

## **Feeding Experience Modifies the Assessment of Ambush Sites by the Timber Rattlesnake, a Sit-and-Wait Predator**

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### **Abstract**

To effectively ambush prey, sit-and-wait predators must locate sites where profitable prey are likely to return. One means by which predators evaluate potential ambush sites is by recognizing high-use areas through chemical cues deposited inadvertently by their prey. However, it is unknown whether ambush predators can use chemical cues associated with past prey items in the assessment of potential ambush sites. I examined selection of ambush sites by timber rattlesnakes (*Crotalus horridus*) exposed to trails made from chemical extracts of the integument of various prey species. I evaluated the role of feeding experience in ambush site selection by comparing the behavior of timber rattlesnakes before and after feeding experience with different sized prey items. Timber rattlesnakes are more likely to select ambush sites adjacent to chemical trails from prey with which they have had feeding experience, but only those fed relatively large prey showed an increase in responsiveness. Increased responsiveness after feeding experience was exhibited in experiments using integumentary extracts of mammals (the natural prey of timber rattlesnakes), but not in those using extracts of fish. These results indicate that ambush predators may learn to recognize chemicals on the integument of profitable food items, and use that experience when subsequently selecting ambush sites. Additionally, these findings provide evidence that size-dependent predation by snakes may be, in some species, a result of active prey selection.

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### **Introduction**

Chemical substances shed from the integument of most organisms are unavoidable by-products of metabolism and excretory processes. Because these chemicals may contain information about an organism, chemosensory abilities for detecting and responding to other species are a key aspect of many predator–prey

interactions (Cooper 1995; Kats & Dill 1998; Banks et al. 2000). Although behavioral ecology strongly emphasizes studies of prey eavesdropping on predator chemical cues, predators also use chemosensory information as an important component of their foraging behavior (Burghardt 1990).

Many predators recognize chemical cues from prey without previous experience (Burghardt 1993; Potting & Otten 1997; Cooper & Hartdegen 2000), and this response can also be modified through learning (Langley 1983; Burghardt 1990; Menzel 1990; Vet et al. 1995; Nams 1997). However, past work has focused on active predators that use cues to locate or identify prey. Chemical cues may also provide information about prey microhabitat use and probability of return to a site – information that is valuable to ambush, or sit-and-wait, predators (Schoener 1971; Huey & Pianka 1981). Ambush foraging is a tactic usually employed by sedentary, cryptic predators commonly found in fish, insects, arachnids, amphibians, lizards, and snakes (reviewed in Shafir & Roughgarden 1998). Tactics used by ambush predators are not as well-studied as those of active predators; most foraging behavior research is usually conducted on fast, active animals (such as birds or mammals) that make many rapid decisions about prey choice and patch use (Stephens & Krebs 1986, Table 9.1).

Although the use of prey-derived chemical cues to evaluate ambush sites has not been studied in depth, it is a strategy that occurs in a wide range of predators and parasites (Greene 1992; Carroll et al. 1996; Persons & Rypstra 2000; Punzo & Alton 2002). Ambush predators invest significant amounts of time waiting for prey. Although metabolic costs for this behavior may be small, an opportunity cost is paid if there are better sites in the environment at which to ambush prey. Therefore, it is important that ambush predators be able to identify a site where profitable (e.g. large, energy-, or nutrient-rich) prey items are likely to be encountered. One means by which ambush predators may do so is to use chemical cues from past feeding experiences with profitable prey to recognize sites associated with these prey. Here, I examine the role of learning and experience in ambush site selection by timber rattlesnakes (*Crotalus horridus*).

Timber rattlesnakes are medium-sized viperids distributed throughout the deciduous forests of the eastern United States. Like many snakes that prey principally on small mammals (Clark 2002), timber rattlesnakes are slow-moving relative to their prey, and hunt primarily by ambush. This is evidenced by field observations of snakes coiled next to fallen logs or other pathways used by rodents (Reinert et al. 1984). Timber rattlesnakes are ideal subjects for studying ambush foraging because their chemosensory response (tongue-flicking) can be evaluated quantitatively (*sensu* Cooper & Burghardt 1990), and they exhibit a stereotyped series of behaviors and postures when waiting to ambush prey (Reinert et al. 1984; R. W. Clark, pers. obs.).

