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Responses of Natricine Snakes to Predatory Threat: A Mini-Review and Research Prospectus

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ABSTRACT.—**Numerous behaviors of natricine snakes are plausibly interpreted as antipredator mechanisms that are useful at different stages of an encounter with a predator. Several of these behaviors have been described in detail, often in the laboratory, but we know little about the factors that influence their expression and effectiveness in the field, especially against real predators. Thus, one question that we might ask is: How effective are humans and artificial stimuli as proxies for real predators? Other areas that would profit from further research include the role of color and pattern in avoidance of predation, the effect of injury on subsequent survival, growth, or other measures of demographic performance, the role of previous experience in shaping future antipredator behavior, and the links among fear, stress physiology, and antipredator behavior.**

> "...*some* defence is probably effective in some cases, but almost no defence works *all* the time." (Greene, 1988)

Like most herpetologists of my generation, I spent much of my boyhood, especially my teenage years, looking for snakes and frogs around local ponds and learning about their natural history. Graduate school extended my boyhood for another few years; earning a faculty position made it permanent. I have been fortunate to have spent the last 40+ years at the University of Victoria indulging in my major passion in life—finding and observing amphibians and reptiles in the wild—and combining that pursuit with my enthusiasm for science, asking questions that I would never have thought of in my youth (and being paid to do so).

Although I have made occasional research forays into "lizards," turtles, anurans, and salamanders, snakes have always been my main obsession and my bread-and-butter study organisms. With my students, I have studied various aspects of the ecology of snakes and used assorted types of modern technology such as radiotelemetry (Charland and Gregory, 1995) and spectrophotometry (Isaac and Gregory, 2013), not to mention elaborate statistical analyses that would have been unimaginable in my pre-computer early days. All of this is richly rewarding, but what I find truly satisfying is time spent in the field and the little events that collectively open up windows into the lives (and deaths) of snakes. I particularly enjoy recapturing snakes that I have marked previously and seeing how much they have grown and wondering what they have been doing since I last saw them (sometimes 10 or more years). I can estimate survivorship from these mark–recapture data, but only rarely do I learn the ultimate fate of individual snakes that I mark and release. Nonetheless, every once in awhile, the hard evidence turns up in my hands. For example, I once found a marked juvenile *Thamnophis sirtalis* in the stomach of an adult *Thamnophis elegans*—no big mystery about what happened there.

This little observation underlines the fact that snakes, like most other animals, play multiple roles in the ecosystems they occupy. At one level, snakes are predators, eating a wide variety of prey. We know this partly because we sometimes see snakes catching or eating prey in the wild but mainly because we can sample stomach contents of snakes, either by dissection (Rodríguez-Robles, 2002) or by gently encouraging live snakes to regurgitate their prey (Tuttle and Gregory, 2009). As a result, we actually know quite a bit about the diets, if not the foraging habits, of many species of snakes.

Snakes are not only predators themselves but also prey for other species of predators. In this case, though, we usually know much less about the particular players involved (but see Shine et al., 2001; Ajtić et al., 2013). Predators are occasionally seen attacking or attempting to attack snakes, but in my experience, such observations are generally few and far between (and my camera never seems to be handy, either). We know that snakes are attacked because unsuccessful attacks often leave evidence in the form of injuries (Gregory and Isaac, 2005; Fig. 1), and also we sometimes see the remains of successful attacks (Fig. 2), but we usually do not know who the guilty party is. This is an important gap in our knowledge as even the mere threat of predation can have potentially significant population-level consequences for prey.

Predation on snakes, and as a consequence, antipredation defenses of snakes, is an enigmatic subject that is ripe for further study. My experiences in the field have left me with many questions. Why do some snakes bite vigorously when captured, whereas others of the same species react more placidly? Why do snakes crossing open spaces, such as roads, often pause and rest immobile and exposed? Why do some snakes flee when approached, whereas others allow close approach and even contact? Why do some snakes play dead when handled? I cannot hope to answer these kinds of questions definitively here, but perhaps I can provide some sort of framework for tackling them.

Throughout my career, I have mostly studied natricine snakes, especially gartersnakes (*Thamnophis*). Why? Partly because they were the first snakes I encountered as a youth and I have a soft spot for them but mainly because they are diverse, widespread, and abundant and usually easily maintained in captivity, making them attractive for all sorts of studies, including comparative work within a restricted phylogenetic framework. Although some natricines bite readily when caught, their bites are usually innocuous; hence, snakes can be caught by hand without the need for tongs, tubes, and other paraphernalia that are needed for handling seriously

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FIG. 1. Examples of injuries in Common Watersnakes (*Nerodia sipedon*). (A) Injury to body. (B) Loss of end of tail.

venomous snakes. True, some natricines are mildly venomous, and people sometimes react to their bites (Hayes and Hayes, 1985; Gomez et al., 1994), but I am not aware of any fatalities or long-term effects from such bites. In fact, *Rhabdophis* is the only natricine genus that has any dangerously venomous species (Greene, 1988, 1997), but when molested, these snakes generally resort to other antipredator measures before biting (Mori and Burghardt, 2001).

Therefore, natricines represent an interesting class of prey. They are all small to medium-sized, even as adults, and thereby susceptible to capture by all manner of predators throughout their lives. Their physical defensive weaponry is weak to nonexistent in most cases (although biting might have an element of surprise). Nonetheless, they are highly successful and, as my mark–recapture records show, often live long lives. How do they do it? How do they avoid being eaten?

