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Don't tread on me: an examination of the anti-predatory behavior of Eastern Copperheads (*Agkistrodon contortrix*)

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Abstract. Venomous snake species across the globe have been historically categorized as aggressive and dangerous, leading to widespread persecution and killings. Despite the conservation importance of educating the public about the docile nature of these species, few studies have attempted to quantify the response of viperid species to human interactions. Here we report the responses of free-ranging copperheads to a potential human encounter using a set of hierarchical behavioral trials. Out of a total of 69 snakes, only two individuals feigned striking and only two attempted to bite (3% of all individuals). Our results support the findings of previous studies documenting the docile nature of other viperid species and can hopefully be used to change the public perception of venomous snakes. Convincing the public and policy makers that viperid species are docile is critical to long-term conservation of these species in the U.S. and around the globe.

Keywords. Human-wildlife conflict, optimality theory, venomous species, Viper, Viperidae.

INTRODUCTION

As human populations continue to grow and encroach further into uninhabited or sparsely populated areas, there is a subsequent increase in the prevalence of human-wildlife conflict (Woodroffe et al., 2005; Skogen et al., 2008; Dickman, 2010). The outcomes of human-wildlife conflict are rarely more pronounced and potentially lethal to both parties than the interaction between humans and venomous snakes. Venomous snakes have long been a source of great fear for the general public, and have been historically (and currently) mischaracterized as being aggressive and dangerous (Blythe, 1979; Seigel and Mullin, 2009; Burghardt et al., 2009; Pandey, 2016). Even scientific medical publications describing envenomations as late as 2002 (Juckett and Hancox, 2002) continued to perpetuate the myth that viperid species like the cottonmouth (*Agkistrodon piscivorus*) are aggressive and readily attack humans. Misinformation and negative public perception have led to the wholesale slaughter of venomous pit vipers across North America and Europe. Events such as Rattlesnake and copperhead roundups in the US (Adams et al., 1994; Fitch, 1998; Burghardt et al., 2009), and the killing of individual snakes, such as the meadow viper (*Vipera ursinii*), the Cyperian Blunt-nosed Viper (*Macrovipera lebetina lebetina*), and the Northern adder (*Vipera berus*) when they are encountered in Europe (Edgar and Bird, 2006; Stumpel et al. 2015, Julian and Hodges, 2019) are examples of direct persecution against viperid species. This widespread persecution continues to take place in both areas, and is a serious conservation concern for many viperid species, despite these species causing very low numbers of fatalities across these two continents (Chip-

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paux, 2012). It is imperative that any conservation action plan seeking to protect these species will need to incorporate some type of public outreach to reduce direct persecution of these species (Seigel and Mullin, 2009).

Despite the largely negative public perception surrounding pit-vipers, papers have been published in the last two decades that clearly demonstrate the passive and even cowardly nature of other viperid species (Shine et al., 2000; Gibbons and Dorcas, 2002; Glaudas et al., 2005). If snakes are confronted by a large potential predator, the decision to no longer rely on passive defensive behaviors and strike could have a host of potentially short and long-term negative consequences for the snake (Gibbons and Dorcas, 2002; Broom and Ruxton, 2005). For cryptic species, optimality theory predicts that the most efficient strategy to both reduce energy waste and avoid potential mortality is to remain in hiding if possible and to flee immediately if detected by the predator (Ydenberg and Dill, 1986; Broom and Ruxton, 2005; McKnight and Howell, 2015). Like other cryptic species responding to large predators, cryptic viperid species should rely primarily on crypsis or fleeing as primary sources of predator evasion, followed only after these two tactics have failed, by striking and envenomation. When confronted and detected by a potential predator, a snake should first attempt to escape, then employ a suite of passive deterrents (e.g., musking, tail vibrating, mouth gaping), and finally commit to active defenses (biting or striking; Roth and Johnson, 2004).

In addition to the decision-making process driven by optimality theory (see Ydenberg and Dill, 1986), there are a host of intrinsic and extrinsic factors that may act to mediate the chance that a snake will strike (Cooper and Vitt, 2002; Roth and Johnson, 2004). Intrinsic factors such as size (Hailey and Davies, 1986; Whitaker and Shine, 1999), body temperature (Layne and Ford, 1984; Goode and Duvall, 1989), sex (Scudder and Burghardt, 1983), time since feeding (Herzog and Bailey, 1987), prior predator exposure (Glaudus, 2004), and gestation may all play a role in the likelihood of striking (Glaudas et al., 2005). However, studies have found contradictory results regarding the role that each of these factors may play, suggesting that the exact influence of these factors are likely species specific (Roth and Johnson 2004). Extrinsic factors like the severity of the threat and the relative location of the snake may also impact strike likelihood (Gibbons and Dorcas, 2002; Shine et al., 2002; Glaudas et al., 2005).

