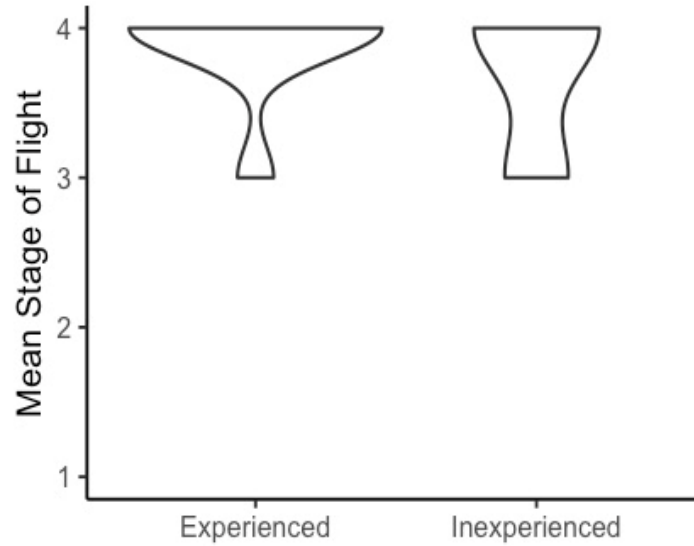


Figure 3. Box and violin plots depicting mean stage of flight for experienced ( $n = 8$ ) and inexperienced ( $n = 6$ ) eastern copperheads (*Agkistrodon contortrix*) that fled during a behavioral trial at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

### Latency to Flee

The number of visible behaviors exhibited before flight was used to determine latency to flee. There was a positive relationship between the number of behaviors exhibited before flight occurred and the number of years an individual had been recaptured, although this relationship was not significant (Likelihood Ratio  $\chi^2 = 2.2069$ ,  $df = 1$ ,  $p = 0.1374$ ) (Figure 4).

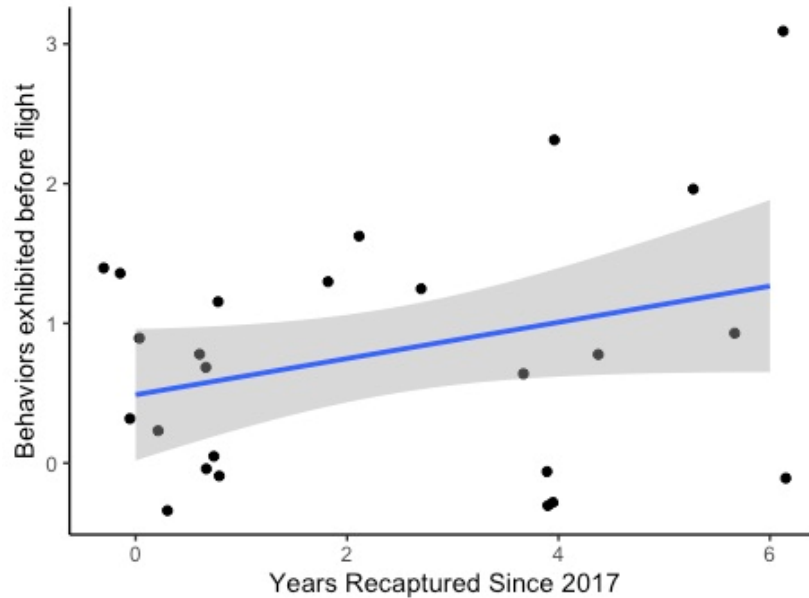


Figure 4. Poisson-distributed regression with number of years recaptured as an explanatory variable for the number of visible behaviors exhibited by an individual eastern copperhead (*Agkistrodon contortrix*) before fleeing a predatory stimulus across the entirety of the four-stage trial (n = 25). All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

### Repeat Trials for Resampled Copperheads

I conducted at least two behavioral trials on ten of the 25 copperheads sampled. There was no difference detected in sign symmetry between resampled copperheads in Stage 1 of the trials (n = 10, plus = 2, tie = 8, minus = 0, p-value = 0.5, z = -1.414). In this stage only two individuals exhibited an increase in the severity of defensive behavior between sampling occasions, while the remaining eight snakes displayed behavior consistent with that of their first trial (Figure 5). Behavior in Stage 2 did not differ significantly between Trials 1 and 2 based on sign symmetry (n = 10, 3+, 2-, 5 tie, p = 1.0, z = -0.447) (Figure 6).

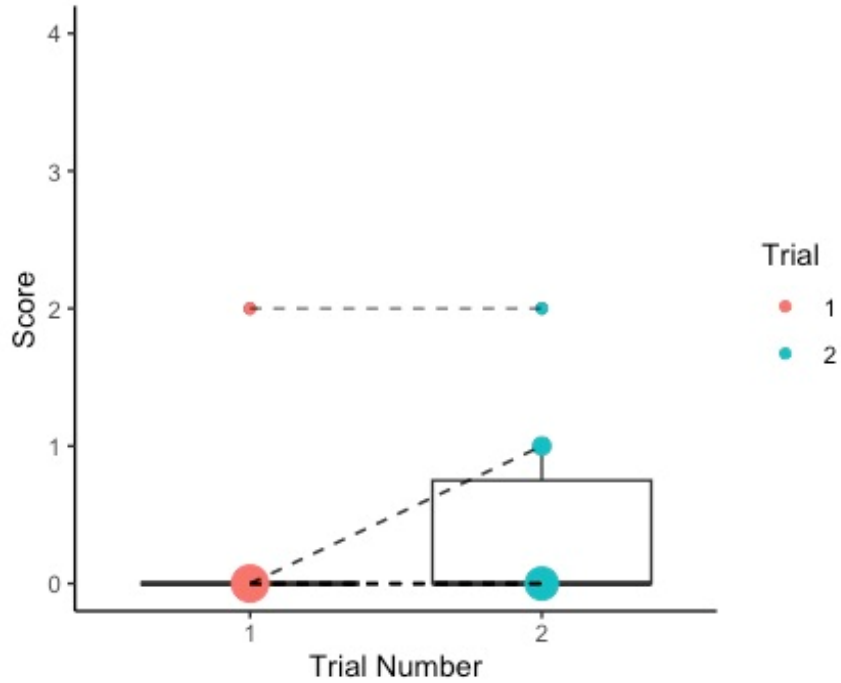


Figure 5. Paired scores for n = 10 eastern copperheads (*Agkistrodon contortrix*) during Stage 1 of the first and second behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky. Lines indicate pairing between an individual's scores. Due to the discrete nature of score data, points of varying sizes are used to represent the number of individuals at each value.

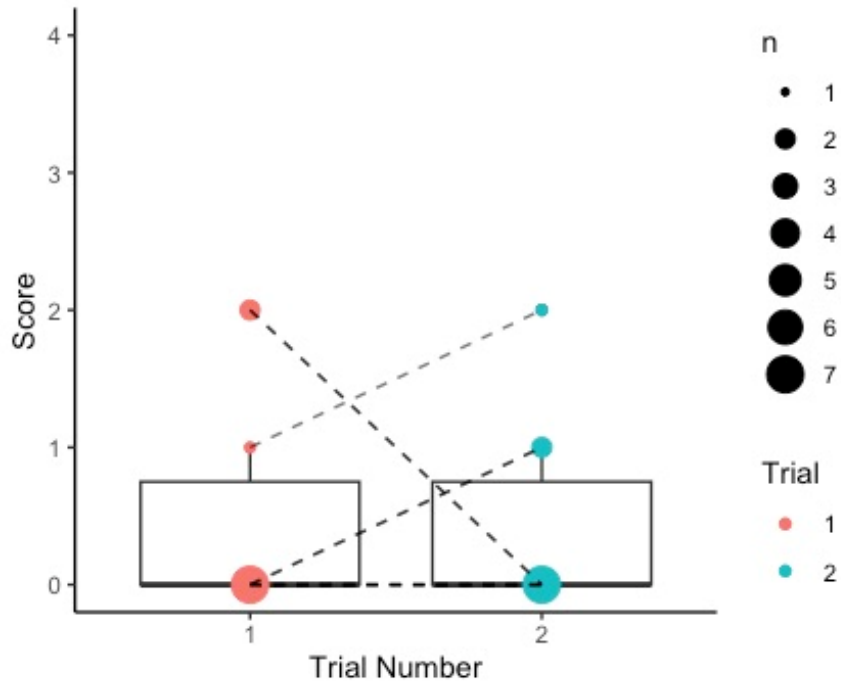


Figure 6. Paired scores for n = 10 eastern copperheads (*Agkistrodon contortrix*) during Stage 2 of the first and second behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky. Lines indicate pairing between an individual's scores. Due to the discrete nature of score data, points of varying sizes are used to represent the number of individuals at each value.

