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Do warning displays predict striking behavior in a viperid snake, the cottonmouth (*Agkistrodon piscivorus*)?

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Abstract: Warning displays are defined as signals designed to intimidate predators or indicate a proclivity to fight. However, support for the idea that warning behaviors signal an intent to fight is largely based on anecdotes and isolated observations, and a complete understanding of antipredator behavior will only be achieved if specific hypotheses are experimentally tested. Herein, we tested in a North American viperid snake, the cottonmouth (*Agkistrodon piscivorus* (Lacépède, 1789)), the hypothesis that warning displays serve as a reliable signal to potential predators that a snake will strike. The cottonmouth exhibits two stereotypical warning displays during predator confrontation, i.e., mouth gaping and tail vibrations, making it an ideal study organism to experimentally test the relationship between warning displays and defensive striking. To test this idea, we recorded the sequence of defensive behavior — gaping, tail vibrating, and striking — of cottonmouths towards a standardized predatory stimulus in the laboratory. As predicted, snakes that gaped during the trials were subsequently more likely to strike than snakes that did not. In contrast, striking behavior was independent of the occurrence of tail vibrations. Our results suggest that gaping behavior — but not tail-vibrating behavior — may provide an honest signal to would-be predators.

Résumé : Les postures d'avertissement se définissent comme des signaux destinés à intimider les prédateurs ou à indiquer une inclination à livrer bataille. Cependant, l'idée que les comportements d'avertissement annoncent une intention de livrer bataille s'appuie en grande partie sur des anecdotes et des observations isolées; une compréhension entière du comportement antiprédateur ne sera possible que lorsque des hypothèses spécifiques auront pu être testées. Nous vérifions ici chez le mocassin aquatique (*Agkistrodon piscivorus* (Lacépède, 1789)), un vipéridé nord-américain, l'hypothèse selon laquelle les postures d'avertissement servent de messages fiables aux prédateurs potentiels que le serpent va contre-attaquer. Le mocassin aquatique utilise deux postures stéréotypées d'avertissement durant la confrontation avec un prédateur, c.-à-d. l'ouverture de la bouche et les vibrations de la queue, ce qui en fait un organisme d'étude idéal pour tester expérimentalement la relation entre les postures d'avertissement et les attaques défensives. Afin de vérifier cette idée, nous avons enregistré les séquences du comportement de défense — ouverture de la bouche, vibration de la queue et contre-attaque — chez des mocassins aquatiques en réaction à un stimulus standardisé de prédation en laboratoire. Tel que prédit, les serpents qui ouvrent la bouche durant les essais sont plus susceptibles de contre-attaquer plus tard que les serpents qui n'ouvrent pas la bouche. En revanche, le comportement de contre-attaque est indépendant des vibrations de la queue. Nos résultats laissent croire que le comportement d'ouverture de la bouche — mais non celui de vibration de la queue — constitue un signal honnête pour les prédateurs potentiels.

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Introduction

When encountered by a predator, many animals use warning displays, which are signals designed to intimidate predators (Edmunds 1974) and (or) indicate an intention to fight (Halliday and Slater 1983). Warning displays have presumably evolved by selection favoring individuals that advertise their dangerousness — whether it is a bluff or not — rather than overtly attack a predator (Edmunds 1974). Selection can subsequently optimize individual signals by reducing the ambiguity between the signaler and the receiver through a process known as ritualization (Cullen 1966; Wiley 1983), which in the case of warning displays can prevent detrimental interactions for both opponents if the prey is potentially

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dangerous to the predator. In this case, the predator–prey interaction may be somewhat analogous to within-species agonistic behaviors in which two individuals first observe and threaten each other (assessment), and eventually fight if neither retreats (Ewer 1968; Swaisgood et al. 1999).

The idea that warning displays communicate a disposition to fight is seemingly based on observations that animals respond to predatory threats in a hierarchical manner as the risk of being killed increases (Klauber 1972; Edmunds 1974; Endler 1986; Greene 1988). This correlated response between threat escalation and prey defensive behavior has been reported for an extensive variety of taxa, including mammals (Ewer 1968), birds (Kruuk 1964), and reptiles (Greene 1988). Within reptiles most of the evidence comes from snakes. For instance, in response to threat escalation in the field, pitvipers typically try to flee when first confronted, then exhibit coiled defensive postures and warning displays, and subsequently strike if the predator is still threatening (Duvall et al. 1985; Gibbons and Dorcas 2002). This stereotyped sequence of snake defensive behaviors led Pope (1958) to conclude that "snakes are first cowards, then bluffers, and last of all warriors". However, support for the idea that warning behavior signal an intent to fight is largely based on anecdotes and isolated observations, and a complete understanding of antipredator behavior will only be achieved if specific predictions and hypotheses are experimentally tested (Endler 1986).