In a previous study, I demonstrated that timber rattlesnakes raised in captivity on pre-killed laboratory mice still recognize chemical trails from prey items sympatric with their population of origin (Clark 2004). Although these subjects responded more strongly to natural prey, they also exhibited some degree of ambush behavior toward rodent species that are not natural prey items.

Additionally, I have found that the chemoattractive substances are a mixture of peptides and proteinaceous compounds present on the integument of mammals, and can be chemically extracted in methanol (R. W. Clark, unpubl. data). This technique allows precise chemical stimuli to be used in evaluating the predatory responses of the subjects. In this study, I examine how captive-raised timber rattlesnakes modify their ambush behavior after feeding experience with untreated prey items, and with prey that has been artificially treated with integumentary extracts from other species.

## General Methods

### Overview

Three experiments were conducted to determine how feeding experience affects ambush site selection. The first experiment was designed to determine whether snake predators increased responsiveness to chemical trails made from species they had eaten in the past, and how prey sizes affected their response. Following positive results from this experiment, the second experiment was conducted to determine if this recognition was based solely on chemical cues present on the integument of their prey. The third experiment was designed to determine whether snakes learn to recognize integumentary chemicals from taxa not present in their natural diet (Clark 2002).

### Test Subjects

Snakes consisted of 24 individuals from three litters of *C. horridus*, born in the laboratory to wild-caught females. Gravid females were caught on Aug. 15, 1999 in Wyoming, Clinton, and Lycoming Counties, Pennsylvania. Experiments were conducted between Dec. 1, 2001 and Nov. 12, 2002, during which the 24 snakes ranged from 76 to 98 cm total length and 305–487 g in body mass. Snakes were housed individually in glass cages (90 × 30 × 30 cm) and reared on a diet of pre-killed laboratory mice. Snakes were maintained in a Cornell University animal holding facility at 22–26°C under a 12L:12D light cycle, with water dishes and heating pad situated at one end of each aquarium.

### Preparation of Extracts

Previous experiments indicate that the chemoattractive integumentary substances present are soluble in methanol (R. W. Clark, unpubl. data). Extracts were prepared by gently washing the integument of a recently killed potential prey species several times with methanol. The methanol effluent was collected, filtered through glass wool to remove particulates, lyophilized, weighed, and stored in a freezer until use. Prior to application, samples were reconstituted in methanol to a concentration of 0.01 g/ml. Extracts were made from individuals of three different species: juvenile and adult laboratory rats (*Rattus rattus*), goldfish (*Carassius*

*auratus*), and woodchucks (*Marmota monax*). These species do not occur in the diet of timber rattlesnakes, and were chosen in part to eliminate any natural predisposition these snakes may have for natural prey. Laboratory rats and woodchucks were chosen because they belong to a taxon on which timber rattlesnakes specialize (rodents), whereas goldfish were chosen to represent a taxon that does not occur in the diet of timber rattlesnakes, but does occur in the diet of other crotaline species.

### Testing Procedure

The testing procedure consisted of placing a snake in a wooden, open-topped enclosure (75 × 75 × 120 cm) lined with clean construction paper and containing a water dish, a cover object, and two rectangular wooden blocks (25 × 5 × 3 cm). The snakes were acclimated to the arena for at least 3 d. At the beginning of each test, both wooden blocks were removed, and their tops were lined with white paper. One of these pieces of paper was treated with 1 ml methanol extract, and, as a control, the other was treated with 1 ml of methanol. Extracts were applied evenly across the paper with a glass pipette, saturating the entire surface. The methanol was allowed to evaporate completely by leaving the blocks at room temperature for approx. 5 min. To minimize disturbance, subjects were not removed from the arena when replacing these blocks. Instead, both wooden blocks were replaced simultaneously, equidistant from the subject and from each other. Snakes were then allowed to respond to these chemical cues for 60 min.