The Eastern copperhead (*Agkistrodon contortrix*) is perhaps the most commonly persecuted snake species in the Eastern US. This wide-ranging species can be found throughout the eastern United States from Massachusetts to Florida, west into Texas and across a wide variety of habitat types (Ernst and Ernst, 2003). Copperheads are an ideal species for a study examining the defensive behavior of a Viperid species to human presence and subsequent interaction, because they are widespread across the heavily populated areas of the Mid-Atlantic and Southeastern US, are responsible for a large proportion (49.2%) of the reported envenomations in the US (Gummin et al., 2017), and are both widely feared and heavily persecuted when located by the general public. While there were 2,048 reported copperhead envenomations in the US in 2016 (Gummin et al., 2017), the overwhelming majority of these envenomations (94%) were either of a moderate or lower health-risk and there were zero reported fatalities (Gummin et al., 2017).

With the continued and rapid expansion of urbanized areas across the copperhead's range, especially in the Southeastern US, where copperheads are still abundant, the number of copperhead-human interactions is likely to increase in the future. Therefore, an understanding of the anti-predatory behavior of copperheads may be used to dispel misinformation, inform the public about the behavior of this common and widespread venomous species, and potentially serve to mitigate the negative consequences of future human-snake encounters.

The aim of the present research is to examine the anti-predatory behavior of the Eastern copperhead when contacted by a potential human predator. Based on optimality theory, we predict that copperheads will rely on crypsis to avoid predation and will very rarely resort to defensive anti-predatory tactics.

MATERIALS AND METHODS

Our study areas (n = 10) were dispersed throughout the state of Maryland, a small state located in the mid-Atlantic region of the US, and included a variety of habitats within each of the state's physiographic provinces. Maryland is comprised of six physiographic provinces, the Atlantic Continental Shelf Province, the Coastal Plain Province, the Piedmont Plateau Province, the Blue Ridge Province, the Ridge and Valley Province, and the Appalachian Plateau Province (Reger and Cleaves, 2002). Copperheads are widely distributed across Maryland and occupy different habitats within these physiographic provinces (e.g., bottomland swamps, rocky stream banks, south facing slopes) across the state. The location of each site was non-random, with study sites chosen based on prior distribution records collected through the Maryland Amphibian and Reptile Atlas (Cunningham and Nadrowicz, 2018) or historical localities gathered from Harris (1975). All encounters occurred within the state of Maryland. Searches were conducted during the copperhead's active season, from 01 May 2017 to 01 November 2017, and again from 01 May 2018 to 01 November

2018. The snakes were located by visually searching each study site by foot (Karns, 1986; Gibbons and Dorcas, 2002). In general, snakes were found in areas adjacent to wintering den sites with a large amount of adjacent cover in the form of rock crevices and piles. Once a snake was visually located, the body position of each individual, either coiled or extended, was recorded prior to any further approach (Shine et al., 2000; Glaudas et al., 2005). Since body surface temperature can play a role in defensive behavior (Arnold and Bennett, 1984), we used a Ryobi Tek4 non-contact infrared digital thermometer (Ryobi, Chicago, IL, USA) to record body temperature at three different locations on the body (head, mid-section, and cloaca) from a distance of ~2 m and then averaged these values together (Garrick, 2008). Ambient environmental temperature was recorded by extracting local weather data from the nearest weather station using the Weather Underground mobile application software (v5.11.9, TWC Product and Technology, Atlanta, GA) from the National Weather Service, operating under the National Oceanic and Atmospheric Administration (2018).

Once located, snakes had 1) an apparatus with a boot attached placed directly adjacent to the snake to simulate a possible human interaction while actively hiking (Gibbons and Dorcas, 2002; Shine et al., 2002). After the initial approach and first trial, the snake then had 2) the apparatus placed gently on top of it (to simulate accidental contact with a hiker; Gibbons and Dorcas, 2002). Finally, the snake was 3) grabbed and picked up using a pair of snake tongs covered with a leather glove to simulate a human hand (Gibbons and Dorcas, 2002; Glaudas, 2004; Glaudas et al., 2005; Maritz 2012). A previous study showed that a human hand elicits a strong anti-predatory response, suggesting that faux gloved hand might elicit a similar anti-predatory response (Herzog et al., 1989). Each stage of the test (1-3) was carried out for 20 seconds and was videotaped using a digital video camera (to allow post hoc analysis of the defensive response).