Cottonmouths (*Agkistrodon piscivorus* (Lacépède, 1789)) are an ideal study organism to experimentally investigate the relationship between warning and striking behaviors for three reasons: (1) they are highly venomous snakes, and are therefore potentially dangerous to many predators; (2) they possess unambiguous warning signals during predator confrontations such as mouth gaping to expose the inner white lining of their mouth (hence their name) and tail-vibrating behavior, which presumably indicate an intent to strike (Gibbons and Dorcas 2002); and (3) they exhibit individual variation in the use of these displays (Gibbons and Dorcas 2002; Glaudas 2004; Glaudas et al. 2006). Our research objective was to test the hypothesis that warning displays serve as a reliable signal to potential predators that a snake will strike. This hypothesis predicts that snakes that exhibit warning displays (i.e., gaping or tail vibrations) during predator confrontations are subsequently more likely to strike than snakes that do not exhibit warning displays.

Methods

Experimental subjects

We tested a total of 101 cottonmouths during the course of this study. We collected 68 cottonmouths (36 females and 32 males; snout–vent length (SVL) = 63.78 ± 15.36 cm (mean ± SD); mass = 348.6 ± 240.78 g (mean ± SD)) from the US Department of Energy's Savannah River Site, located in Aiken and Barnwell counties, South Carolina, during the spring and summer of 2003. Additionally, we obtained 33 neonates (SVL = 23.97 ± 1.29 cm; mass = 16.8 ± 1.8 g) from six litters (N = 3, 4, 5, 6, 6, 9) born in the laboratory in 2003. Subsequent to the present experiment, we used the neonates and 36 of the adults in an antipredator habituation study that we report elsewhere (Glaudas et al. 2006). Ultimately, we released all snakes at their capture location.

Prior to the trials, we housed all snakes individually in polyethylene containers (Rubbermaid™ Commercial Products, Winchester, Virginia; adults: 58 cm × 42 cm × 14 cm; neonates: 34 cm × 25 cm × 14 cm), with water provided ad libitum and bark mulch as a substrate, within a walk-in environmental chamber (14 h light : 10 h dark, 26 °C). To minimize human scent, we used latex gloves when setting up the containers. We allowed the snakes to acclimate to the containers for 48–72 h prior to being tested. We did not feed the snakes during the experiment to eliminate the effect of recent feeding on defensive behavior (Herzog and Bailey 1987).

The predatory stimulus

An approaching human is likely to be perceived as a threat and trigger high defensive responses in snakes (Goode and Duvall 1989); consequently, humans have been widely used to elicit defensive behaviors in snakes in general (Herzog et al. 1989; Glaudas et al. 2005) and cottonmouths in particular (Gibbons and Dorcas 2002; Glaudas 2004; Roth and Johnson 2004; Glaudas and Gibbons 2005; Glaudas et al. 2006). In this study, we approached each snake with an artificial human arm at an angle of approximately 45° from the horizontal plane, and then gently tapped the snake's midbody three successive times at 1 s intervals. Our stimulus has the advantage of being a highly repeatable standardized test that elicits and allows cottonmouths the opportunity to deploy their full range of defensive responses (Glaudas et al. 2006).

The artificial arm consisted of 1 m snake tongs (Whitney tongs, Midwest Products™, Greenwood, Missouri) customized with a shirt sleeve to resemble a human arm (Gibbons and Dorcas 2002). In this study, we did not warm the artificial arm because a previous study using the same stimulus demonstrated that thermal cues do not influence the defensive strike of cottonmouths (Glaudas and Gibbons 2005). We covered the anterior part of the arm with polyethylene and replaced it between trials so that chemical cues from a previous snake would not influence the response of the subsequent snake. We hand-held the polyethylene-wrapped tip for 1 min prior to each trial to ensure the presence of human olfactory cues on the stimulus.

