Natural History Note

When Dinner Is Dangerous: Toxic Frogs Elicit Species-Specific Responses from a Generalist Snake Predator

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ABSTRACT: In arms races between predators and prey, some evolved tactics are unbeatable by the other player. For example, many types of prey are inedible because they have evolved chemical defenses. In this case, prey death removes any selective advantage of toxicity to the prey but not the selective advantage to a predator of being able to consume the prey. In the absence of effective selection for postmortem persistence of the toxicity then, some chemical defenses probably break down rapidly after prey death. If so, predators can overcome the toxic defense simply by waiting for that breakdown before consuming the prey. Floodplain death adders (*Acanthophis praelongus*) are highly venomous frog-eating elapid snakes native to northern Australia. Some of the frogs they eat are nontoxic (*Litoria nasuta*), others produce gluelike mucus when seized by a predator (*Limnodynastes convexiusculus*), and one species (*Litoria dahlii*) is dangerously toxic to snakes. Both the glue and the toxin degrade within about 20 min of prey death. Adders deal with these prey types in different and highly stereotyped ways: they consume nontoxic frogs directly but envenomate and release the other taxa, waiting until the chemical defense loses its potency before consuming the prey.

Keywords: antipredator tactics, coevolution, evolution, predator-prey systems, prey release.

In many predator-prey systems, predators exhibit species-specific tactics that enable them to capture particular types of prey, and prey exhibit a range of antipredator tactics that reduce their vulnerability to predation (Edmunds 1974). Prey defenses range from behavioral (e.g., shifts in diel activity patterns, enhanced vigilance) to morphological (e.g., spines, tail autotomy) and physiological (e.g.,

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toxins) traits. In all cases, the individual fitness benefit derived from a particular defense is straightforward: the antelope that escapes the lion lives another day and thus has a greater chance to reproduce.

Predators tend to exert asymmetrically strong selection on their prey whereby selection is strong on prey to evade capture (the prey risks its life) but selection is weak on the predator (which only risks its meal; Abrams 1986, 2000; Vermeij 1994). This selective asymmetry may well become more equitable, however, when prey are dangerous (Brodie and Brodie 1999). Nevertheless, in all cases there is strong selection on prey to avoid predation. In this article, we explore a loophole in these adaptive pathways: a route by which predators can deal with prey defenses in a way that is not opposed by selection working on the prey. This pathway results from an asymmetry in the time course over which selective forces operate on prey versus predator during a predator-prey interaction. Individual selection on the prey effectively ceases when the prey animal dies because anything that happens after that time does not affect the animal's fitness (excepting instances where kin selection operates; Fisher 1930; Brodie and Brodie 1999). In contrast, the benefit to a predator from consuming a prey item persists long after prey death, until other factors such as putrefaction or theft by scavengers removes the nutritional benefit available from the prey. Hence, we might expect that many of the antipredator tactics exhibited by prey items cease to be effective soon after the prey dies and that predators will evolve to exploit that fact by judicious waiting after prey death until the antipredator mechanism becomes ineffective. Our data on a generalist snake predator reveal an example of this scenario, whereby specific predator behaviors, manifested after prey death, enable snakes to overcome the chemical defenses of toxic frogs.

First, we briefly review the conceptual basis for the asymmetry posited above. In the absence of group or kin selection, there is no fitness advantage for a prey individual to maintain its antipredator defenses after death. Nonetheless, some antipredator mechanisms remain effective:

for example, a porcupine's spines are still capable of wounding after the death of the porcupine. Similarly, toxic prey will likely remain toxic for some time postmortem. Parsimony suggests that such situations are not the result of selection but instead are accidental flow-on effects of a defensive strategy that worked in life. Nevertheless, postmortem persistence of antipredator mechanisms does exert selection on the predator; a predator that kills or maims itself on a dead prey item has had its fitness curtailed. Thus, although dead prey can still exert selection on their predators, postmortem prey defenses will not evolve in direct response to selection by predators, and thus coevolution (sensu stricto) will not proceed with regard to postmortem prey defenses. Therefore, predators should evolve strategies to deal with these risks: if a predator can defeat the defensive tactics of its live prey, it can also develop strategies to ameliorate any postmortem danger posed by that prey, and there is no selection acting on the prey to prevent this from happening.