During each phase, the observers recorded the defensive behavior of the snake from the anterior end. Behaviors were categorized into four separate categories during each stage of the experiment (fleeing, tail vibrating, feigning a strike, and striking; Gibbons and Dorcas 2002) to represent escalating levels of anti-predatory responses. A feigned strike was classified as a lunge forward without any discernible opening of the mouth. To test the effect of human activity, environmental temperature, snake's body temperature, and the snake's initial posture on anti-predatory behavior, we categorized each snake's response across trials into one ordered value based on their most defensive response to any of the trials (no-response [0], fleeing [1], benign anti-predatory response [2; tail vibrating], or defensive anti-predatory response [3; feigning a strike or striking]). To test for associations between ambient and body temperatures and behavior we used an ANOVA. Both environmental temperature and the snake's body temperature were normally distributed (Shapiro-Wilk W Test, W = 0.94 and 0.97 respectively). To test for associations between initial body condition and anti-predatory behavior we used a Mann-Whitney U-Test. All statistical analyses were conducted in JMP Pro (v14, SAS Institute Inc., Cary, NC).

We did not collect and individually mark snakes since it would have been impossible to collect many of the snakes that rapidly fled into adjacent cover (e.g., deep rock crevices, den sites, heavy vegetation) in a manner that did not harm the snakes or lead to the potential envenomation of the researchers. Additionally, since contact prior to the trials would have biased behavior, marking could not have been performed prior to the initiation of the trials. To help prevent "double-testing" of the same snake, integument patterns (specifically the darker "hourglass" bands that may have been thin or wide, uneven, broken on the dorsal side, etc.) were used as a basis for individual recognition and were supplemented by recordings of scale abnormalities (Carlstrom and Edelstam, 1946; Shine et al., 1988; Moon, et al., 2004). Post-hoc visual photo comparison between each individual snake was conducted to remove any duplicate trials. In total, we removed one snake trial from all analysis after post-hoc comparison confirmed that it had been tested during a prior sampling period.

RESULTS

In total, we recorded encounters with 69 snakes across all 10 sites (Fig. 1). Of these 69 snakes, 15 escaped immediately upon discovery without performing any other anti-predatory behavior and were not available for any further trials. During the initial approach, one snake performed tail vibrating before fleeing, one snake performed tail vibrating and a feigned strike before fleeing, and one snake attempted a strike. After accounting for these 18 snakes, 52 snakes remained for further trials. For a summary of the responses to each of the individual trials (stepped next to (N = 52), stepped on (n = 33), and picked up (n = 14)), see Fig. 2. In total across all trials, five snakes displayed tail-vibrating behavior and one exhibited a feigned strike followed by fleeing (Fig. 2). Across all trials, we recorded only two instances of striking (3% of all snakes).

There was no relationship between snake anti-predatory behavior and either ambient temperature (ANOVA: $F_{3,65}$, P = 0.92) or snake body temperature (ANOVA: $F_{3,62}$, P = 0.45). Similarly, there was no difference in anti-predatory behavior between snakes that were initially coiled or extended (U = 255, P = 0.496). Thus, across all conditions snakes showed similarly low percentages of anti-predatory behavior.

DISCUSSION

Overall, our results provide evidence to support the hypothesis that copperheads respond to potential predators in a manner consistent with their cryptic patterning. Specifically, copperheads are more likely to either remain in crypsis or flee in the presence of a human rather than display defensive behavior. Across the various trials of