Testing procedures

We performed all tests in the individual housing containers to eliminate pre-test and post-test handling. Since container heights were small (14 cm), prior to the test we placed each container in a larger plastic-wall arena (to prevent escape), where we left the closed container undisturbed for 1 min. Containers were always oriented in the arena with the snake facing the tester. After removing the container lid, the snake was briefly allowed to orient towards the tester and, then, the snake's midbody was approached and gently tapped three successive times at 1 s intervals with an artificial arm (see above). At the start of each trial, all snakes tongue-flicked and (or) pointed their heads toward the approaching stimulus, indicating that snakes were aware of the tester's presence. We tested all snakes between the hours of 1100 and 1400. At the time of the experiment, the tester was not aware of the hypothesis. All trials were videotaped using a DM-GL1A Video Camcorder (Canon, Inc., Lake Success, New York) and later reviewed by an independent observer who was unaware of the hypothesis.

Defensive behaviors

We recorded the sequence of defensive behaviors — gaping, tail vibrating, and striking — exhibited by cottonmouths for all trials. We defined a strike as any motion forward with an opened mouth and the snake's neck fully or partially extended toward the stimulus, regardless of whether strikes successfully contacted the arm (i.e., we assumed accurate and inaccurate strikes were derived from equal intent to strike the arm). No distinction was made between envenomation and dry bites (i.e., no venom injected), or between "feint" (e.g., half-hearted) and "real" strikes, since no reliable method was available to assess whether venom was injected, and because the intent of a strike may be difficult to interpret (Glaudas et al. 2006). Gaping behavior was defined as a snake exposing the white lining of its mouth, and tail-vibrating behavior was defined as the snake twitching its tail against the substrate to generate a weak auditory signal.

Data analysis

We first used a logistic regression to investigate a potential relationship between body size (SVL) and snake striking behavior. Body size did not affect a snake's likeliness to strike (logistic regression, $\chi^2_{[1]}$ = 2.39, P = 0.12), so we disregarded this variable. We used contingency table analyses and log-linear analyses to investigate the effect of three categorical independent variables (gaping, tail vibration, sex), as well as their interactions, on striking behavior (Zar 1999). For each test, we set the level of significance to be α = 0.05. All χ^2 values reported are corrected for continuity using Yate's correction (except for the interaction analyses). We performed all statistical tests using STATISTICA® version 6.0 (StatSoft Inc. 2000).

Results

Overall, 42.57% of the snakes (43/101) gaped during the predatory encounter and 40.59% of the snakes (41/101) vibrated their tails. Gaping and tail-vibrating behaviors were significantly associated with one another: 58.14% (25/43) of the snakes that gaped also vibrated their tail compared with only 27.59% (16/58) of the snakes that did not gape (contingency table, $\chi^2_{[1]}$ = 9.55, P = 0.002). For all subsequent analyses, we considered snakes to be nondisplaying (e.g., not gaping or not tail vibrating) if they used warning displays only after striking.

Of the 32 snakes that both gaped and struck during a trial, 81% (26/32) gaped prior to — as opposed to after — striking, which indicates the warning character of gaping behavior. Two × two contingency table analyses revealed that gaping was significantly associated with striking ($\chi^2_{[1]}$ = 4.54, P = 0.03). Snakes that gaped during the trials were subsequently more likely to strike than snakes that did not (Fig. 1A). In contrast, striking behavior was independent of sex ($\chi^2_{[1]}$ = 0.29, P = 0.58) and the occurrence of tail vibrations ($\chi^2_{[1]}$ = 2.72, P = 0.10; Fig. 1A). Moreover, the nonsignificant association between tail-vibrating and striking behaviors was in the opposite direction of our prediction; that is, snakes that vibrated their tails were less likely to strike than snakes that did not (Fig. 1A). Interestingly, of the 30 snakes that exhibited both tail-vibrating and striking behaviors over a single trial, 76% (23/30) vibrated their tail after striking, indicating that tail-vibrating behavior was not used as an initial warning mechanism.

To alleviate potential concerns of pseudoreplication for the neonatal snakes (e.g., litter mates may not be independent samples), we restructured the data set to include all of the adults and only a single, randomly chosen neonate from each litter. Using the same analyses on the reduced data set yielded similar results: striking was significantly associated with gaping behavior ($\chi^2_{[1]}$ = 3.7, P = 0.05) but not with tail-vibrating behavior ($\chi^2_{[1]}$ = 0.027, P = 0.86) or sex ($\chi^2_{[1]}$ = 0.32, P = 0.57).