To a large extent, my interest in antipredator defenses has been fuelled by my experience with Grass Snakes (*Natrix natrix*), which often feign death when captured. This is curious behavior. I well remember the first grass snake I ever caught. As the snake hung limply from my hand, mouth agape, I was initially convinced that I somehow had accidentally killed it. It was a thoroughly persuasive display, but playing dead really seems like an odd thing to do when one's life is potentially at stake. Several colleagues, especially behavioral ecologists, have expressed their skepticism that this could be effective antipredator behavior. I have argued elsewhere why and under what circumstances it might be effective (Gregory, 2008a), but this remains an open question. On the one hand, questions about death-feigning underscore the fact that we know little or nothing about how (or even whether) most presumed antipredator behaviors of natricines are used against natural predators and their adaptive value; this is a general, if difficult, problem that demands attention (Lind and Cresswell, 2005). On the other hand, though, it makes me wonder whether there are any actions of natricines that do not have elements of predator avoidance or other antipredator behavior. From the perspective of a small animal, it must indeed be a scary world.

My first aim in this review is to summarize what we know about defensive armaments and behavior in natricine snakes. Because this is a "Perspectives" paper, my review is selective (perhaps idiosyncratic), rather than exhaustive but relies on both field and laboratory studies, with occasional reference, as appropriate, to studies of other animal taxa. Much of what I present about natricines also applies to other groups of snakes, but restricting my review to a single diverse clade is a practical constraint. Second, I discuss some current issues about predatory threat and defensive behavior that have broader ecological implications and merit further study. Collectively, they comprise a potential agenda for future research that we might profitably address using natricines as "model organisms." At my advancing age, it is unlikely that I will tackle even a small fraction of this agenda, but I hope to inspire others to do so.

Because my focus here is on snakes as prey, further use of words like "predation" or "predators" herein refers to predation on snakes rather than by snakes.

Antipredator Behaviors of Natricine Snakes

The wide variety of antipredator behaviors exhibited by snakes, including natricines, has been cataloged elsewhere (Greene, 1988), and it is not my intention to repeat this list in detail here but to cover antipredator defenses under broad categories. There are various ways that one could categorize such behaviors. Perhaps the most comprehensive is by Mori and Burghardt (2004), who categorized antipredator behaviors in three dimensions: 1) whether prey move toward or away from predators; 2) how much movement is involved; and 3) apparent function. More simply, Arnold and Bennett (1984) placed antipredator behaviors of neonate Plains Gartersnakes (*Thamnophis radix*) on a spectrum from defensive to offensive. Another convenient approach, which I adopt here, is to classify antipredator behaviors according to when they occur during a predator–prey interaction; different tactics may be called for at different points in an encounter with a predator. I pool predator avoidance and antipredator mechanisms (Brodie et al. 1991), but there is potential utility in making the distinction between them in other contexts.

Any interaction between predator and prey consists of sequential stages. The interaction can be terminated at any stage, by the prey escaping or being consumed, or by the predator giving up (Lima and Dill, 1990; Toledo et al., 2011; Sherbrooke, 2013). Presumably, it is in the prey's interest to end the encounter, in its favor, as soon as possible (Bowers et al., 1993; but see Bateman et al., 2014). Generally speaking, the stages of predation include: localization (detection), approach, attack, handling (including subjugation), and consumption.

FIG. 2. A recently killed *Natrix natrix* found in the field.

Approach and attack may be combined as one single action but can also be separate, as in the case of a predator approaching a prey but failing to attack because of aggressive defense posturing by the prey (Arnold and Bennett, 1984; Greene, 1997) or because of "flash" or "startle" coloration that is exhibited when the prey's body is flattened defensively (Shine et al., 2000; Westphal, 2007). This sequence can be simplified even further as a continuum from avoiding detection through avoiding capture to avoiding consumption.

By "avoiding detection," I refer to detection of the prey by the predator, but the detection of the predator by the prey is equally important. Avoiding detection by the predator essentially means hiding (e.g., under cover; Gregory, 2009) or otherwise not stimulating the predator's senses (e.g., immobility coupled with visual crypsis; Isaac and Gregory, 2013). Hiding under cover may be more important for smaller snakes (Fig. 3) because they are presumably more vulnerable to predators than are large snakes (Bittner, 2003); small juvenile snakes also are slower than adults (Pough, 1977). Gartersnakes (*Thamnophis*) hiding under cover during the day are smaller than those basking or moving in the open (Gregory et al., 1983; Gregory, 1984), as are *N. natrix* (Fig. 4).

If a predator detects a prey, but not vice versa, the prey may be doomed unless it detects the predator as the latter approaches. However, prey sometimes detect predators before the predator detects them. Once a prey animal has detected a predator, one option is to flee, but this entails the risk of drawing the predator's attention. If unsure about whether it has been detected by the predator, the prey's other option is to remain immobile (and perhaps thereby remain undetected), especially if cryptically colored, until the predator comes within some critical distance, usually called approach distance or flight initiation distance (FID), at which point the prey should flee.

Flight initiation distance has been well studied in diverse taxa (Stankowich and Blumstein, 2005), including lizards (Cooper, 2011; Cooper et al., 2012; Martín et al., 2009), but has been studied in only a few natricines (Layne and Ford, 1984; Weatherhead and Robertson, 1992; Burger, 2001; Shine et al., 2000, 2003a; Brown and Shine, 2004; Cooper et al., 2008). The point at which FID occurs is determined by the relative costs of fleeing versus remaining in place (Lima and Dill, 1990). More recent models emphasize the "decision" to remain still or flee as one that maximizes fitness (Cooper and Frederick, 2007, 2010). Flight initiation distance is influenced by multiple factors (Stankowich and Blumstein, 2005) and might even be reduced to zero in cases in which the prey has effective post-capture defensive behaviors (e.g., death-feigning; Cooper and Frederick, 2010) or the prey stands its ground with intimidating (even if bluffing) aggression toward the predator. Also, proximity to cover should allow closer approach of a predator (Stankowich and Blumstein, 2005); many natricines favor edge habitats when in the open (Wisler et al., 2008), presumably because they allow ready escape while basking or engaging in other activities. Finally, walking past snakes without stopping may be less likely to cause flight than approaching them directly (Burger, 2001; pers. obs.). One puzzle is why some snakes do not flee at all as they are approached and fail to move even when the human predator is lunging at them (Gregory, 2013).