The above is true in the absence of kin selection. In situations where kin selection is strong (e.g., social insects), however, selection can proceed postmortem via indirect fitness benefits accrued by the dead individual's close relatives. Thus, postmortem prey defenses may be selected for if they give an individual's relatives increased fitness by, for example, killing a predator that may have preyed on relatives in the future. More realistically, postmortem prey defenses may increase predator handling time and give relatives time to escape. While kin selection can be invoked to explain the evolution or maintenance of postmortem prey defenses, kin selection is far from ubiquitous (Griffin and West 2002), and so in the absence of strong evidence suggesting its operation, the evolution of postmortem prey defenses should be seen as most likely an accidental by-product of defenses that act in life (as described in the previous paragraph).

Toxic food items provide clear examples of prey that remain dangerous after death. Although toxin detectability and distastefulness may evolve in response to selection from predators (Brodie and Brodie 1990; Vanhoye et al. 2003; Pukala et al. 2006), there is unlikely to be selection for toxin longevity postmortem. Thus, although some prey may remain toxic for days or months after death, others may remain toxic only briefly after the prey has died. Toxin longevity likely will depend on the chemistry of the toxin involved rather than on the toxin's defensive role. Thus, a prey item that is too poisonous to eat nonetheless may become edible sometime after its death. Hence, a predator that is able to kill the prey without ingesting a fatal dose of toxin may circumvent this prey defense simply by delaying its ingestion of the item.

Methods

Study System and Species

All animals were collected from the Adelaide River floodplain, near Darwin in the Northern Territory. The Adelaide River floodplain contains many snake and frog species; most snake species in the area eat frogs (Shine 1991; B. Phillips, unpublished data).

The floodplain death adder (*Acanthophis praelongus hawkei*; Wuster et al. 2005) is a dangerously venomous, ambush-foraging elapid snake of northern Australia. Floodplain adders grow to a maximum size of 750 mm (mean of 99 field-captured animals = 460 mm, SD = 136 mm; B. Phillips, unpublished data). Most of their diet consists of frogs, although juvenile adders feed primarily on lizards, and very large death adders commonly take rats (Webb et al. 2005).

Of the prey species, one (the rocket frog *Litoria nasuta*) is relatively nontoxic and relies on its prodigious leaping ability to escape predation (hence the common name). The marbled frog (*Limnodynastes convexiusculus*) is a burrowing species with short legs (and concomitantly low jumping ability), which secretes a gluelike substance when irritated. Adhesive secretions are common antipredator devices in amphibians (see, e.g., Williams et al. 2000; Kizirian et al. 2003) and can be devastatingly effective against snake predators (Arnold 1982; Evans and Brodie 1994). Although the chemical basis of *Lim. convexiusculus* secretions is unknown, the glue dries rapidly and is difficult to remove from skin (B. Phillips and R. Shine, personal observation), which presumably poses a risk to snakes. The third species (Dahl's aquatic frog *Litoria dahlii*) is highly toxic to most snake species, including floodplain adders (Madsen and Shine 1994). The toxin is composed of active peptides (the dahleins; Wegener et al. 2001) that strongly inhibit neuronal nitric oxide synthase, a molecule of major importance to intracellular communication (particularly in the circulatory and nervous systems; Pukala et al. 2006). The low antimicrobial activity of dahleins suggests that they have a purely antipredator function (when force-fed *L. dahlii*, most snakes died within 20 min; Madsen and Shine 1994).

The likelihood of kin selection is low in this system. None of our study species show parental care; all simply deposit offspring/eggs and have nothing further to do with them. In the frog species there may be a temporary spatial concentration of relatives around the period when tadpoles first metamorphose, but this represents only a brief moment in the life history, and there is no evidence that death adders concentrate their feeding effort around bodies of water or on metamorph amphibians. Thus, any postmortem prey defenses in this system are most likely accidental by-products of defenses that work in life.

Snakes were housed individually in glass terraria (floor area = 400 mm × 200 mm), with a paper substrate and ad lib. water in a small dish. Once every six nights, a prey item was introduced to each snake's cage in the evening (within an hour of sunset), and a video recorder was set to record the following 2 h of activity. Lighting was provided by a red lamp. Prey items were weighed and then introduced to each snake in random order, and each snake was tested with each type of prey item only once.

After a successful strike from an adder, the following variables were recorded: (1) whether the prey item was released after the initial bite and, if so, the time between bite and release; (2) whether the snake gaped following the release of the prey and, if so, the time between releasing the prey and cessation of gaping; (3) whether the snake commenced trail-following activity (characterized by sweeping head movements and repeated tongue flicking) after gaping/release and, if so, the time between gape/release and the commencement of trail following; (4) the time it took the snake to find the prey item after the commencement of trail following; (5) the total time between striking the prey and commencing to ingest the prey (defined as the moment the prey was picked up again following a release or the moment the jaw began moving for those prey held); and (6) the time taken to ingest the prey item (all prey items that were struck were eventually ingested).