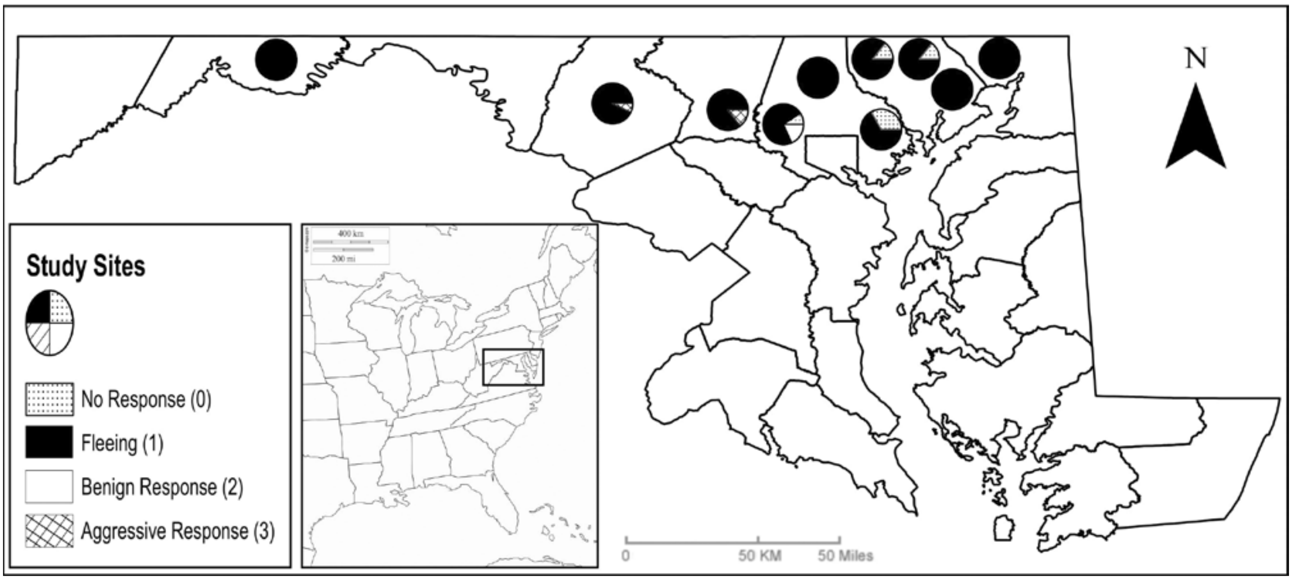

Fig. 1. Geographic distribution of the study sites across the state of Maryland. Each study site is represented by a pie chart with the binned behavioral responses from all individuals at that site.

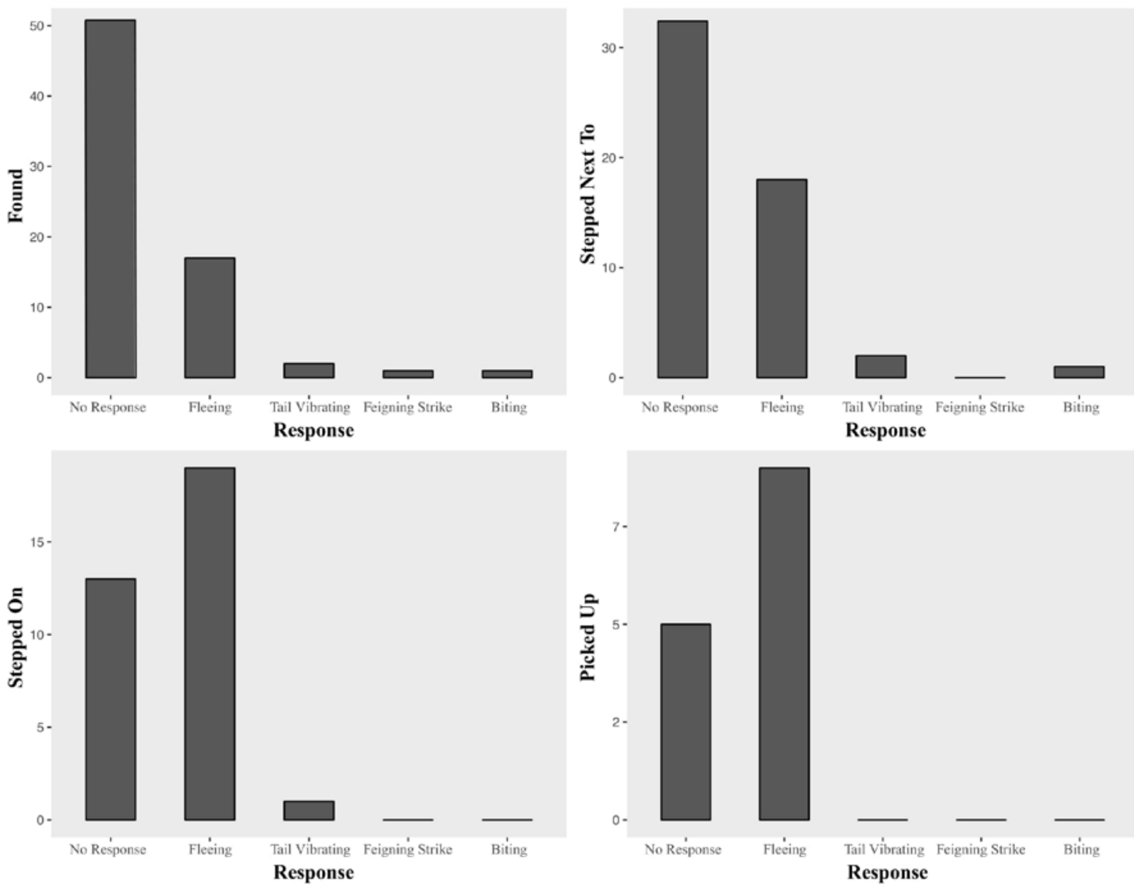

Fig. 2. Responses of copperheads to four increasing threat levels in a hierarchical anti-predatory trial (Found, Stepped Next To, Stepped On, Picked Up).