A prey animal cannot be vigilant in all ways and in all directions all the time and I've caught my fair share of snakes that probably simply did not see me because their heads were hidden. But even snakes that are aware that a predator is approaching or close by might sometimes take the chance that the predator has not detected them and continue to try to evade detection by remaining immobile. I think I have a pretty good search image for snakes, but it's not perfect, and every once in awhile I put my foot down right beside a snake without seeing

FIG. 3. An adult female *Storeria occiptiomaculata*. Although individuals of this small species are sometimes found in the open, they are typically found hiding under cover such as rocks.

it. I am usually alerted to this if somebody else notices the snake or if the snake decides to move away soon after I've nearly stepped on it, but if the snake does not move, I easily might not see it at all and simply move on. In any case, the snake faces a dilemma—whether to move or to remain frozen in place. Either action could be the correct one, but either also could be an error. A decision has to be made especially quickly if the predator surprises the snake (and perhaps itself) by coming upon the snake suddenly and at close quarters, an experience I have had as a snake hunter many times.

This issue is similar to one I raised earlier: Why do snakes crossing open spaces, such as roads, often pause and rest immobile and exposed? Are they simply being wary? Snakes

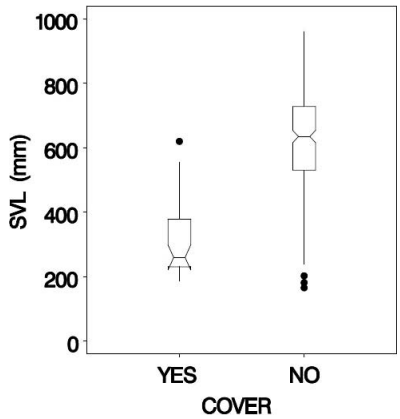

FIG. 4. Boxplots of body sizes (snout–vent length, SVL) of Grass Snakes (*Natrix natrix*) found under cover and in the open at Fordwich, Kent, U.K., from 1999–2012 (unpubl. data; $N = 302$, of which 36 were under cover). Median is shown by horizontal line. Top and bottom of box are 75th and 25th quartiles, respectively; ends of vertical line are the furthest points not exceeding 1.5 times the distance between the quartiles; and dots are more extreme values. Lack of overlap of notches of boxes indicates significant difference between medians at $P = 0.05$.

that have to cross open spaces have two main options: 1) cross the space and reach safety as quickly as possible but risk drawing the attention of predators through conspicuous movement; or 2) cross slowly with barely detectable movement but risk longer exposure. I have seen snakes do both of these, but what factors determine the direction of this apparent trade-off in any given case is an open question. I suspect that temperature plays a role—warmer snakes are faster than cooler snakes; furthermore, lingering on a dangerously hot substrate could be fatal.

However, temperature, which has a profound effect on the general ecology of snakes (Peterson et al., 1993), shows no consistent influence on FID—colder snakes flee earlier (Shine et al., 2000) or later (Layne and Ford, 1984) than warmer snakes or there is no difference in FID between warm and cold snakes (Weatherhead and Robertson, 1992; Brown and Shine, 2004; Cooper et al., 2008).

Trade-offs between putative antipredator behaviors should be common. Individual hatchling *N. natrix* that move quickly rely on flight to counter a perceived threat, whereas slower snakes rely more on aggression; locomotory speed, in turn, varies among clutches and is influenced by developmental temperature (Hagman et al., 2015). In DeKay's Brownsnakes (*Storeria dekayi*), the duration of death-feigning behavior is negatively related to maximum swimming speed, again indicating a trade-off between these two traits (Gerald, 2008).

Color and pattern play a role in avoiding detection through background matching and crypsis (King and Lawson, 1997; Isaac and Gregory, 2013), but also they are linked to flight behavior. For example, striped snakes should use flight readily because uniformity of body landmarks makes it difficult to follow the snake's movement (Jackson et al., 1976; Allen et al., 2013; but see von Helversen et al., 2013). In contrast, blotched snakes are cryptic when immobile and should be more likely to defend themselves than flee once detected by a predator (Jackson et al., 1976). Brodie (1992) tested the escape response

of naïve newborn Northwestern Gartersnakes (*Thamnophis ordinoides*) from litters containing both striped and blotched individuals and found that the two morphs indeed had different responses. Laboratory work, coupled with mark–recapture studies in the field, showed that fitness was maximized in young snakes for two combinations of traits: snakes with stripes that fled in one direction when chased versus snakes without stripes that tended to reverse their movement and stop when chased instead of fleeing steadily in a single direction (Brodie, 1992). The sudden disappearance of the snake (and its blotches) when the snake stops is likely to confuse a predator and make it difficult to locate the prey. Color pattern and behavior are genetically correlated in this species (Brodie, 1989b). This correlational selection helps explain the color polymorphism. That is, neither pattern, by itself, has an advantage over the other—the advantage emerges only through correlation with behavior.

Also, sex and reproductive state should affect how snakes react to predatory situations. Male snakes that are preoccupied with searching for mates allow much closer approach than snakes not so engaged (Shine et al. 2003a; Brown and Shine, 2004). Because of their increased mass, gravid females are typically limited in their mobility (Seigel et al., 1987), which affects their antipredator options. Female *T. ordinoides* change their antipredator behavior during pregnancy, exhibiting a significantly higher frequency of reversals in movement direction than when not gravid and, thus, a higher reliance on sudden crypsis than on flight (Brodie, 1989a). By changing their behavior while pregnant, gravid females reduce their dependency on locomotion at a time when they are disadvantaged in this respect, thereby also reducing the cost of reproduction. Also, presumably because of their reduced locomotory ability, gravid Keelback Snakes (*Tropidonophis mairii*) flee at greater FID than do nongravid snakes (Brown and Shine, 2004). In contrast, when confronted with an immediately adjacent threat in the confines of the laboratory, gravid *T. sirtalis* are less likely to flee and more likely to be aggressive than males or nongravid females (Maillet et al., 2015).