Results of the exact sign test failed to reject the null hypothesis of sign symmetry for resampled copperheads in Stage 3, scores of this stage did not significantly differ between trials ( $n = 10$ , 3+, 3-, 4 tie,  $p = 1.0$ ,  $z = 0$ ) (Figure 7).

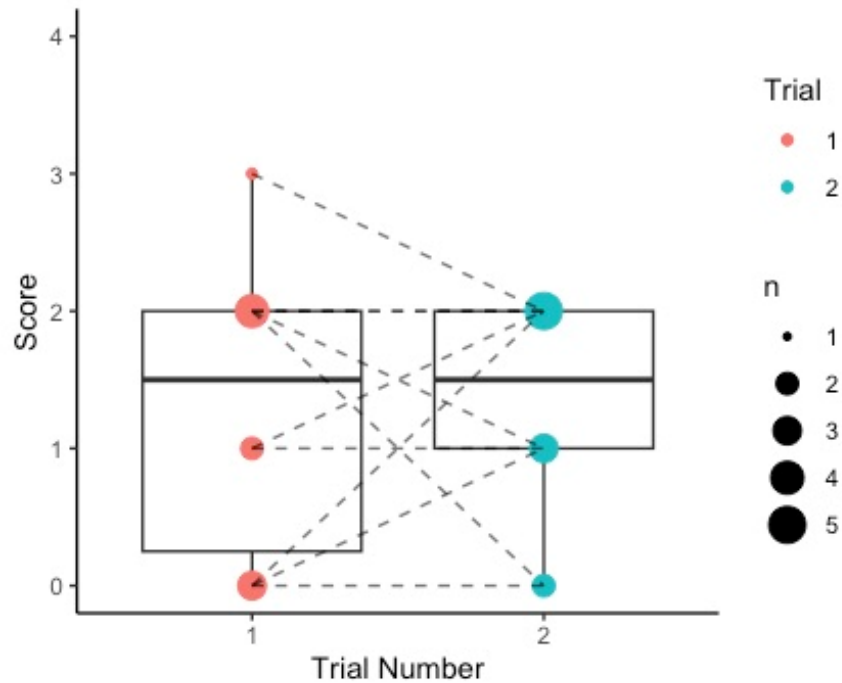


Figure 7. Paired scores for  $n = 10$  eastern copperheads (*Agkistrodon contortrix*) during Stage 3 of the first and second behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky. Lines indicate pairing between an individual's scores. Due to the discrete nature of score data, points of varying sizes are used to represent the number of individuals at each value.

Mean behavioral score in the second administration of Stage 4 was found to be higher than that of the first, though this difference was insignificant based on results from two-tailed exact sign test ( $n = 10$ , 6+, 1-, 6 tie,  $z = -1.889$ ,  $p = 0.125$ ) (Figure 8).

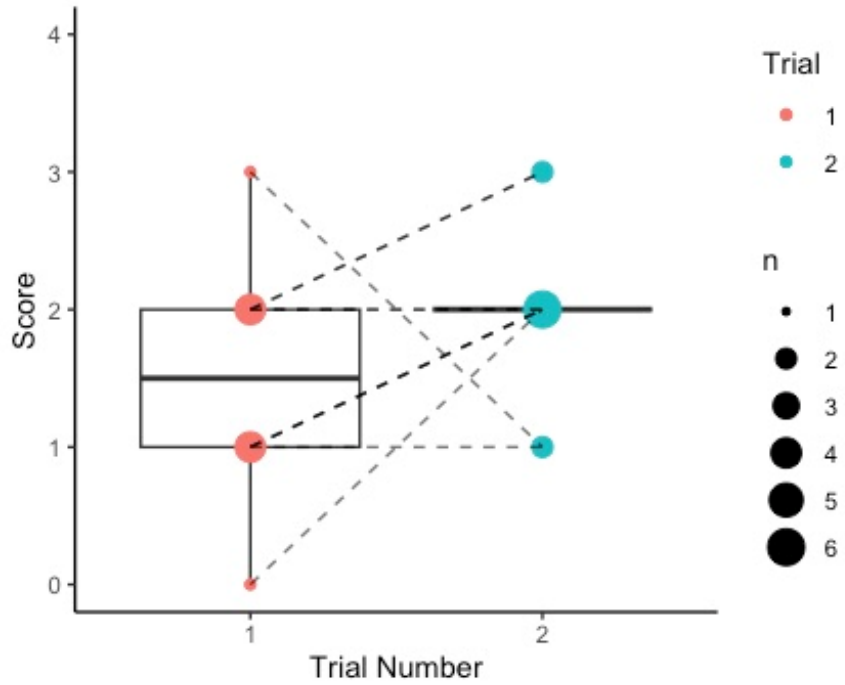


Figure 8. Paired scores for  $n = 10$  eastern copperheads (*Agkistrodon contortrix*) during Stage 4 of the first and second behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky. Lines indicate pairing between an individual's scores. Due to the discrete nature of score data, points of varying sizes are used to represent the number of individuals at each value.

## Site Visitation Analysis

The number of years an individual had been recaptured was significantly, positively associated with the number of nights an individual visited the site in 2022 (Likelihood Ratio  $\chi^2 = 18.169$ ,  $df = 1$ ,  $p < 0.001$ ) (Figure 9).

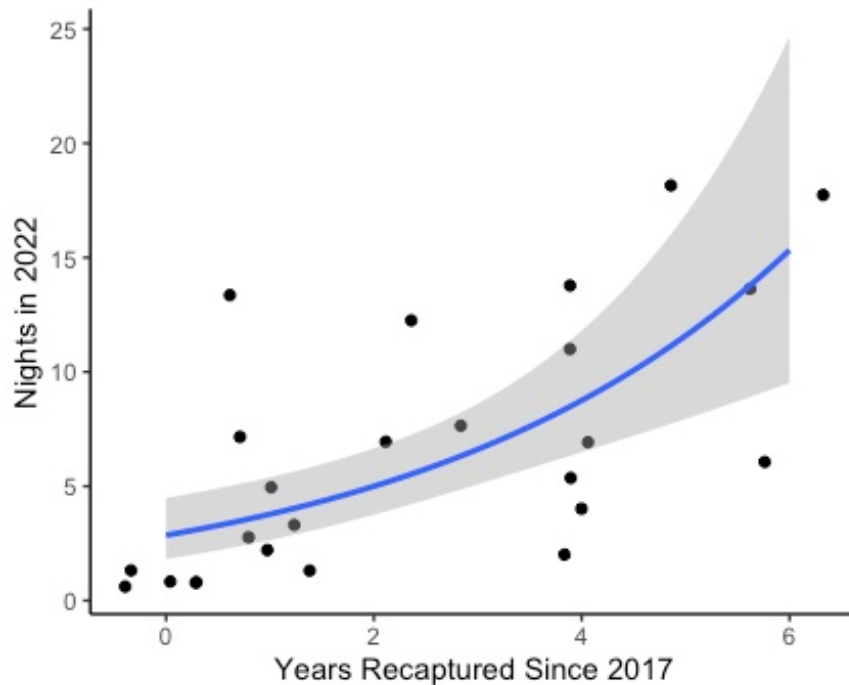


Figure 9. Negative binomial regression with 95% CI between the number of years an individual eastern copperhead (*Agkistrodon contortrix*) had been captured and the number of nights they were documented foraging at the site in 2022. All trials and captures were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

## Copperhead Behavior Models

### *Behavior Analysis by Stage*

The null model produced the lowest  $AIC_C$  values for Stage 1 behavioral scores. The best supported model containing an *a priori* parameter was the effect of Nights Detected which accounted for 0.35 of  $AIC_C$  weight (Table 2). Based on model-



averaging, none of the four predictor variables had a significant impact on copperheads' likelihood to respond or severity of response (Table 3) (Figure 10).