When initial results showed that adders waited some time after the initial bite before attempting to consume *Lim. convexiusculus* (see "Results"), we hypothesized that this delay might enable the frog's gluey secretions to dry before the predator ingested it. If so, we would expect that the secretory glue rapidly becomes ineffective (i.e., nonsticky) within the time interval that most snakes waited. To test this hypothesis, we quantified this effective duration of "glueyness" with a procedure modified from that of Evans and Brodie (1994). Three replicate samples of glue were collected from each of five *Lim. convexiusculus* by lightly scraping their skin surface with a pair of forceps. The resulting secretion was smeared onto a 1-cm² area of cardboard (the test patch). One of the samples was tested immediately, another was tested after 6 min, and the third was tested after 12 min. The bonding capacity of the secretion was tested by pressing a fresh 1-cm² piece of cardboard onto the test patch for 1 min before forcibly separating the two pieces of cardboard. The amount of force required to separate the two pieces of cardboard was measured using a spring balance.

Statistical Treatment

All categorical comparisons (e.g., prey item vs. held/released) were made using a simple contingency table and the likelihood ratio test. Most of the data on feeding times (with the exception of ingestion time) were highly left skewed, so we used Kruskal-Wallis tests on these data. Ingestion time was approximately normally distributed, so in this case we used multiple regression. We analyzed the effect of time on the adhesive strength of *Lim. convexiusculus* secretions using a simple least squares regression.

Results

Hold/Release

Adders never released *Litoria nasuta* after the initial strike, they occasionally released *Limnodynastes convexiusculus* (35% of encounters), and they always released *Litoria dahlii* after the strike and before attempting ingestion (likelihood ratio $\chi^2 = 46.9$, df = 2, $P < .0001$; fig. 1). Some frogs were bitten, released, and then bitten and released again.

Gaping

On releasing prey, snakes often gaped (fig. 2). After excluding all instances where a prey item was held (which included all interactions with *L. nasuta*), prey types differed in the tendency to elicit gaping by the snake (likelihood ratio $\chi^2 = 8.8$, df = 1, $P = .003$; fig. 2). Snakes gaped in 33% of release encounters with *Lim. convexiusculus* and in 94% of encounters with *L. dahlii*.

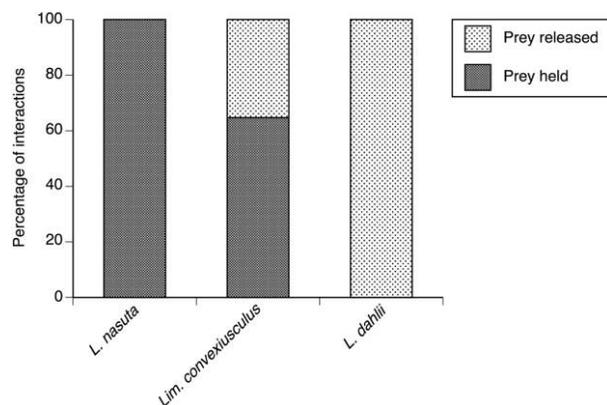The amount of time spent gaping also varied signifi-

Figure 1: Percentage of interactions in which a snake either released or held the prey item. *Litoria nasuta* were always held, *Limnodynastes convexiusculus* were released occasionally, and *Litoria dahlii* were always released.

cantly between prey types (Kruskall-Wallis $\chi^2 = 4.8$, df $= 1$, $P < .03$), with adders gaping for longer after biting a *L. dahlii* than after biting a *Lim. convexiusculus* (fig. 2*B*).

Trail Following

Typically, trail following commenced immediately after gaping (median delay of 60 s, no significant difference between prey types: Kruskall-Wallis $\chi^2 = 2.5$, df $= 1$, $P = .12$). Prey were usually dead (from envenomation) well before trail following commenced.

Tasting

Occasionally, a trail-following snake would taste and reject the prey item after locating it. This behavior involved grasping the dead prey gently and then releasing it (sometimes with further gaping). One snake tasted and rejected the same *L. dahlii* 18 times before eating it. The two toxic frog species were equally likely to elicit tasting by the predator (*L. dahlii* were tasted 47% of times, *Lim. convexiusculus* 33% of times: likelihood ratio $\chi^2 = 0.4$, df $= 1$, $P = .56$).