Other characteristics of pregnant snakes also might be seen as part of their antipredator repertoire. For example, pregnant *Thamnophis* are typically anorexic, especially late in pregnancy (Gregory et al., 1999). I interpret this as a physiological suppression of appetite at a time when foraging might conflict with the more important function of thermoregulation. But not foraging also means that snakes can bask near shelter to which they can readily escape if a predator turns up; snakes that cannot move fast should ensure that they do not have to move far.

Gartersnakes often aggregate in the open when pregnant, sometimes touching, sometimes not (Gregory et al., 1987). Aggregation might be social behavior or merely common attraction to particular physical conditions, but it also might be antipredator behavior. Although an aggregation of prey might be somewhat more conspicuous to a predator than an isolated individual, there might be safety in numbers (the "selfish herd"; Hamilton, 1971) if the predator can focus on and catch only one or two prey while the others make good their escape, especially if they all move in different directions. A few years ago, I came across four pregnant *T. elegans*, all piled in a heap on a patch of open ground. The snakes all started to flee before I could touch them. I managed to catch them all, but then I am a specialized predator with grasping hands and a cloth bag in which to store the snakes while I process them one by one at my leisure. Other predators do not have this suite of attributes and probably would not have been able to catch, hold, and consume all four snakes very easily.

Snakes whose locomotion is affected by a full stomach (Garland and Arnold, 1983) might be expected to respond to threats in similar ways to gravid females. A large meal obviously represents a large payload of energy for future use, but also it can be costly. On at least two occasions, I have encountered snakes (one *T. sirtalis* and one *N. natrix*) that had eaten such large meals that they could hardly move. Their bodies were so distended in the stomach region that they mainly rocked back and forth when they tried to flee—easy pickings for me and no doubt for other predators.

Snakes that do not flee as the predator approaches may be confronted with exploratory examination by the predator before attack or a direct attack. Many studies mimic this situation of close approach and/or initiation of attack by approaching the snake with a finger, either held stationary or moving (Herzog and Burghardt, 1986), or touching the snake directly on some part of the body (Mori and Burghardt, 2000; Langkilde et al., 2004). In other cases, a model of an actual predator may be used to simulate approach and attack of a predator (Shine et al., 2000). Finally, attack may be simulated simply by catching the snake by hand and handling it (Gregory, 2008a). Collectively, these approaches have yielded a rich diversity of responses of snakes to approach and capture by simulated predators.

Studies in which snakes are exposed to escalating levels of threat (e.g., from approach to actual contact) show that defensive behaviors change as the approach of a predator becomes more threatening (Schieffelin and de Queiroz, 1991; Bowers et al., 1993). Although the sequence of behaviors employed as threat increases varies among species, the general pattern is to shift from more aggressive defense (e.g., striking) toward either more passive displays (e.g., head hiding, Fig. 5) or flight (Schieffelin and de Queiroz, 1991; Bowers et al. 1993). Aggressive behaviors are presumably attempts to intimidate the predator, buying time to escape, especially if directed at vulnerable parts of the body (e.g., eyes; Herzog and Bern, 1992), whereas behaviors such as head hiding (typically under or within the coiled body) protect the more vulnerable parts of the body from attack. Similarly, tail-waving, which also is a common behavior in such situations (Bowers et al., 1993), may serve to direct the predator's attention toward a less vulnerable part of the body (Langkilde et al., 2004). Tail injuries, including loss of parts of the tail, are common in natricines (Gregory and Isaac, 2005; Placyk and Burghardt, 2005, references therein). Given this variation in vulnerability of different parts of the body, where the body is touched by the "predator" may influence what behavior is shown in response (Arnold and Bennett, 1984; Langkilde et al., 2004). Finally, even when caught and handled, natricine snakes may continue to exhibit antipredator behaviors, such as struggling and twisting, biting, or expelling the contents of their cloacal glands, as well as feces and urine ("musking" behavior; cloacal smearing); the latter presumably makes the snake malodorous and unattractive to predators (Gangloff et al., 2014; Gray, 2015). Some behaviors, such as death-feigning, may be exhibited only when the snake is handled (Gregory et al., 2007; Gregory, 2008a). Studies of Tiger Keelbacks (*Rhabdophis tigrinus*), for example, often fail to reveal death-feigning behavior (Mori and Burghardt, 2001) unless significant handling is involved (Mutoh, 1983). Death-feigning is much easier to induce in *N. natrix*, but degree of handling and where on the body the snake is held still influence occurrence of

FIG. 5. Head-hiding behavior in a *Thamnophis radix*.

this behavior (Gregory, 2008a; Fig. 6). Among other natricines, at least four species of *Thamnophis* (Gregory and Gregory, 2006; Schield and Waye, 2012; Enge, 2015), two species of *Storeria* (Jordan, 1970; Gerald, 2008), and one species of *Regina* (Oldham et al., 2015) may exhibit elements of death-feigning behavior when handled.