Table 2. Candidate set of hurdle models used to explain eastern copperhead (*Agkistrodon contortrix*) behavioral scores in Stage 1 of the behavioral trial (count distribution = Poisson, zero distribution = binomial). Models with  $\Delta AICc \leq 10$  were used for model averaging. Full and null models were included in analysis but excluded from table. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Model components</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>Wt.</b>	<b>LL</b>
Nights	4	31.49	0.11	0.35	-10.75
Years	4	34.2	2.82	0.09	-12.1
Soil.temp	4	34.66	3.28	0.07	-12.33
Mass	4	36.32	4.94	0.03	-13.16
Mass+Nights	6	36.48	5.1	0.03	-9.91
Soil.temp+Nights	6	37.21	5.83	0.02	-10.27
Mass+Soil.temp	6	38.15	6.77	0.01	-10.74
Soil.temp+Years	6	39.01	7.63	0.01	-11.17
Mass+Years	6	40.26	8.88	0	-11.8
Mass+Soil.temp+Nights	8	43	11.62	0	-9
Mass+Soil.temp+Years	8	46.41	15.03	0	-10.71

Table 3. Model-averaged beta estimates, unconditional SE, and 85% CI for explanatory variables used in hurdle models assessing the initiation and severity of eastern copperheads' (*Agkistrodon contortrix*) defensive response in Stage 1 of the behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Predictor</b>	<b>Model-averaged estimate</b>	<b>UnSE</b>	<b>85% confidence interval</b>	
			<b>Lower</b>	<b>Higher</b>
<b>Zero</b>				
Mass	0.009364	0.010651	-0.005968	0.024695
Nights	-0.242647	0.189827	-0.515909	0.030615
Years	-0.052782	0.273909	-0.447082	0.341518
Soil temp.	0.594467	0.492074	-0.113889	1.302823
<b>Count</b>				
Mass	-0.067730	0.065467	-0.160067	0.026512
Nights	3.801770	110.977684	-155.9541	163.5576
Years	2.539560	417.465473	-598.4151	603.4942
Soil temp.	1.906330	2.949157	-2.339074	6.151734

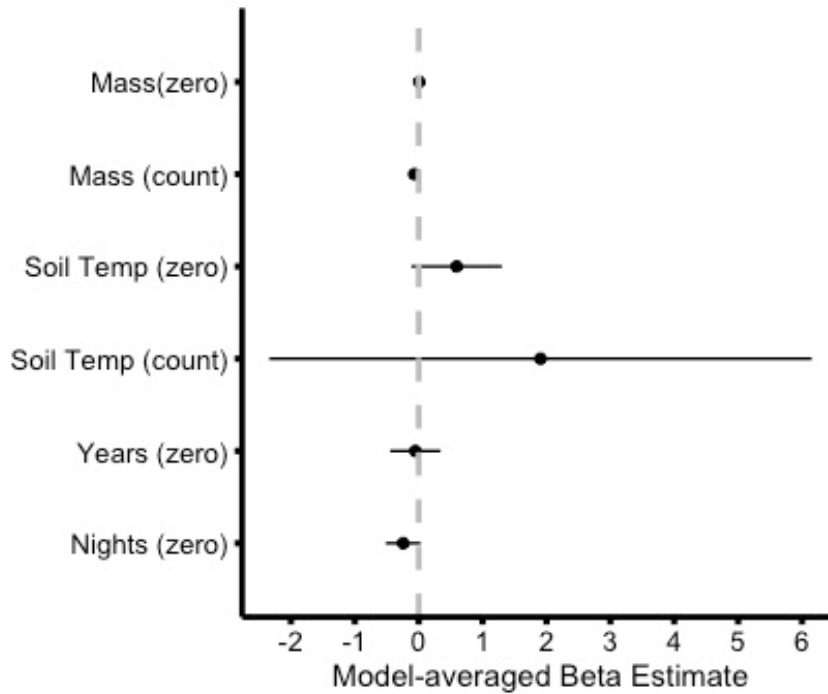


Figure 10. Model averaged beta estimates for four parameters used in hurdle models to explain initiation (zero) and intensity (count) of eastern copperhead (*Agkistrodon contortrix*) defensive behavior in Stage 1 of the behavioral trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

The null model produced the lowest  $AIC_C$  score in Stage 2, the next best model containing soil temperature accounted for only 0.1 of total weight (Table 4). Based on model-averaged estimates, none of the four predictor variables were significantly associated with initiation of defensive behavior or magnitude of behavioral score (Table 5, Figure 11).

Table 4. Candidate set of hurdle models used to explain eastern copperhead (*Agkistrodon contortrix*) behavioral scores in Stage 2 of the behavioral trial (count distribution = Poisson, zero distribution = binomial). Models with  $\Delta AICc \leq 10$  were used for model averaging. Full and null models were included in analysis but excluded from table. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Model components</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>Wt.</b>	<b>LL</b>
Soil.temp	4	43.01	3.87	0.1	-16.5
Mass	4	43.82	4.68	0.07	-16.91
Nights	4	43.93	4.8	0.06	-16.97
Years	4	44.23	5.1	0.05	-17.12
Soil.temp+Nights	6	48.05	8.92	0.01	-15.69
Mass+Soil.temp	6	49.04	9.9	0	-16.19
Soil.temp+Years	6	49.46	10.33	0	-16.4
Mass+Years	6	49.52	10.39	0	-16.43
Mass+Nights	6	50.04	10.9	0	-16.69
Mass+Soil.temp+Nights	8	55.94	16.81	0	-15.47
Mass+Soil.temp+Years	8	56.18	17.05	0	-15.59

Table 5. Model-averaged beta estimates with unconditional standard error (UnSE) and 85% confidence intervals for explanatory variables included in hurdle models assessing initiation and severity of eastern copperheads' (*Agkistrodon contortrix*) defensive behavior in Stage 2 of the Trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Predictor</b>	<b>Model-averaged estimate</b>	<b>UnSE</b>	<b>85% confidence interval</b>	
			<b>Lower</b>	<b>Higher</b>
<b>Zero</b>				
Mass	-0.004360	0.008433	-0.016499	0.007779
Nights	-0.078439	0.106993	-0.232458	0.075581
Years	0.106236	0.241967	-0.242082	0.454555
Soil temp.	-0.071832	0.384617	-0.625500	0.481836
<b>Count</b>				
Mass	0.015881	0.024872	-0.019922	0.051684
Nights	0.011612	0.357069	-0.502400	0.525624
Years	-0.120898	0.312718	-0.571065	0.329269
Soil temp.	-0.525077	0.585800	-1.368353	0.318200

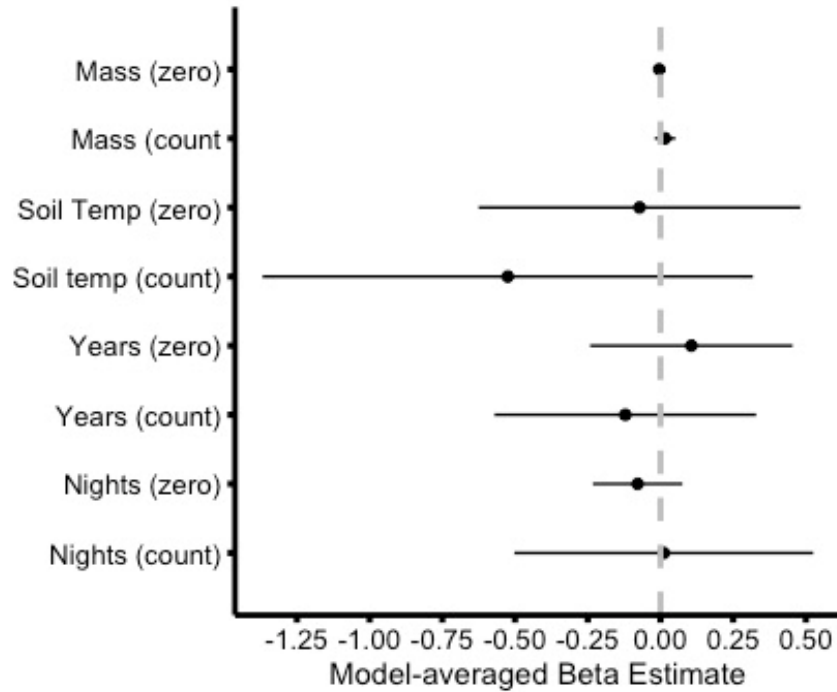


Figure 11. Model averaged beta estimates for hurdle model parameters used to explain initiation (zero) and intensity (count) of eastern copperhead (*Agkistrodon contortrix*) defensive behavior in Stage 2 of the behavioral trial at Koomer Ridge Campground. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

Soil temperature best explained copperhead behavior in Stage 3 ( $AIC_C$  wt. = 0.26) (Table 6). Based on model-averaging, soil temperature significantly and positively influenced initiation of defensive behavior but did not significantly affect severity of behavior (Table 7) (Figure 12).