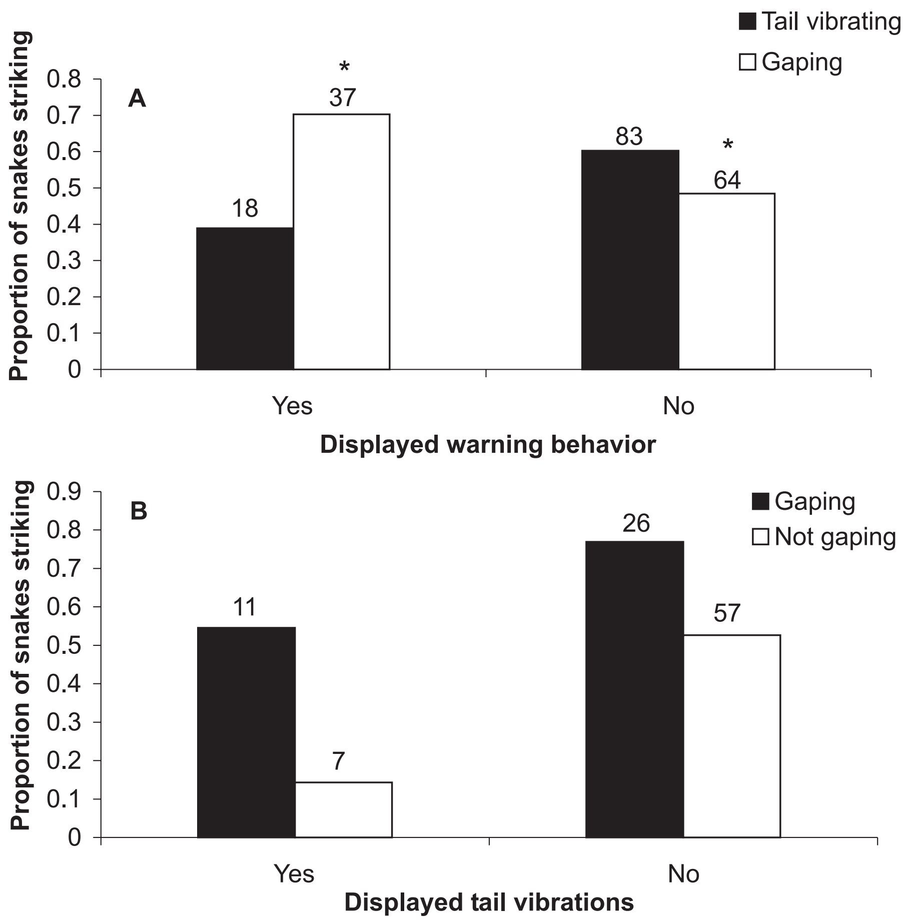
Finally, we used log-linear analyses to investigate possible interactions between the following variables on striking behavior: (*i*) tail-vibrating and gaping behaviors, (*ii*) sex and gaping behavior, and (*iii*) sex and tail-vibrating behavior. We observed a significant interaction of gaping and tail-vibrating behaviors on striking behavior (Fig. 1B). That is, the probability that a snake struck after gaping was lower if the snakes also vibrated its tail (log-linear analysis, $\chi^2_{[4]}$ = 11.23, P = 0.02). The remaining interactions were nonsignificant (sex and gaping behavior: $\chi^2_{[4]}$ = 7.03, P = 0.13; sex and tail-vibrating behavior: $\chi^2_{[4]}$ = 8.10, P = 0.08).