Once an animal is caught by a predator, its options for escape are much more limited, but until the prey is dead, all is not necessarily lost. Escape from consumption might be possible via some of the behaviors discussed above. For example, struggling while held by the predator may cause the predator to lose its grip (L. A. Isaac, pers. comm.); many natricines also spin their bodies when held by the tail, apparently attempting to break the tail and escape (Cooper and Alfieri, 1993). Biting the predator while in its clutches also might deter the predator or perhaps simply irritate it further (Fig. 7). Some species, such as Watersnakes (*Nerodia*) are renowned for reacting to capture by biting vigorously. Not only do *Nerodia* bites sting, but they often bleed profusely. Of course, the hardened herpetologist ignores all this and hangs onto the snake, but biting might be an effective deterrent against other predators (including humans) in this case.

Prey with chemical defenses have other options for deterring predators. *Rhadophis tigrinus* have dorsal nuchal glands, shared by only a few other species, just behind the head. Snakes sequester steroid toxins in these glands, obtained from Japanese Common Toads (*Bufo japonicus*) that they eat, and present the glands to oncoming predators; snakes from sites where toads are not present do not exhibit this behavior (Mori and Burghardt, 2000; Hutchinson et al., 2007; Hutchinson et al., 2013). Such behavior is clearly associated with nuchal glands because it is absent in close relatives that eat toads but lack nuchal glands (Takeuchi and Mori, 2012). Young *R. tigrinus* also obtain toxins as maternal provisions during embryonic development (Hutchinson et al., 2008); this provision presumably is enhanced by selective foraging of gravid females in habitats where they are likely to encounter toads (Kojima and Mori, 2014). Other natricines that eat poisonous prey also might use ingested toxins in their own defense (Williams et al., 2012), especially if paired with aposematic coloration (Williams et al., 2004).

Death-feigning, discussed above, is an example of a last-ditch attempt, perhaps a desperate one, to avoid death. Predators that relax their grip when a prey is apparently dead may momentarily look away, allowing the prey to escape. Alternatively, predators that cache their prey may mistakenly cache a death-feigning prey, which could escape when left alone. Clearly, however, this strategy will not work against a predator that kills and consumes its prey immediately. Unfortunately, we do not know how often death-feigning snakes use this behavior against real predators or whether they use it only against certain predators (see quotation at beginning of this article). This is true of virtually all the antipredator behaviors that we have described for snakes—we simply do not know whether they are used against real predators and in what context. This leads to the first of several overlapping areas in which we need to increase our knowledge about how snakes interact with their predators.

SOME AREAS FOR FURTHER RESEARCH

Context.—Context is of paramount importance in eliciting (and understanding) antipredator behavior of natricine snakes (and other animals). Defensive behaviors within species can vary geographically (Placyk, 2012), even at small scales (Shine et al., 2003b). Different species have different morphological, physiological, and ecological attributes that influence their "decision" about defensive tactics in a given situation. Small (often young) snakes face different risks from large ones, and gravid snakes, whose locomotion is compromised (Seigel et al., 1987), face

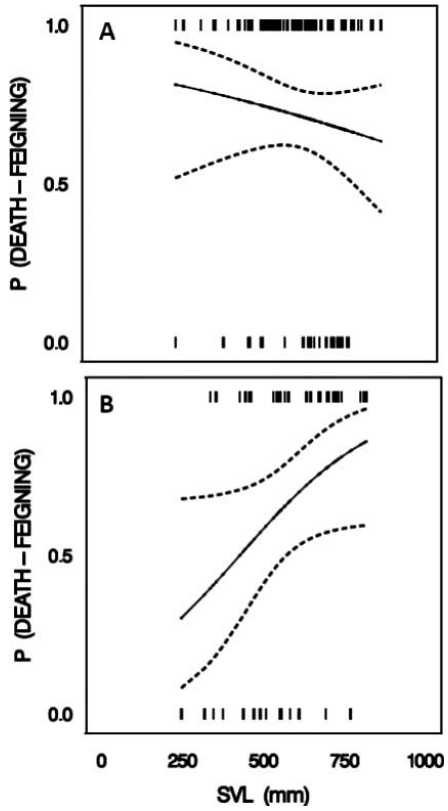

FIG. 6. Logistic regressions of probability of death-feigning vs. SVL for Grass Snakes (*Natrix natrix*) subjected to one of two treatments. (A) "Fully handled" snakes that were passed back and forth in the hands for 30 sec immediately upon capture and then subjected to routine handling and measurement plus being grasped at back of head for measurement of head size. (B) "Less-handled" snakes subjected to routine handling and measurement only. Solid line is predicted logistic regression, and dashed lines are 95% confidence limits around that prediction; vertical lines at top and bottom are data (snakes that feigned death and those that did not, respectively). Regression statistics: (A) $\chi^2_1 = 0.72$, $P = 0.40$, $N = 97$; (B) $\chi^2_1 = 3.69$, $P = 0.055$, $N = 43$. Data from Gregory (2013), but figure not shown there. For further details, see that reference.

different challenges from nongravid snakes. Thus, it is no surprise that the display of different defensive behaviors is influenced by multiple factors (e.g., Greene, 1988), including both genetic and environmental (Arnold and Bennett, 1984; Garland, 1988; Webb et al., 2001; Placyk, 2012), and that those factors can interact in complex ways (Shine et al., 2000). Often, no clear patterns exist, as is the case for the effects of temperature on many defensive behaviors (e.g., Mori and Burghardt, 2004). However, locomotory speed (and, hence, potential flight speed) typically increases with temperature (e.g., Isaac and Gregory, 2007).

Numerous informative studies have been done in the laboratory, where conditions can be controlled and standardized, and have revealed consistency of behaviors within individuals (Arnold and Bennett, 1984; Brodie, 1993; Brodie and Russell, 1999). Unfortunately, the laboratory setting may lack numerous aspects of essential context for interpretation of what is observed. We need to take more advantage of natural situations in the field, where we can assess the effects of multiple factors simultaneously on defensive behavior. Situations where we can generate sufficient sample size in a short time to detect often relatively weak signals in the data are fairly rare (Shine et al., 2000), but many species of natricines are abundant and easily found in the field (Gray, 2015).