Table 6. Candidate set of hurdle models used to explain eastern copperhead (*Agkistrodon contortrix*) behavioral scores in Stage 3 of the behavioral trial (count distribution = Poisson, zero distribution = binomial). Models with  $\Delta AICc \leq 10$  were used for model averaging. Full and null models were included in analysis but excluded from table. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Model components</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>Wt.</b>	<b>LL</b>
Soil.temp	4	70.93	1.47	0.26	-30.47
Nights	4	73.63	4.16	0.07	-31.81
Mass	4	74.05	4.59	0.05	-32.03
Years	4	74.77	5.3	0.04	-32.39
Soil.temp+Nights	6	76.38	6.92	0.02	-29.86
Mass+Soil.temp	6	76.42	6.96	0.02	-29.88
Soil.temp+Years	6	77.21	7.74	0.01	-30.27
Mass+Nights	6	79.87	10.4	0	-31.6
Mass+Years	6	80.65	11.19	0	-31.99
Mass+Soil.temp+Nights	8	84.08	14.61	0	-29.54
Mass+Soil.temp+Years	8	84.61	15.14	0	-29.8

Table 7. Model-averaged beta estimates with unconditional standard error (UnSE) and 85% confidence intervals for explanatory variables included in hurdle models assessing initiation and severity of eastern copperheads' defensive behavior in Stage 3 of the Trial. Bold font indicates variables found to be significant. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Predictor</b>	<b>Model-averaged estimate</b>	<b>UnSE</b>	<b>85% confidence interval</b>	
			<b>Lower</b>	<b>Higher</b>
<b>Zero</b>				
Mass	0.002316	0.009172	-0.010887	0.015518
Nights	-0.035445	0.092888	-0.169159	0.098269
Years	0.094497	0.26658	-0.289253	0.478246
<b>Soil temp.</b>	<b>0.894911</b>	<b>0.514352</b>	<b>0.154485</b>	<b>1.635336</b>
<b>Count</b>				
Mass	0.003994	0.004315	-0.002217	0.0102065
Nights	0.046687	0.043187	-0.015481	0.1088552
Years	0.032448	0.124343	-0.146547	0.2114430
Soil temp.	0.041972	0.207247	-0.256366	0.3403107

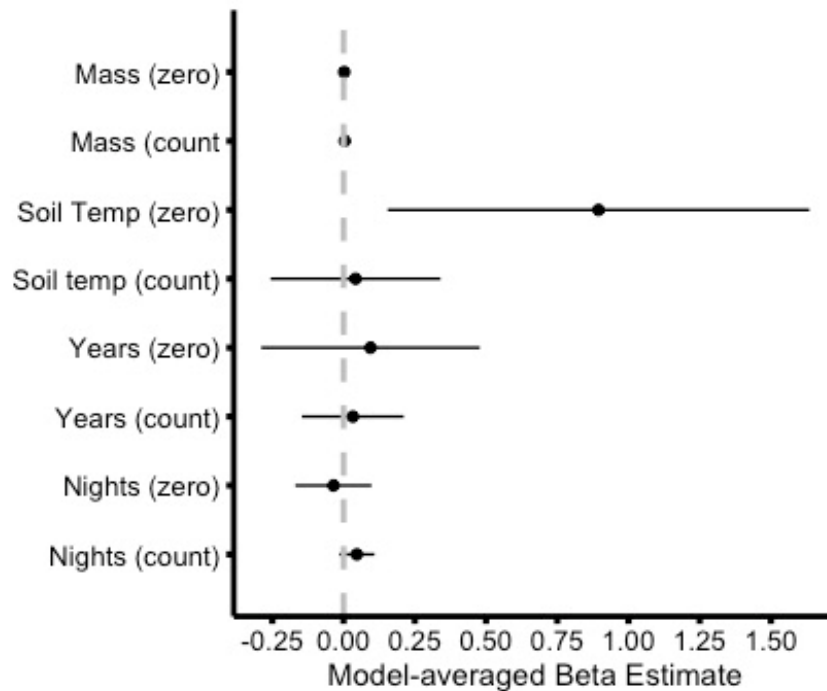


Figure 12. Model averaged beta estimates for parameters used in hurdle models explaining the initiation (zero) and intensity (count) of eastern copperhead (*Agkistrodon contortrix*) defensive behavior in Stage 3 of the behavioral trial at Koomer Ridge Campground.

Three individuals fled during Stage 3, yielding a sample size of  $n = 22$  for Stage 4 analyses. Behavior in Stage 4 was best explained by the null model ( $AIC_C$  wt. = 0.34), followed by model containing the effects of Nights Detected ( $AIC_C$  wt. = 0.15) (Table 8). None of the four predictor variables were significantly associated with the severity of defensive behavior (Table 9) (Figure 13).

Table 8. Candidate set of hurdle models used to explain eastern copperhead (*Agkistrodon contortrix*) behavioral scores in Stage 4 of the behavioral trial (distribution = Poisson). Models with  $\Delta AICc \leq 10$  were used for model averaging. Full and null models were included in analysis but excluded from table. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Model components</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>Wt.</b>	<b>LL</b>
Nights	2	60.13	1.6	0.15	-27.75
Soil.temp	2	60.84	2.31	0.11	-28.1
Years	2	60.91	2.37	0.1	-28.14
Mass	2	60.95	2.42	0.1	-28.16
Soil.temp+Nights	3	62.52	3.99	0.05	-27.59
Mass+Nights	3	62.73	4.2	0.04	-27.7
Soil.temp+Years	3	63.46	4.93	0.03	-28.06
Mass+Soil.temp	3	63.54	5.01	0.03	-28.1
Mass+Years	3	63.57	5.04	0.03	-28.12
Soil.temp+Mass+Nights	4	65.47	6.94	0.01	-27.56
Soil.temp+Mass+Years	4	66.46	7.93	0.01	-28.05

Table 9. Model-averaged beta estimates with unconditional standard error (UnSE) and 85% confidence intervals for explanatory variables included in generalized linear models assessing magnitude of eastern copperheads' (*Agkistrodon contortrix*) defensive score in Stage 4 of the Trial. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Predictor</b>	<b>Model-averaged estimate</b>	<b>UnSE</b>	<b>85% confidence interval</b>	
			<b>Lower</b>	<b>Higher</b>
Mass	-0.000508	0.003113	-0.005173	0.004157
Nights	0.029460	0.030758	-0.016624	0.075545
Years	0.021290	0.082386	-0.102153	0.144735
Soil.temp	0.050166	0.124231	-0.135992	0.236325

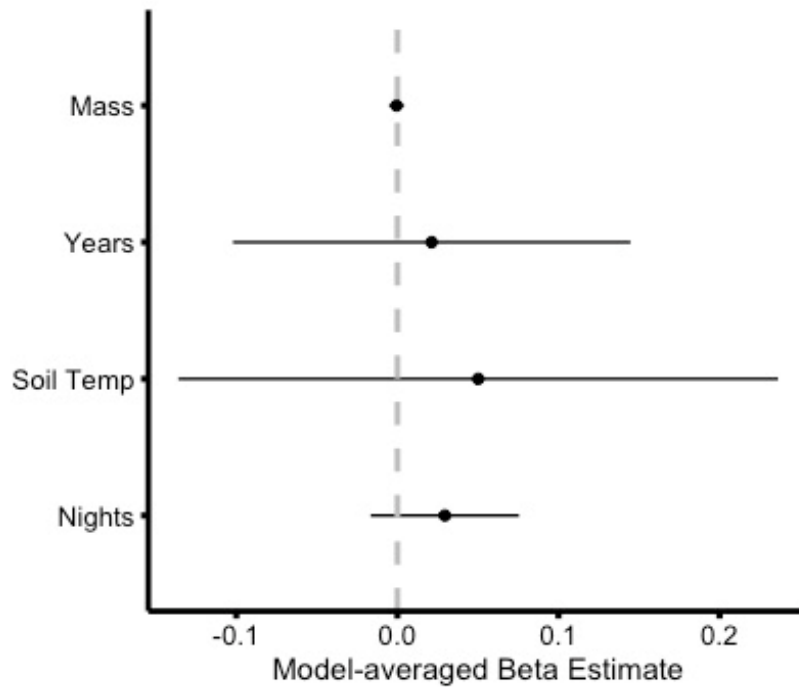


Figure 13. Model averaged beta estimates for parameters used in a generalized linear model to explain intensity of eastern copperhead (*Agkistrodon contortrix*) defensive behavior in Stage 4 of the behavioral trial at Koomer Ridge Campground.