Discussion

Overall, cottonmouths that employed their stereotypical gaping display were more likely to strike than cottonmouths that did not gape. In this regard, our results are consistent with the hypothesis that the use of a warning behavior accurately signals an individual's willingness to retaliate. In a similar study, Shedao pitvipers (*Gloydius shedaoensis* (Zhao, 1979)) that used tail vibrations as a warning display during human encounters struck more often than individuals that did not display (Shine et al. 2002). In cottonmouths, however, the use of tail vibrations as a warning display was not a good predictor of defensive striking. In fact, our results revealed that most of the snakes that vibrated their tails did so after striking, and that the probability of a snake striking after it gapes decreases if the snake also vibrates its tail. Taken together, our results suggest that (*i*) gaping behavior is a reliable signal of the cottonmouths' willingness to strike, (*ii*) tail-vibrating behavior may not be a warning display but rather a mechanism used to redirect predators' attention to a less vulnerable part of the body (Greene 1988), and (*iii*) the relationship between gaping and striking behaviors is affected by tail-vibrating behavior. However, cottonmouths did not always signal their intent to strike; approximately half of the snakes struck without warning. This suggests that the use of warning displays may vary by species or experimental protocols because Shedao pitvipers almost always warned the predator prior to striking (Shine et al. 2002).

In the distantly related Shedao pitviper, the tendency to use warning displays is influenced by habitat (arboreal vs.

Fig. 1. (A) Relationship of gaping and tail-vibrating behaviors to striking behavior of cottonmouth (*Agkistrodon piscivorus*). Snakes that gaped, but not those that vibrated their tails, struck significantly more often. Asterisks denote statistically significant difference at $P < 0.05$. (B) Effect of the interaction between gaping and tail-vibrating displays on striking behavior of cottonmouth. The probability that a snake would strike after gaping was lower if it also vibrated its tail during an encounter (log-linear analysis: $P = 0.02$). The numbers above the bars indicate the number of snakes that did or did not display warning behaviors, not the absolute number of snakes that struck.



terrestrial) and body temperature (Shine et al. 2002). We performed our experiment in a controlled laboratory setting, and therefore, neither habitat nor body temperature varied among snakes in our study. Consequently, the individual variation we observed in the use of warning and striking behaviors raises interesting questions. First, what determines whether a snake will use a warning display? Possibly, the use or non-use of warning displays may reflect two diametrically opposed strategies. Using a warning display (specifically gaping) may serve an aposematic function in venomous cottonmouths, which are fully capable of defending themselves against most predators (Ernst and Ernst 2003) and experience low rates of mortality, particularly adults (Ford 2002); whereas, not using a warning display during a predatory encounter may be beneficial to a snake relying on crypsis to avoid detection. It seems likely that these alternative strategies may vary within or among individuals, based on habitat and predator characteristics, and as a result of prior experience with a predator (Glaudas et al. 2006). Alternatively, variation in the use of gaping behavior may simply depict temporal or individual variation in disposition towards a potential predator. Thus, one possible interpretation of the significant relationship between gaping and striking behaviors in cottonmouths is that snakes which used gaping as a warning behavior either felt more threatened by the stimulus or were feistier than snakes that did not display. However, a large number of snakes that struck at the stimulus did not exhibit a warning display, suggesting that the latter interpretation may not be correct.

Second, what is the adaptive significance of warning signals in cottonmouths? In predator–prey interactions, the function of signals is to modify the predator’s behavior (Hasson 1991) so as to alter the outcome of the encounter (Leal and Rodriguez-Robles 1997). The presumed intent of these displays is to maximize the prey’s survival by decreasing the probability that the predator will attack, and interrupt the predator–prey interaction as early as possible to decrease the cost of defense (Endler 1986, 1991). However, the intimidating significance (and supposedly the survival value) of warning displays has been reported mostly anecdotally in mammals (reviewed in Edmunds 1974) and reptiles (reviewed in Greene 1988). Carefully designed experiments that investigate the adaptive significance of warning displays are clearly needed to further our understanding of the evolution of antipredator behavior.

In summary, we provide a direct experimental test of the relationship between warning signals and striking behaviors in a reptile. Typically, snakes that gaped — but not those that vibrated their tails — subsequently struck at the stimulus. The interaction between gaping and tail-vibrating behaviors observed in our study also underlines the complex nature of the relationships between these displays and striking behavior. Our results demonstrate an association between striking and gaping behaviors, and this suggest that gaping possibly provides an honest signal to would-be predators. On the other hand, we found no significant association between tail-vibrating displays and striking behavior in cottonmouths. Possibly, the use of warning displays (gaping vs. tail vibrating) varies with habitat or predator types, or alternatively tail-vibrating behavior may not function as a warning display (e.g., a majority of snakes that both exhibited striking and tail-vibrating behaviors vibrated their tails after striking), and these ideas could be tested in future experiments.

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