the study, 93% of the snakes fled when we approached or made physical contact with them. Furthermore, a higher proportion of snakes (6%, n = 4) displayed no response to any of our interactions (including being picked up) than those snakes that struck during one of the trials (3%, n = 2). While the proportion of strikes was low, these results mirror the findings of other studies examining pit-vipers' responses to humans and consistently demonstrate that despite the public's perception of these species as being dangerous and aggressive, that Pope (1958) was correct when claiming that snakes are "first cowards, then bluffers, and last of all, warriors."

To examine how different intrinsic and extrinsic factors influenced anti-predatory response, we analyzed the effect of the initial body posture and body temperature of each individual, and ambient environmental temperature on anti-predatory responses. While we did not collect individuals to gather morphometric data, the extremely low prevalence of snake strikes makes it highly unlikely that any effect of sex or size class on a snake's anti-predatory response would have been detected. However, with a larger sample size, differences in anti-predatory behavior based on various intrinsic or extrinsic factors may be detected. The published literature on the anti-predatory behavior of snakes is full of conflicting results regarding the role of intrinsic and extrinsic factors on anti-predatory behaviors both between and among species (Shine et al., 2000; Roth and Johnson, 2004). Unfortunately, our work does little to elucidate the differences between these conflicting studies, except perhaps to further emphasize that differences in evolutionary history may be prohibitive when attempting to produce general models of anti-predatory behavior in snakes.

While for obvious safety reasons we were unable to approach the snakes with an exposed hand or forearm, other studies have also used a gloved apparatus to simulate the human hand (Gibbons and Dorcas, 2002; Glaudas 2004; Glaudas et al., 2005). While it is possible that the difference in temperature between the gloved apparatus and a human hand may have modified the anti-predatory behavior of the copperheads due to their heat-sensing capabilities, no study has yet assessed the importance of thermal cues in the modification of anti-predatory behavior in free-ranging pit-vipers. Since no studies have examined the effect of predator temperature on anti-predatory behavior, examining the literature on the influence of temperature on predatory behavior may be instructive. However, in the only field studies conducted to this point examining the importance of thermal cues on predatory behavior, Shine and Sun (2003) found that while adult snakes were more likely to strike at warmer objects, temperature was not a predictor of juvenile strikes, and Schraft et al. (2018) found that absolute temperature was not an important predictor of predation attempts.

The public perception of venomous snakes as aggressive and dangerous leads to a suite of problems for the conservation of viperid species (see Seigel and Mullin, 2009 for an overview). Most notable among these issues are the large organized round-ups that may lead to localized extirpation of rattlesnakes (Adams et al., 1994; Fitch, 1998; Burghardt et al., 2009) and the lack of resources that are made available for habitat protection or management of these species (Seigel and Mullin, 2009). While some studies provide cautionary tales about the potential backfiring of educational material (Hoff and Maple, 1982), it is clear that increasing the public's positive perception of snakes will be a necessary component of any long-term conservation plan (Seigel and Mullin, 2009). More recent studies have shown that well designed education programs focusing on biodiversity conservation, the ecological role or snakes, or the use of antivenom for medicinal use can improve feelings and attitudes about snakes (Murphy and Xanten, 2007; Markwell and Cushing, 2009). As part of this public outreach and education, providing examples demonstrating the docile nature of most venomous species may convince some individuals to support legislation to prevent the organized killings that persist to this day.

The results of this research provide previously unavailable information to inform the public of the docile nature of copperheads and potentially assuage fears surrounding the perceived aggressive nature of viperid species. These striking results should prove useful in convincing the proportion of the public that is still impressionable of the copperheads' benign nature and may result in an increase in positive public perception. Future conservation of imperiled viperid species may hinge on the ability of scientists to persuade policy makers and the public of the importance and docile nature of these species (Seigel and Mullin, 2009). This study provides further evidence that common venomous species are not aggressive and rely on striking only as a last resort. As Charas (1677) noted over 300 years ago, "The viper is taken by many for an image of malice and cruelty; but in reality, she is guilty of no such thing".

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