#### *Total Score Analysis*

Mean total score of all copperheads (i.e., sum of behavioral scores across the four stages) was 3.2 ( $n = 25$ ,  $SE = 0.245$ ). Total score was best explained by the model containing the effect of years of capture at the site ( $AIC_C$  wt. = 0.16), although six other competing models were within  $2 \Delta AIC_C$  (Table 10). Model-averaging results indicated that Years Recaptured had a significant positive association with total score (Table 11, Figure 14).



Table 10. Candidate set of linear models used to explain summed scores of eastern copperhead (*Agkistrodon contortrix*) behavior (n = 25) across all four stages of the trial. Full and null models were excluded from the table. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky.

<b>Model components</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta</math> AICc</b>	<b>Wt.</b>	<b>LL</b>
Years	3	29.55	0.00	0.16	-11.20
Mass	3	29.69	0.14	0.15	-11.27
Soil.temp+Mass	4	30.71	1.16	0.09	-10.35
Soil.temp+Years	4	30.81	1.26	0.08	-10.41
Nights	3	30.89	1.34	0.08	11.87
Mass+Years	4	31.12	1.57	0.07	-10.56
Soil.temp	3	31.53	1.98	0.06	-12.19
Mass+Nights	4	31.84	2.29	0.05	-10.92
Soil.temp+Nights	4	31.98	2.43	0.05	-10.99
Soil.temp+Mass+Years	5	32.1	2.55	0.04	-9.47
Soil.temp+Mass+Nights	5	32.55	3.00	0.03	-9.7

Table 11. Model-averaged beta estimates with unconditional standard error (UnSE) and 85% confidence intervals for explanatory variables included in linear models assessing total behavioral scores of individual copperheads summed across all four stages. All trials were conducted at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky. Bold font indicates parameters found to be significantly associated with total score.

<b>Predictor</b>	<b>Model-averaged estimate</b>	<b>UnSE</b>	<b>85% confidence interval</b>	
			<b>Lower</b>	<b>Higher</b>
<b>Years</b>	<b>0.0597</b>	<b>0.0404</b>	<b>0.0016</b>	<b>0.1178</b>
Mass	0.0021	0.0014	0.000	0.0041
Nights	0.0172	0.0159	-0.0057	0.0401
Soil temperature	0.076	0.0618	-0.013	0.1649

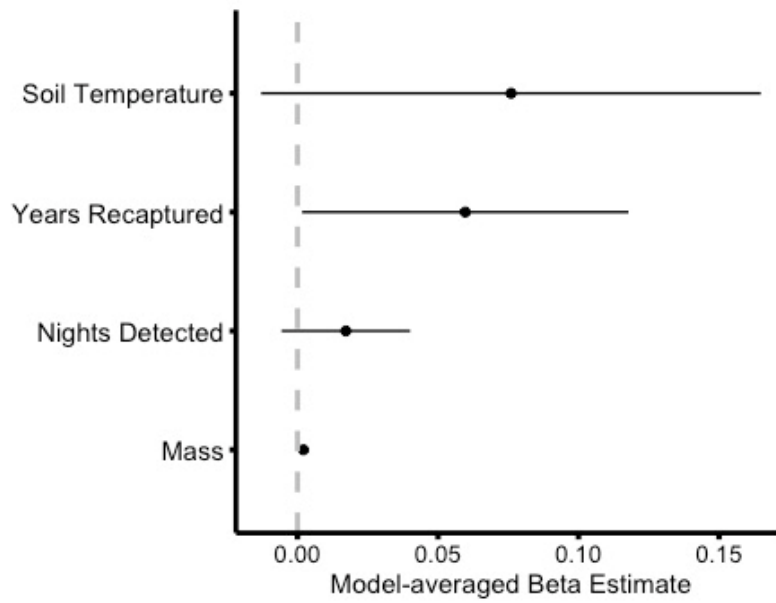


Figure 14. Model averaged beta estimates and 85% CI for variables used to explain copperhead total score across all four stages of the behavioral trial at Koomer Ridge Campground, Daniel Boone National Forest, Kentucky. Confidence intervals that do not contain 0 indicate variable significance.

## Discussion

### Overview of Copperhead Behavior

The objective of this study was to elucidate the role that individual experience plays in shaping defensive behaviors and foraging decisions of free-ranging eastern copperheads. I aimed to determine whether repeated captures by, and exposure to, humans cause copperheads to alter the frequency at which they forage at a recreational campsite, as well as their defensive behavior toward human approach while foraging. The responses of sampled copperheads were largely consistent with established hypotheses regarding anti-predator behavior of cryptic species (Broom and Ruxton 2005, McKnight and Howell 2015). Copperheads primarily did not react to approach and exhibited avoidance behaviors like flight to escape predatory stimuli. Interestingly, results support these hypotheses even in conditions where cryptic capabilities of an individual are limited, such as locomotion during active foraging. Copperheads are typically ambush predators that rely on envenomating strikes followed by strike-induced chemosensory searching (SICS) to locate the incapacitated prey (Greenbaum 2004, Teshera and Clark 2021). When primed to ambush, copperheads and other viperids typically position their body in a coil providing maximum crypsis (Glaudas et al. 2005). However, copperheads at our study site forgo this specialized strategy to capitalize on the emergence of annual cicadas, which do not require envenomation and SICS to consume (Lagesse and Ford 1996, Gull 2021). Due to this shift in foraging method, most copperheads sampled at the site were in an extended body position as they locomoted toward the presumed location of a cicada ( $n= 21$  of 25). It is possible that the prevalence of extended snakes was also influenced by the grass substrate of the

site, which provides limited cryptic abilities for a species adapted to hiding in red-brown leaf litter.

While my dataset did not have a large enough sample of coiled snakes to include body position as a predictor variable in behavioral models, comparisons to previous studies of viperid behavior can help clarify the role of body position in shaping defensive behavior. Research suggests that extended pygmy rattlesnakes (*Sistrurus miliarius*) are more likely to strike, presumably because cryptic patterning is less effective in this state (Glaudas et al. 2005). However, a study of the baseline response of copperheads to human approach did not detect an effect of body position on the snakes' overall intensity of response or willingness to strike (Adams et al. 2020). Disparity in the effect of body position between studies could be confounded by body size of focal species. Adult copperheads are significantly larger than their pygmy rattlesnake counterparts. Smaller species or individuals often face greater predation risk (Endler 1986), and intensity of viperid response to predation is negatively associated with body size (Roth and Johnson 2004), though I did not detect this pattern in my study. Therefore, it is logical that small-bodied species like pygmy rattlesnakes would be more likely than larger copperheads to resort to striking if a cryptic coil is not an option. This is supported by the fact that extended snakes sampled at KRC exhibit a similar pattern in the progression of defensive behavior to coiled copperheads sampled in Maryland by Adams et al. (2020). The majority (80%) of snakes in my study did not respond to initial human approach, consistent with a 75.3% frequency of non-responsiveness in Maryland copperheads. Both Adams et al. (2020) and I found that copperheads are unlikely to respond when being approached and stepped next to by a human. Both of

our results also indicate that after physical contact by a human, flight or movement away becomes the most frequently exhibited copperhead behavior. These results suggest that copperheads' defensive response to humans is not influenced by their body position.