Watching snakes for long periods of time is usually a tricky proposition that is only sometimes feasible, and I generally lack the patience for it in any case, but much can be learned from short-term observations. Generally speaking, we can readily observe what snakes are doing when they are first encountered, how they respond to being approached and captured, and how they behave upon release. Capturing a snake is essentially an act of predation, albeit lacking the violence with which serious predators may act. Therefore, the capture occasion represents an opportunity to collect data on antipredator behavior and to test hypotheses by comparing responses to different experimental treatments (e.g., handling regime following capture) and by comparing different categories of animals (e.g., small vs. large, gravid vs. nongravid), along with relevant covariates (e.g., body temperature).

Laboratory experiments will continue to be important in this area, but perhaps we could bring more context into play. For example, given that snakes have highly developed chemical senses, how might odors of different potential predators influence how snakes respond? Juvenile *T. elegans* avoid shelters with odors of adults, which are sometimes cannibalistic (Waye and Gregory, 1983). Both *T. elegans* and *T. sirtalis* flick their tongues at a heightened rate in response to odors of ophiophagous snakes compared to odors of other snakes or blank controls (Weldon, 1982); this indicates both an ability to discriminate different species and increased arousal at evidence of a threat. Combining chemical and visual stimuli might be a useful approach to studying antipredator behavior in these animals.

Humans as Proxies for Real Predators.—According to the instructions for writing this paper, I am limited in the extent to which I can use anecdotes. Fair enough—anecdotes are not data and are not collected in any kind of systematically rigorous way. They do, however, often cause us to ask questions and, in that sense, form the basis for hypotheses that we might want to test formally. I raise this issue in the context of considering whether humans are suitable proxies for real predators in studies of antipredator defenses of snakes. Humans (or novel objects resembling predators) are often used this way and do appear to induce defensive behaviors in snakes, but are those behaviors the same as would be used in response to actual predators or as intense as natural responses? I offer two pertinent anecdotes; a third is described in Gregory (2004).

First, observations of natural encounters between snakes and their predators are generally rare and opportunistic, but we do occasionally make them. In this case, I observed a mink, nose to the ground, moving along the grass bordering a fish hatchery channel, evidently foraging. The wind direction being favorable and the mink's head pointed away from me, I quietly followed this animal for a few minutes. The mink was ambling along at a fairly leisurely pace until it came across a clump of longer grass, and its attention suddenly became focused on that clump. Just as suddenly and almost simultaneously, a gartersnake (*T. sirtalis*) shot out from the clump of grass at what seemed to me a record speed, whereupon it was immediately pursued by the mink. The snake dived into the channel, rapidly followed by the mink. Fortunately for the snake, the mink veered off in the wrong direction once in the water and the snake made good its escape. What impressed me about this encounter, though, was the speed and intensity of the snake's response to the mink—I obviously took no measurements, which makes this truly

FIG. 7. A newly captured *Thamnophis elegans* vigorously bites the author's wrist. Photograph by G. Gregory.

anecdotal, but I do not think I have seen any gartersnake move with such urgency in response to my approach. Real life-and-death situations call for desperate effort, but can snakes somehow distinguish the differential threat posed by a mink and a benevolent human?

I do not know the answer to that question, but I will mention one more anecdote that suggests that snakes do not always "see" humans as serious threats. Terrestrial Gartersnakes (*T. elegans*), which are often aquatic, occasionally bite vigorously when caught (Fig. 7; Gregory, 2008b), but they also often respond to handling by humans as if capture itself poses little threat. When I catch a snake that has food in its stomach, I sometimes gently palpate the food up to the snake's mouth to identify it and, then, if possible, gently push it back into the snake's stomach so that I do not deprive it of its meal. Individuals of many species resist re-swallowing their food, and I sometimes have to abandon the effort. But *T. elegans* are different. First, they will often start to re-swallow food that I have brought up to their mouths before I can properly identify it. Second, even if they regurgitate the food, I often just have to put it back in the snake's mouth and the snake will swallow it while sitting in my hands. This sort of behavior does not seem to me to be one that a snake should engage in if in a life-threatening situation, which would be the case if I were a real predator. Perhaps despite the various measurements that I take from snakes, including prodding and poking here and there, this handling is simply too gentle to be recognized as a serious threat, at least for some snakes. Real predators bite and claw their victims, cutting them and breaking their bones. It is perhaps not surprising then that "rougher" handling can stimulate stronger putatively defensive behavior than does gentle handling (Greene, 1997; Gregory, 2008b; Placyk, 2012). However, there are ethical limits to how far we can use humans as proxies for real predators.

Perhaps there is a difference between a snake's perception of a human as a potential predator when first approached and when actually handled. Therefore, studies of approach distance using humans might be generally valid, whereas studies based on handling may require more care. Corticosterone (CORT) levels in natricines do increase in response to capture and handling, indicating stress (Moore et al., 2000; Palacios et al., 2012). The question is: how does this level of stress and attendant behavior compare with those observed in more threatening captures by predators with serious intent?

Color and Pattern.—Snakes exhibit considerable variation in color and pattern, both interspcifically and intraspecifically, the latter including geographic variation between populations (Isaac and Gregory, 2013) and polymorphism within populations (Brodie, 1990). Color and pattern are two separate and distinct characters of snakes that I lump together here for convenience. However, they may or may not be correlated genetically in different populations of the same species (Westphal, 2007). Color and pattern have various functions (e.g., heat absorption and reflection), but, as indicated earlier, they also play a major role in avoiding predation.