Total Delay

Overall, the total delay between striking and the onset of ingestion differed strongly between prey types (Kruskall-Wallis $\chi^2 = 24.13$, df $= 2$, $P < .0001$; fig. 3*A*). The median delay between initial strike and ingestion was 42 min for *L. dahlii*, 10 min for *Lim. convexiusculus*, and 0 min for *L. nasuta*.

Consumption Time

The total consumption time is likely to depend not only on the prey type but also on relative prey size. Consumption times were approximately normally distributed, so to test these effects we used standard multiple regression. After removal of the nonsignificant interaction term (prey × relative prey mass, $F = 1.67$, df $= 2, 38$, $P = .20$), there was no significant effect of relative prey weight on consumption time ($F = 0.61$, df $= 1, 40$, $P = .44$), but there was a slight effect of prey type ($F = 3.54$, df $= 2, 40$, $P = .04$), with *L. nasuta* being consumed the fastest, followed by *Lim. convexiusculus* and *L. dahlii* (fig. 3*B*).

Adhesive Strength of Lim. convexiusculus *Secretions*

The skin secretions of *Lim. convexiusculus* rapidly lost their bonding capacity ($F = 32.5$, df $= 1, 13$, $P < .0001$; fig. 4). The mean force required to separate cardboard squares
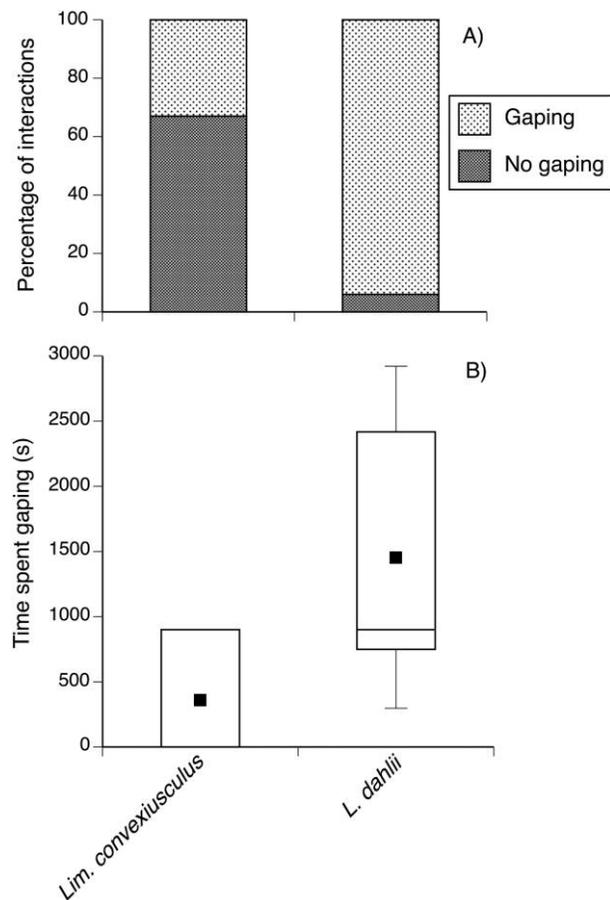

Figure 2: *Top*, death adder gaping after biting a *Litoria dahlii*. *A*, Percentage of postrelease interactions in which the snake gaped. Snakes gaped more often with *L. dahlii* prey than with *Limnodynastes convexiusculus*. *B*, Snakes spent a greater amount of time gaping with *L. dahlii* prey (box-and-whisker plot). Black square represents the mean, the box describes the median and upper and lower quartiles, and whiskers represent the range.