Biotic factors driving copperhead aggregation at KRC may also be important in interpreting these data. Other examinations of viperid defensive behavior have been either conducted in labs or based on opportunistic encounters in the field. For field studies, the opportunistic nature of snake location complicates the identification of specific behaviors in which an individual was engaged. At KRC, however, copperhead abundance and site use is closely associated with seasonal cicada emergences (Sockman 2020), suggesting that individuals arriving at the site are foraging. Unlike the coil that is characteristic of ambush-ready vipers, actively foraging snakes are extended and locomoting. Similarities in behavior between coiled snakes in previous studies and extended snakes in this study could be a product of trade-offs between foraging and predation pressure (Brown and Kotler 2004). If an individual is in a forage patch with abundant food they should require a more intense predatory stimulus to cause them to flee (Verdolin 2006). In this context, it is possible that KRC copperheads exhibited similar levels of non-responsiveness as coiled snakes in other studies not because body position is unimportant in shaping behavior, but because the net fitness gain of non-responsiveness and continued foraging is greater than the cost of visibility to a human.

## **Variables Influencing Defensive Behavior and Likelihood to Forage**

Under the context of optimal risk allocation, I hypothesized that frequent captures and encounters with humans would decrease copperhead expression of defensive behaviors, resulting in lower behavioral scores. However, based on results of model averaging I reject this hypothesis. Total score across all stages was significantly, positively associated with number of years that individuals had been recaptured, though this effect was not detected in the per-stage models. Disparity between total and per-stage analysis may be caused by the ordinal and hierarchical nature of scoring. Per-stage, copperheads could score integer values of 0-3 while an individual's total score was the sum all trials and could theoretically be 0-12. I believe this low variation in scores within the per-stage analyses may have limited statistical power.

### *Soil Temperature and Mass*

Increasing soil temperature was associated with an increased likelihood to respond in Stage 3 but was not associated with an increase in the intensity of response. The effect of soil temperature may have only been detected in Stage 3 because physical contact was necessary to detect it. For poikilotherms, it is logical that the transitional stage between hiding from predators and responding once detected would be influenced by temperature (Hertz et al. 1993). In this context, the absence of temperature as significant in other stages could be a result of copperheads' low propensity to respond until touched and their tendency to avoid predators once touched. Once touched (i.e., Stage 3), soil temperature exhibited a relationship with defensive behavior that is consistent with results of previous studies. Although the nature of the behavioral trial

used for this study complicates direct comparison to others with different methods, research has demonstrated that within species' ranges of thermal tolerance, warmer reptiles are more reactive to predatory stimuli than cooler individuals (Hertz et al. 1993). For example, eastern garter snakes (*Thamnophis sirtalis*) with higher body temperatures flee human approach more readily than their cooler counterparts (Passek and Gillingham 1997), and warmer rattlesnakes (*C. oreganus helleri* and *C. scutulatus*) strike faster and gape more quickly during the strike than cooler snakes (Whitford et al. 2020).

Mass did not significantly explain variation in per-stage behavioral score or total score. Previous research found that cottonmouth defensive responses to humans decrease with body size, presumably because larger individuals face lower likelihoods of predation (Roth and Johnson 2004). This pattern is also present in other groups of squamates (Cooper Jr. and Vitt 1985). Cottonmouth populations sampled by Roth and Johnson (2004) exhibited a similar variation in body size (30.5 – 82.5 cm SVL) to copperheads in my research (44.5 – 79.5 cm SVL), suggesting that that the range of body sizes sampled was not responsible for body mass having little explanatory power. Disentangling the roles of size and ontogeny can be difficult, but research suggests adults are more capable of habituating to humans than neonates (Glaudas et al. 2006). Although ages of individual copperheads are unknown, the size range of sampled snakes indicates no juveniles were present, suggesting that differences in behavior were not produced by ontogeny. Due to the insignificance of mass and temperature variables that the total score level, I primarily base my discussion around the two experience variables of Years Recaptured and Nights Detected in 2022.

### *Experience Influences Defensive Behavior and Foraging Frequency*

To interpret these results in the context of individual experience, it is crucial to understand the behavioral foundation on which scoring relied. Increases in score represent an increase in diversity and intensity of individual defensive behaviors. Also, important to note is that in each stage scoring was based on the most severe behavior exhibited, as viperid responses to predation typically occur in progression (Table 1). I predicted that if foraging copperheads were exhibiting some form of acclimatization to capture and increase in tolerance to human presence at a foraging site, it would occur in the form of an overall reduction of defensive investment (Lima and Bednekoff 1999), resulting in an overall lower score. Instead, increasing frequency of capture led copperheads to be less likely to immediately flee human approach, and more likely to exhibit both passive and active defensive responses before fleeing, thus producing higher scores.

Although the relationship between number of years recaptured and total score was the inverse of what was predicted, the underlying pattern of copperhead behavior supports the optimal risk allocation hypothesis. Results suggest that copperheads with prior experience being approached and captured by humans are more likely to defend a foraging opportunity when approached and less likely to immediately flee relative to their naïve counterparts. Despite receiving a score of 1, escape behavior like fleeing has associated energetic and opportunity costs (Endler 1986, Broom and Ruxton 2005). In the context of scoring defensive responses of a foraging snake, the value 1 is not representative of low energy investment, but of low tolerance to human approach.



Snakes who exhibited passive or active defense and were scored as a 2 or 3 may have invested more energy into defensive behavior in a caloric sense, but the fact that they did not flee and remained foraging at the site to display these more costly behaviors indicates a level of tolerance and willingness to defend a foraging opportunity not present in snakes that fled immediately. The relationship between flight propensity and human contact or disturbance is well-studied, and flight initiation distance (FID) is a common metric used to assess reactivity of wild animals (Weston et al. 2012). Although I did not measure FID, patterns of copperhead behavior mirror results of studies that focused specifically on flight. Evidence suggests that populations experiencing frequent interactions with humans or occupying human-dominated areas exhibit decreased reactivity to human approach relative to their low interaction or rural counterparts (Rodriguez-Prieto et al. 2008, Kitchen and Price 2010, Atkins et al. 2022). By reducing energetic investment in reaction to humans, species occupying urban or high-disturbance areas can maximize their energy gain. I suspect this phenomenon is occurring with KRC copperheads at an individual level, as the likelihood to flee immediately generally decreases with years recaptured.

Due to the cryptic life histories of many snake species, mark-recapture studies are logistically challenging (Spellerberg 1977). I am only aware of one other study that assessed the defensive behaviors of wild snakes in relation to their capture history. Spencer et al. (2015) observed that brown tree snakes in Guam were significantly more likely to strike at researchers when caught in areas with extensive history of snake trapping. They did not find, however, evidence to support the hypothesis that individual capture history influenced strike propensity at the high-intensity trapping site. This

would suggest that individual experience was not the driving factor in producing variation in strike propensity between sites. Conversely, my results indicate that longer capture histories are associated with increased total behavioral scores and are likely a product of increased tolerance toward familiar, low-intensity predatory stimuli (Atkins et al. 2022). Understanding differences in study methodologies is critical in interpreting the results of Spencer et al. (2015) in the context of my own. Brown tree snakes were caught using traps checked by researchers at regular intervals, whereas copperheads in my study were free-ranging and likely foraging when approached. Researchers in Guam were only able to check traps daily at one of three trapping sites. Prolonged time in traps may have caused some snakes at the other two sites to acclimate to confinement and be less likely to strike relative to snakes in traps checked daily, which may explain why a difference was detected between sites, but not between individuals with varying capture histories. The nature of trapping complicates behavioral interpretations, as hormonal stress responses to being captured may linger and influence behavior (Mathies et al. 2001). Comparatively, copperheads in my study were not captured until the conclusion of behavioral trials. I also accounted for a range of possible behavioral responses, whereas Spencer et al. (2015) focused specifically on defensive striking. Although the disparity between strike propensity at high- and low-intensity trapping sites in Guam is apparent, it remains unclear what drives this behavioral difference.