Ontogenetic change in color and pattern is common in snakes and can be expected to be correlated with antipredator behavior, but this issue has not been explored extensively in natricines. In Mexican Black-Bellied Gartersnakes (*Thamnophis melanogaster*), subadults are more variable in color and pattern than are adults (Gregory et al., 1983), but whether this results from ontogenetic change or selective mortality is unknown. Body patterns of *T. ordinoides* become somewhat brighter during growth in early life (Brodie, 1993); striped individuals become more markedly striped, whereas unstriped individuals do not change. Although individuals are consistently different in their pattern-related antipredator behaviors, there is an overall increase in sprint speed, whereas reversals in escape direction decline with age

(Brodie, 1993). In western populations of *T. sirtalis*, red pigmentation increases in intensity with age in some populations but not in others (Westphal and Morgan, 2010), but how this is related to antipredator behavior is unknown. Juvenile *N. natrix* have a much brighter yellow collar (nuchal spot) behind the head than do adults, although the color varies with developmental temperature (Hagman et al., 2015). Madsen (1987), based on experiments with plasticine models in the field in which models with collars were attacked by birds less than those without, suggested that the yellow collar of juveniles is aposematic, mimicking the color of unpalatable insects. Perhaps correspondingly, small *N. natrix* feign death less readily than do adults (Gregory et al., 2007; Gregory, 2008a; Hagman et al., 2015). The area of ontogenetic change in color pattern and coincident antipredator behavior is rich with possibilities for further study.

Melanism is widespread in natricines, either as an occasional occurrence within populations (Mollov, 2012) or as a regularly occurring morph (Lawson and King, 1996), often at high frequency. It may play a modest role in thermoregulation, but differences between melanistic and "normal" striped morphs of *T. sirtalis* are small (Gibson and Falls, 1979; Bittner et al., 2002). Black specimens are conspicuous on many backgrounds, but clay models of melanistic and striped morphs of *T. sirtalis* are attacked equally often by birds (Bittner, 2003).

Most studies of color and pattern in snakes have relied on relatively subjective and/or human-based assessments of, for example, color and contrast with background. We can now assess snake and background colors from the point of view of the visual systems of different types of predators using spectrophometry. Such work is in its infancy, but two geographically separated color types of *T. elegans* exhibit chromatic crypsis against bird and mammal visual systems (Isaac and Gregory, 2013). That study suggests that snakes use basking sites nonrandomly and that sites used for basking provide more crypsis than do sites chosen at random. Do snakes actively select basking sites for their cryptic characteristics? If so, how do they do it? Whatever the answers to these questions, spectrophotometry offers an objective way to measure color, opening the door to quantitative assessment of the extent to which color is correlated with antipredator behaviors.

Experience.—Can snakes learn from the experience of escaping predation to modify their subsequent behavior in similar situations? This should apply particularly to individuals that have had a close brush with predation. Such close calls evidently happen often, given the high frequency of injury in many populations of natricine snakes (Gregory and Isaac, 2005). In laboratory tests, adult *T. sirtalis* with previous injuries do not differ in their antipredator responses from uninjured adults (Placyk, 2012). In contrast, in the field, "experienced" (i.e., injured or captured previously) *N. natrix* are more likely to attempt to flee before capture than are "naïve" snakes that have not been injured or caught previously (Gregory, 2013), but evidence on this point is otherwise lacking. In the laboratory, chronic differences in handling of young *T. sirtalis* result in differences in frequency of subsequent antipredator behaviors (Herzog, 1990; Placyk, 2012).

Snakes might also habituate to apparently threatening stimuli (e.g., movements of non-predator animals) if they have experiences with them that do not lead to predation attempts (Hampton and Gillingham, 1989; Herzog et al., 1989), just as captive snakes adjust to handling by humans by decreasing their defensive behavior.

Injuries and Predation Regime.—Predators can have direct effects on the population dynamics of prey, by killing prey, or indirect effects, simply by their presence influencing critical activities of the prey, such as foraging (Lima and Dill, 1990; Ferrari et al., 2009). In between these two extremes are close encounters with predators that leave the prey alive but injured. Injuries are common in animals, including natricines (e.g., Gregory and Isaac, 2005). Although some injuries may be routine "wear and tear" or derived from non-predatory misadventure, most authors assume that most injuries result from failed predation attempts. Injury rates may be higher when predators are more abundant (Santos et al., 2011), but it does not follow that injury rate is indicative of mortality rate attributable to predation (see below). Studies that address the population-level consequences of injury are sorely needed. Body condition of *N. natrix* that have been injured previously is lower than that of uninjured snakes, although differences are nonsignificant (Gregory, 2013). Whether future survivorship or reproductive output is impaired in injured individuals is unstudied.

One idea that is unexplored in snakes is that some individuals may be injury avoiders and others injury survivors (Seligmann et al., 2003). As noted above, *N. natrix* with injuries are more likely to move before capture than are those without injuries, which I attribute to negative experience with a predator (Gregory, 2013). However, an alternative hypothesis, offered by Richard Shine (University of Sydney, pers. comm.), is that snakes that move early are more likely to be detected by predators and, therefore, more likely to receive injuries as they try to escape. I think this unlikely, especially given that snakes that have been captured previously also show the same effect, independent of injury (Gregory, 2013), a result best attributable to prior experience. However, Seligmann et al.'s (2003) ideas of different strategies with respect to injury might well be worth exploring.

Another idea from the same authors that merits investigation is that frequency of injury is lower with specialized predators, which are likely to be especially effective killers, than with opportunistic generalist predators (Seligmann et al., 1996, 2003). Thus, for example, we might predict that snakes from within the range of specialized snake-eaters (e.g., Short-Toed Eagles, *Circaetus gallicus*; Gil and Pleguezuelos, 2001) are more often killed rather than escape and, therefore, have a lower rate of injury than do conspecifics from outside that range. This parallels my earlier suggestion that death-feigning might be an effective antipredator behavior only where predators are generalists because a specialized predator would quickly adapt to the ruse (Gregory, 2008a).