glued together with the secretion fell by 76% (from 133 g/cm^2 to 31 g/cm^2) within 10 min, the median time that snakes waited between strike and ingestion.
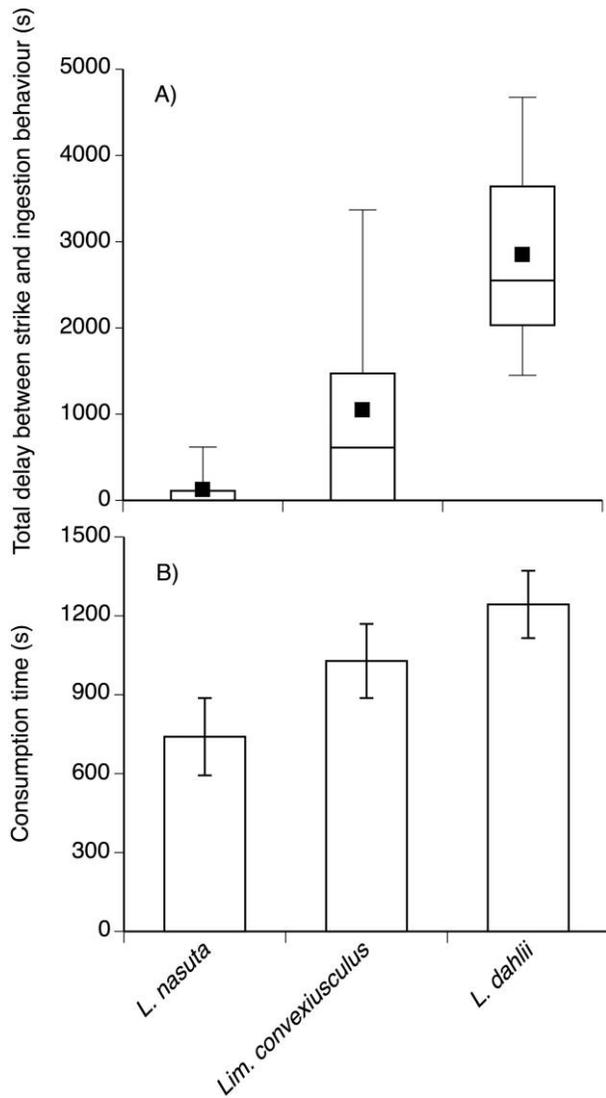
Figure 3: *A*, Box-and-whisker plot of the total delay (in seconds) between strike and the onset of ingestion behavior for death adders offered three prey types. *B*, Average ($\pm$ SE) consumption time for death adders offered three prey types.

Discussion

Floodplain adders distinguished among the three frog species and handled them appropriately. When dealing with the nontoxic *Litoria nasuta*, adders never released the frog and generally began to ingest it immediately. Many *L. nasuta* were consumed while still alive and may not even have been envenomated (B. Phillips and R. Shine, personal observation). *Limnodynastes convexiusculus* (the glue-secreting species) were often held rather than released, they elicited less (and shorter periods of) gaping, and ingestion generally commenced within 10 min of the strike. In con-

trast, *Litoria dahlii* (the highly toxic species) were released after the initial strike, elicited long periods of gaping, and typically were not ingested until about 40 min poststrike.

These species-specific prey-handling responses overcome prey defenses effectively. When the snake deals with the nontoxic frog, the optimal tactic is to hold onto the prey so that it cannot escape and to consume it as rapidly as possible. Presumably, there is a cost associated with releasing prey or delaying consumption (both of which increase the chance of losing the meal), so holding the prey and consuming it immediately should be the safest strategy unless a prey item has a chemical defense. Thus, for the glue-secreting species, a rapid decline in adhesive strength allows snakes to circumvent the defense by delaying ingestion for about 10 min postmortem, but snakes seldom waited much longer than this period, suggesting a carefully timed response. The advantages of the predator's behavioral flexibility are even more apparent when dealing with the toxic frog species. No adders in our trials died after eating these prey, even though a freshly killed *L. dahlii* can be fatal if ingested (based on trials in which adders from the same population were force-fed freshly killed frogs; Madsen and Shine 1994). Instead, a 40-min delay between frog death and ingestion suffices to break down the toxic dahleins, and adders wait for this chemical change to occur before ingesting the frog. Hence, death adders have evolved behavioral flexibility (complex stereotyped prey-handling behavior elicited by specific prey cues)
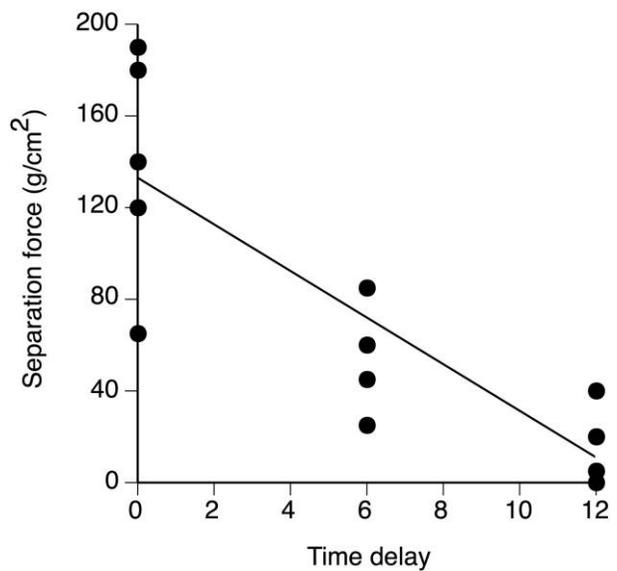

Figure 4: The adhesive power of *Limnodynastes convexiusculus* secretions declines rapidly with time. Line represents the least squares regression fit to the data.

appropriate to their culinary environment and balanced against the costs associated with losing the prey item.