Although the extent of long-term learning and habituation abilities of many squamates is unclear, there is evidence to suggest that some snakes are capable of modulating their behaviors based on experience (Greene 1988, Herzog et al. 1989). Habituation to human approach is unlikely to be the mechanism for behavioral

alteration in my study based on the results of sign tests between resampled snakes; however, copperheads experiencing repeated foraging success at KRC may learn to perceive risks posed by humans at the site to be minimal since no predation pressure is exerted. Originally proposed by Glaudas et al. (2006), this non-predatory contact could produce degrees of tolerance toward human presence that may be mechanistically similar to the Dear Enemy hypothesis (Owen and Perrill 1998, Wilson 2000). Originally proposed in the framework of conspecific territorial aggression, this hypothesis posits that individuals benefit from reducing aggression toward neighbors with whom they are familiar (Werba et al. 2022). Applied to the context of my copperhead system, individuals may become more tolerant of familiar predatory stimuli relative to unfamiliar ones if it increases their likelihood of successful foraging (Rodriguez-Prieto et al. 2008, Rodríguez-Prieto et al. 2010, Fernández-Juricic and Rodriguez-Prieto 2010). This hypothesis is supported by results of the site visitation analysis, as copperhead capture history was a significant, positive predictor of foraging frequency in 2022. Within this system, familiarity with the predatory stimuli of human approach and capture is dictated by the frequency at which an individual forages there during the summer. Frequency of foraging increased with number of years recaptured, though this relationship was not linear, as the most experienced individuals foraged far more frequently than the sample average (Figure 9). This relationship between experience and nights detected foraging suggests that the most experienced individuals forage at the site more successfully than less experienced snakes. Although it was not possible to record the number of cicadas each copperhead consumed across the field season, I would hypothesize that more experienced snakes would exhibit a higher foraging success rate

than their counterparts. Further research could attempt to identify a relationship between copperhead visitation rate and foraging success, as results could potentially support conclusions drawn in this thesis. Additionally, the relationship between foraging success and defensive behaviors could be investigated to determine if copperheads who frequently consume cicadas respond to human approach differently than copperheads who are less successful at foraging.

If forage patches with abundant prey also tend to be predator-dense, animals may avoid foraging there in favor of other locations with reduced forage availability but lower predation risk (Newman and Caraco 1987). However, if predator density increases with patch resources, as is the case at KRC, it may be more beneficial for individuals to forage in a predator-dense patch (Jones 2010). Although the process of capture elevates corticosterone levels in western cottonmouths, human foot traffic near snakes did not produce a similar elevated hormonal response, suggesting this species may be fairly resilient to habitat with high human use (Bailey et al. 2009). My results, though lacking hormonal data, support the same conclusion in the congeneric eastern copperhead. Neither annual capture and measurement nor human use of KRC for recreation deterred copperheads from returning to the site in 2022. Individuals with the most extensive capture histories visited the site to forage most frequently and tended to have the highest total behavioral score across the trial. This pattern appears to be driven by more experienced individuals fleeing less readily and exhibiting more visible behaviors in response to human approach than less experienced snakes, though this result was not significant.

In human-altered landscapes, eastern copperheads, as well as other squamate species, may reduce initial reactivity to human approach in favor of investing energy in active or passive responses should the approach progress and risk of predation increase. Doing so will allow individuals to experience increased foraging success relative to those who remain highly reactive to human approach (Rodríguez-Prieto et al. 2010). Although variation in conspecific behavior is often attributed to temperament (Gibert et al. 2022) or habitat-level selective pressures (Atkins et al. 2022), my study provides evidence that repeated captures by, and exposure to, humans may produce behavioral variation on an individual level. Namely, copperheads frequently encountering humans may learn a degree of behavioral tolerance toward human presence that is consistent with their ability to survive in anthropogenically modified habitat (Novak et al. 2020).

### **Management Implications and Conclusions**

By becoming more tolerant to human presence, copperheads can more effectively predate a seasonal food source at a recreational site. My study provides further evidence that squamates alter their behavior to maximize fitness in response to human disturbance and land-use change. However, increased tolerance and subsequent willingness to expose oneself to humans may also promote human-snake conflict. Copperheads' are responsible for a disproportionately large number of North American snake envenomations (Gummin et al. 2022), though, as discussed, this is a product of their abundance and range. Increased tolerance could facilitate even more conflict between humans and copperheads, as these snakes are not only living near humans, but they are also more willing to defend themselves from humans as opposed to

immediately fleeing. This behavioral shift could lead to more copperhead envenomations and a continued negative public view of this species. Although evidence overwhelmingly suggest that vipers rarely resort to striking (Gibbons and Dorcas 2002, Shine et al. 2002, Glaudas et al. 2005, Adams et al. 2020), any interaction between humans and venomous snakes can escalate to that level. To avoid conflict, land managers should identify sites frequently used by venomous snakes and attempt to limit human use of them. During the annual cicada emergence at KRC, I recommend the Forest Service consider closing the primitive site to reduce the likelihood of a camper being bitten. If this option is not feasible, I recommend increasing public education via camp host and signage that explains the phenomenon to campers. Although there have been no documented bites at KRC, the abundance of copperheads at the primitive site during the summer must be considered. I would also suggest continued monitoring of the copperhead population to provide more demographic and behavioral information regarding the impacts of humans on viperid defensive and foraging behavior. Overall, my study suggests that eastern copperheads modulate their foraging decisions and defensive behavior based on previous experience to increase fitness and more efficiently consume a seasonal food source. Further research should continue to explore how various anthropogenic factors influence the distribution and behaviors of North American vipers to better inform conservation measures and ensure health of the recreating public.

## References

- Adams, A., J. Garrison, S. McDaniel, E. Bueche, and H. Howell. 2020. Don't tread on me: an examination of the anti-predatory behavior of eastern copperheads (*Agkistrodon contortrix*). *Acta Herpetologica* 15:31–37.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management* 74:1175–1178.
- Atkins, M. C. P., C. R. Howarth, M. A. Russello, J. H. Tomal, and K. W. Larsen. 2022. Evidence of intrapopulation differences in rattlesnake defensive behavior across neighboring habitats. *Behavioral Ecology and Sociobiology* 76:3.
- Bailey, F. C., V. A. Cobb, T. R. Rainwater, T. Worrall, and M. Klukowski. 2009. Adrenocortical effects of human encounters on free-ranging cottonmouths (*Agkistrodon piscivorus*). *Journal of Herpetology* 43:260–266.
- Bateman, P. W., and P. A. Fleming. 2014. Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *Journal of Zoology* 294:93–98.
- Bracis, C., E. Gurarie, J. Rutter, and R. Goodwin. 2018. Remembering the good and the bad: memory-based mediation of the food–safety trade-off in dynamic landscapes. *Theoretical Ecology* 11:305–319.
- Broom, M., and G. D. Ruxton. 2005. You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology* 16:534–540.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.

- Burnham, K. P., and D. R. Anderson, editors. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY.
- Cooper, J. W. E., and L. J. Vitt. 2002. Optimal escape and emergence theories. *Comments on Theoretical Biology* 7:283–294.
- Cooper Jr., W. E., and L. J. Vitt. 1985. Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. *Zeitschrift für Tierpsychologie* 70:265–276.
- Cragg, J. G. 1971. Some statistical models for limited dependent variables with application to the demand for durable goods. *Econometrica* 39:829–844.
- Creel, S., J. A. Winnie, D. Christianson, and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* 76:1139–1146.
- Duvall, D., M. B. King, and K. J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. *National Geographic Research* 1:80–111.
- Endler, J. 1986. Defense against predators. Pages 109–134 *in* M. E. Feder and G. V. Lauder, editors. *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*. University of Chicago Press, Chicago, IL.
- Fagan, W. F., M. A. Lewis, M. Auger-Méthé, T. Avgar, S. Benhamou, G. Breed, L. LaDage, U. E. Schlägel, W. Tang, Y. P. Papastamatiou, J. Forester, and T. Mueller. 2013. Spatial memory and animal movement. *Ecology Letters* 16:1316–1329.