Predation regime, or the diversity of potential predators to which snakes might be exposed, therefore might influence the kinds and intensity of antipredator behaviors displayed. Adult *T. sirtalis* from sites with more kinds of predators exhibit various defensive displays more frequently than do snakes from sites with fewer predators; however, this pattern is not seen in neonates, which generally display more intensely than adults (Placyk, 2012).

Fear, Stress, and Physiology.—Can snakes detect and assess levels of predatory risk in their surroundings? Such perceived risk constitutes a so-called landscape of fear (Laundré et al., 2001; Zanette et al., 2011), which can change spatially and temporally. Predators, merely through their regular presence in an area, may exert population-level consequences on prey above and beyond any actual or attempted predation. For example, animals under fear-induced stress may spend more time in refuges and less time foraging, ultimately reducing growth and reproduction. Thus, snakes in areas with particularly dangerous or abundant predators might be under greater stress and exhibit different

antipredator behavior from those in less risky environments. Chronic stress can be determined directly by measuring CORT levels or indirectly by measuring the ratio of heterophils to lymphocytes in blood (Bell and Gregory, 2014). In *T. elegans*, both baseline and handling-stress CORT levels differ between two life-history ecotypes (Palacios et al., 2012), with the slow life-history ecotype showing higher levels than the fast life-history ecotype (Palacios et al., 2012); the former ecotype exhibits higher rates of bird-induced injury, but the latter ecotype is exposed to more predators (Sparkman et al., 2013), which might translate into higher mortality rather than injury. Thus, without measures of actual intensity of predation (tricky to measure, to be sure), we cannot determine how baseline levels of CORT vary between areas with different risks of predation. Similarly, whether and how baseline CORT levels are linked to expression of different defensive behaviors is an open question, but such effects have been seen in other animals (Mateo, 2007).

Stress aside, the effects of physiological variation in general on defensive behavior would benefit from more study. For example, ecdysis, or shedding of the outer epidermis, is a time of physiological change in snakes that should be expected to affect susceptibility to predators and, hence, antipredator behavior, especially during the "cloudy" or "blue" phase preceding actual ecdysis when a snake's vision is expected to be compromised. During ecdysis (and at rest at other times), blood vessels in the spectacle over the eye remain dilated, but non-shedding snakes may improve their visual acuity when threatened by constricting the blood vessels in the spectacle, thereby making those blood vessels less visible and less occluding (van Doorn and Sivak, 2013). Cloudy-eyed snakes feed less than clear-eyed snakes and are presumably less active (King and Turmo, 1997) and likely seek shelter (choosing warm over cool shelters in the laboratory; Gibson et al., 1989). Cloudy-eyed *T. sirtalis* modify their response to predatory stimuli, showing a greater latency to move and a longer response distance to disturbance than do clear-eyed snakes, as well as a greater strike rate at a moving target (but not a stationary one; King and Turmo, 1997). Overall, however, the relationship between ecdysis and antipredation behavior is relatively unstudied.

Conclusion

A colleague once described my approach to research as "analytic natural history." Whether I am sufficiently analytic or not is a question I leave for others to answer, but the term "natural history" is certainly one I embrace, including (perhaps inadvisably) in grant applications. By natural history, I mean the study of organisms in their natural habitats. In my view, natural-history research is not necessarily purely observational, as some would argue, but can readily accommodate tests of hypotheses. Controlled experiments in both field and laboratory obviously play a central role in ecology and behavior, but studies of the unrestrained, free-ranging animal bring another kind of truth, a different window into the animal's daily life. My bias toward this kind of field study underlies much of what I have written in this review.

Studying behavior of snakes can be tricky, especially in the field. Snakes are built low to the ground and generally cryptic, even when active, which makes them difficult to observe directly. Also, they can sometimes be difficult to watch simply because the observer might fall asleep waiting for something to happen. I once found the same individual gartersnake, preparing to shed its skin, under the same cover object for several days in a row. I have occasionally seen snakes feeding in the field but not often, and, in most of my study sites, I probably could spend another career waiting for another observation. However, encounters with predators, or predator-like stimuli, including humans, always elicit measurable behavioral responses from snakes, even in the form of immobility. These responses and their correlates can be measured in the field.

Reptiles often are excellent "model organisms" for studies of various general phenomena in biology (Luttershmidt, 2013). Like any other organism, reptiles have their own unique combinations of traits and cannot be perfect models for all other organisms, but broad principles should apply. Natricine snakes are smallish animals that presumably encounter risks similar to those faced by other vertebrates in the same size range. Although details of their antipredator tactics differ from those of other animals, they are faced with similar trade-offs in their behavioral "decisions." Thus, studies of antipredator behavior of natricines should bear extrapolation not only to other snakes but, with a wider view, to other animals.

In this review, I have sketched out the broad patterns of defensive behavior in natricine snakes and suggested areas in which we might profitably extend our knowledge. My review has necessarily been selective, and I have ignored important areas such as phylogenetic distribution of traits and what that might tell us about evolutionary patterns and adaptive convergences. Similarly, although size and age must have profound effects on antipredator strategies, I have only hinted here and there at the complexities of ontogenetic change. Finally, body temperature, especially in interaction with other factors, is sure to play an important role in the expression of antipredator defenses, but again I have only touched upon it; it deserves a separate treatment.

Natricine snakes exhibit a diversity of antipredator behaviors that they deploy at various points in an encounter with a predator. However, we know little about use of these behaviors against predators other than humans nor about their adaptive value. Furthermore, antipredator behavior presumably has links to other phenomena such as acquisition of injury and stress, which in turn have potential population-level consequences. We need to integrate the study of antipredator behavior in these animals more closely with population and physiological ecology.

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