If the predator can circumvent the prey's toxic defenses so easily, why do complex (and presumably costly) chemical defenses persist in these frogs? The answer probably lies in the fact that anurans are consumed by a diverse array of snake taxa, many of which are nonvenomous. For example, the Adelaide River floodplain contains high densities of anurophagous nonvenomous colubrids such as *Dendrelaphis punctulatus*, *Stegonotus cucullatus*, and *Tropidonophis mairii* (Shine 1991; Brown and Shine 2002; Brown et al. 2002). Releasing a bitten prey item and waiting until its chemical defenses degrade is not an option for a nonvenomous snake because the potential prey item would escape if released, and prolonged retention of the frog in the snake's mouth likely would result in the death of both parties. Hence, the chemical defenses of native frogs may function effectively against such predators (and be maintained by selection) even if those defenses can be circumvented by venomous snakes. We might expect nonvenomous snakes to adapt to prey toxicity by a more direct route—evolving physiological tolerance to the toxins. Indeed, both *D. punctulatus* and *T. mairii* are resistant to *L. dahlii* toxin (Madsen and Shine 1994), whereas the other nonvenomous snake taxa in the area simply avoid these potentially fatal meals (B. Phillips and R. Shine, unpublished data). Additionally, *T. mairii* appear to have been forced into a trade-off between resistance to *L. dahlii* and locomotor performance (Phillips et al. 2004). That such an important trait (locomotor capacity) is traded off against resistance to *L. dahlii* toxin supports the likelihood of an arms race between *T. mairii* and *L. dahlii*. Plausibly then, these nonvenomous snakes may have driven the evolution (or maintenance) of high toxicity in *L. dahlii*. Given that these nonvenomous species arrived on the Australian continent relatively recently (early Pleistocene, well after the radiation of the elapids in Australia; Cogger and Heatwole 1981; Greer 1997), they may have engaged in this arms race well after adders had already evolved bite-and-release tactics in response to an earlier arms race. Thus, bite-and-release tactics may be a very old adaptation that not only circumvents an arms race between "bite-and-release" predators and their toxic prey but also successfully avoids heightened prey defenses induced by coevolutionary arms races with other nonvenomous predators.

Our results also hint that coevolution with dangerous prey may influence the evolution of snake venoms and tactics of prey capture. Coevolution could work directly on the venom components themselves through two avenues. First, rapid prey immobilization/death is critical to minimizing the possibility of prey loss in cases where prey are released, so venoms should be under strong selection for maximum impact on prey (while prey are under se-

lection to evolve resistance to the venoms; see, e.g., Heatwole and Poran 1995). A second intriguing possibility is that the venoms may interact directly with the defensive secretions of the prey, such that the prey are rendered less toxic as a consequence of envenomation.

Prey capture tactics are also expected to experience strong selection during coevolution with dangerous prey. Strike-and-release tactics (as opposed to simply retaining the prey item in the mouth until it dies) are exhibited by venomous snakes from several phylogenetic lineages (Greene 1997; Deufel and Cundall 2006), suggesting multiple origins of the tactic. The most obvious advantage of immediately releasing a bitten food item is to avoid direct retaliation by the injured prey (such instant retaliation can be fatal; Fleay 1981). The predator exploits the same selective asymmetry we have noted above: prey behavior (such as defensive biting) ceases to be effective when the prey item dies. Our work suggests that the suite of antipredator defenses terminating soon after prey death is wider than we have previously envisaged and includes chemical processes (i.e., adhesive secretions and poisons) as well as behaviors. Hence, feeding on toxic prey may have provided an additional selective force both for strike-and-release behavior and for venoms that kill prey items quickly enough to prevent escape after envenomation. More generally, snakes may exhibit diverse behaviors associated with the time course of prey ingestion, as well as with prestrike behaviors (such as habitat selection; Clark 2007) and methods for prey capture and subdual (such as venom and constriction; Greene 1997). Further detailed studies on the routes by which predators circumvent postmortem prey defenses could well reveal many cases of prey-specific adaptations to the ingestion phase, as well as the prey-capture phase, of foraging biology.

Acknowledgments

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