- Fernández-Juricic, E., and I. Rodriguez-Prieto. 2010. Risk allocation in anti-predator behavior. Pages 75–78 in M. D. Breed and J. Moore, editors. *Encyclopedia of Animal Behavior*.
- Gibbons, J. W., and M. E. Dorcas. 2002. Defensive behavior of cottonmouths (*Agkistrodon piscivorus*) toward humans. *Copeia* 2002:195–198.
- Gibert, R. G., D. W. Maag, L. N. Sanders, and R. W. Clark. 2022. Investigating personality in vipers: individual rattlesnakes exhibit consistent behavioral responses in defensive and exploratory contexts. *Behavioral Ecology and Sociobiology* 76:132.
- Glaudas, X. 2004. Do cottonmouths (*Agkistrodon piscivorus*) habituate to human confrontations? *Southeastern Naturalist* 3:129–138.
- Glaudas, X., T. M. Farrell, and P. G. May. 2005. Defensive behavior of free-ranging pygmy rattlesnakes (*Sistrurus miliarius*). *Copeia* 2005:196–200.
- Glaudas, X., C. T. Winne, and L. A. Fedewa. 2006. Ontogeny of anti-predator behavioral habituation in cottonmouths (*Agkistrodon piscivorus*). *Ethology* 112:608–615.
- Greenbaum, E. 2004. The influence of prey-scent stimuli on predatory behavior of the North American copperhead *Agkistrodon contortrix* (Serpentes: Viperidae). *Behavioral Ecology* 15:345–350.
- Greene, H. W. 1988. Antipredator mechanisms in reptiles. Pages 1–152 in C. Gans and R. Huey, editors. *Biology of the Reptilia* Vol. 16, Ecology B, Defense and life history. Alan R. Liss Inc., New York, NY.

- Griffin, A. S., D. T. Blumstein, and C. S. Evans. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology* 14:1317–1326.
- Gull, H. C. 2021. Evidence of non-strike-induced chemosensory searching by eastern copperheads (*Agkistrodon contortrix*) during cicada predation. Eastern Kentucky University.
- Gummin, D. D., J. B. Mowry, M. C. Beuhler, D. A. Spyker, L. J. Rivers, R. Feldman, K. Brown, P. T. P. Nathaniel, A. C. Bronstein, and J. A. Weber. 2022. 2021 Annual Report of the National Poison Data System<sup>©</sup> (NPDS) from America's Poison Centers: 39th Annual Report. *Clinical Toxicology* 60:1381–1643.
- Helfman, G. S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology* 24:47–58.
- Hendricks, J. J. 2019. Population demographics and unique foraging behavior of copperheads (*Agkistrodon contortrix*) at a recreational site in eastern Kentucky. Eastern Kentucky University.
- Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *The American Naturalist* 142:796–818.
- Herzog, H. A., B. B. Bowers, and G. M. Burghardt. 1989. Development of antipredator responses in snakes: IV. Interspecific and intraspecific differences in habituation of defensive behavior. *Developmental Psychobiology* 22:489–508.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19:101–108.

- Jones, E. I. 2010. Optimal foraging when predation risk increases with patch resources: an analysis of pollinators and ambush predators. *Oikos* 119:835–840.
- Kalisz, P. J., and J. E. Powell. 2003. Effect of calcareous road dust on land snails (*Gastropoda: Pulmonata*) and millipedes (*Diplopoda*) in acid forest soils of the Daniel Boone National Forest of Kentucky, USA. *Forest Ecology and Management* 186:177–183.
- Kitchen, K. I. M., and M. Price. 2010. Tolerance of human disturbance by urban magpie-larks. *Australian Field Ornithology* 27:1–9.
- Krishnamoorthy, K., and M. Lee. 2014. Improved tests for the equality of normal coefficients of variation. *Computational Statistics* 29:215–232.
- Lagesse, L. A., and N. Ford. 1996. Ontogenetic variation in the diet of the southern copperhead, *Agkistrodon contortrix*, in northeastern Texas 48:48–54.
- Laszlo, J. 1975. Probing as a practical method of sex recognition in snakes. *International Zoo Yearbook* 15:178–179.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the Predation Risk Allocation Hypothesis. *American Naturalist* 153:649–659.
- Lukacs, P. M., K. P. Burnham, and D. R. Anderson. 2010. Model selection bias and Freedman’s paradox. *Annals of the Institute of Statistical Mathematics* 62:117–125.
- Marwick, B., and K. Krishnamoorthy. 2019. cvequality: Tests for the equality of coefficients of variation from multiple groups. R software package version 0.1.3. Retrieved from <https://github.com/benmarwick/cvequality> on 06/01/2023

- Mathies, T., T. A. Felix, and V. A. Lance. 2001. Effects of trapping and subsequent short-term confinement stress on plasma corticosterone in the brown treesnake (*Boiga irregularis*) on Guam. *General and Comparative Endocrinology* 124:106–114.
- McKnight, D., and H. Howell. 2015. A comparison of the flight initiation distances of male and female American bullfrogs (*Lithobates catesbeianus*) and green frogs (*Lithobates clamitans*). *Herpetological Conservation and Biology* 10:137–148.
- Newman, J. A., and T. Caraco. 1987. Foraging, predation hazard and patch use in grey squirrels. *Animal Behaviour* 35:1804–1813.
- Novak, M. V., D. P. Crane, L. Bell, L. Keiner, C. R. Gatto, C. T. McNabb, and S. L. Parker. 2020. Spatial ecology of eastern copperheads in fragmented and unfragmented habitats. *Journal of Herpetology* 54:97-106.
- O'Donnell, K., and J. delBarco-Trillo. 2020. Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: a meta-analysis. *Journal of Urban Ecology* 6:014.
- Owen, P. C., and S. A. Perrill. 1998. Habituation in the green frog, *Rana clamitans*. *Behavioral Ecology and Sociobiology* 44:209–213.
- Passek, K. M., and J. C. Gillingham. 1997. Thermal influence on defensive behaviours of the eastern garter snake, *Thamnophis sirtalis*. *Animal Behaviour* 54:629–633.
- Rodriguez-Prieto, I., E. Fernández-Juricic, J. Martín, and Y. Regis. 2008. Antipredator behavior in blackbirds: habituation complements risk allocation. *Behavioral Ecology* 20:371–377.

- Rodríguez-Prieto, I., J. Martín, and E. Fernández-Juricic. 2010. Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology* 64:1937–1945.
- Roth, E. D., and J. A. Johnson. 2004. Size-based variation in antipredator behavior within a snake (*Agkistrodon piscivorus*) population. *Behavioral Ecology* 15:365–370.
- Shettleworth, S. J. 2001. Animal cognition and animal behaviour. *Animal Behaviour* 61:277–286.
- Shine, R., L.-X. Sun, M. Fitzgerald, and M. Kearney. 2002. Antipredator responses of free-ranging pit vipers (*Gloydius shedaoensis*, Viperidae). *Copeia* 2002:843–850.
- Smith, J. M. 1978. Optimization theory in evolution. *Annual Review of Ecology and Systematics* 9:31–56.
- Sockman, J. C. 2020. Impacts of driving factors on annual cicada emergence in relation to the seasonal abundance of eastern copperheads (*Agkistrodon contortrix*). Eastern Kentucky University.
- Spellerberg, I. F. 1977. Marking live snakes for identification of individuals in population studies. *Journal of Applied Ecology* 14:137–138.
- Spencer, M. M., B. Lardner, M. J. Mazurek, and R. N. Reed. 2015. Factors affecting defensive strike behavior in brown treesnakes (*Boiga irregularis*) provoked by humans. *Herpetological Conservation and Biology* 10:703–710.

- Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65:13–21.
- Teshera, M. S., and R. W. Clark. 2021. Strike-induced chemosensory searching in reptiles: A review. *Herpetological Monographs* 35:28–52.
- Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* 60:457–464.
- Werba, J. A., A. M. Stuckert, M. Edwards, and M. W. McCoy. 2022. Stranger danger: A meta-analysis of the dear enemy hypothesis. *Behavioural Processes* 194:104542.
- Weston, M. A., E. M. McLeod, D. T. Blumstein, and P.-J. Guay. 2012. A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu - Australian Ornithology* 112:269–286.
- Whitford, M. D., G. A. Freymiller, T. E. Higham, and R. W. Clark. 2020. The effects of temperature on the defensive strikes of rattlesnakes. *Journal of Experimental Biology* 223:38–59.
- Wilson, E. O. 2000. *Sociobiology: The New Synthesis, Twenty-Fifth Anniversary Edition*. Harvard University Press.