Subjects were not tested more than once in a 30-d period, and all tests were conducted at least 21 d after the subject had last been fed ( $\bar{x} \pm SD = 29 \pm 4$  d since last feeding). Subjects undergoing ecdysis were not tested. All subjects were fed their standard prey (pre-killed mice) in their cages at least once in between their use in experimental trials. Because *C. horridus* forages nocturnally (Reinert et al. 1984), all trials were conducted during the dark half of the light cycle and recorded with a video camera with low-light recording capability (Sony® Handycam CCD-TRV57, New York, USA).

From the videotapes, the latency for the head of the snake to encounter the chemical extract was noted. All videotapes were scored blindly with respect to the subject and treatment. The length of the first encounter was recorded as the time from the initial encounter to the time the snake removed its head from contact with the chemical extract for more than 60 s. The snake's head did not have to be in contact with the chemical extract for the entire time of the initial encounter, so long as it was not out of contact with the chemical extract for more than 60 s. The number of tongue flicks that the snake delivered to the chemical extract (defined as a tongue flick where the tongue actually contacted the block or was directly above the block) was recorded. I also noted whether the subjects adopted the stereotyped ambush posture response (Reinert et al. 1984) after encountering the chemical extract. Qualitatively, this response is a stereotyped, overt behavior, consisting of the snake

coiling in a tight coil adjacent to the chemical extract, with the head and neck oriented toward the trail in a ready-to-strike position. To quantify this behavior, an ambush posture was defined as the snake not moving, with its head and anterior one-third of its body in a recoiled position, oriented toward and within 15 cm of the chemical extract, adopted within 2 min of tongue-flicking the chemical extract, and maintained for at least 5 min. In the majority of cases, the ambush posture was maintained for the entire duration of the trial, if it was adopted.

### Statistical Analysis

For statistical analysis, I used a scoring system to create a composite measure of the ambush response and the number of tongue flicks given upon first encountering an extract. This scoring system is based on a widely used measure developed for actively foraging snakes, the tongue flick attack score, or TFAS (reviewed in Cooper & Burghardt 1990). Under this scoring system, individuals that attack the stimulus receive the base unit score of TFmax, modified by the latency to attack. Individuals that do not attack are scored as the number of tongue flicks emitted toward the stimulus. I modified this score by substituting the ambush response for the attack response. In so doing, a tongue flick ambush score (TFAM) is created,

$$\text{TFAM} = \text{TFmax} + (\text{TL} - \text{latency})$$

where, TFmax is the maximum number of tongue flicks emitted during initial encounter of the chemical extract by any individual in any trial (thus weighting ambushes more than any number of tongue flicks), TL is trial length in minutes, and latency is the latency in minutes to adopt the ambush posture toward the chemical extract. This composite measure, like TFAS, assumes that an ambush posture indicates a stronger response than any number of tongue flicks, and that the latency to ambush posture decreases with increasing stimulus.

As response data violated the assumptions of parametric statistics, non-parametric statistics were used for analysis. The responses of the subjects to each chemical extract before feeding experience were compared with the responses after feeding experience with Wilcoxon signed ranks tests. In trials where two sets of snakes were tested before and after feeding experience with different sized prey items, comparisons of the mean change in TFAM after feeding experience were made with the Mann-Whitney U-test. All statistics were conducted with the software program Minitab<sup>®</sup> (Minitab Inc., State College, PA, USA).

## Experiment 1: Effect of Past Feeding Experience

### Methods

Twelve randomly chosen snakes were tested for their response to methanol extracts made from either weanling or juvenile rats, and the other 12 snakes were

tested with adult rat extract, following the procedures outlined above. Following these trials, snakes were placed back in their cages and fed either a weanling rat (3045 g), or an adult rat (250–275 g). Rats were killed by carbon dioxide inhalation and placed in the snake cage with the snake for 4 h. Any uneaten rats were then removed. Approx. 30 d later (after being replaced in clean cages and fed untreated pre-killed laboratory mice), all individuals were retested for their response to juvenile or adult rat methanol extract ( $\bar{x} \pm SD = 34 \pm 4$  d between retesting).

### Results

All snakes offered small rats consumed them; however, only the two largest snakes consumed large rats. Based on the visual appearance of the rats, six of the remaining 10 individuals attempted to consume a large rat but could not proceed beyond the head (at least in the 4 h time period allotted them) and regurgitated the item. Table 1 presents summary data for all trials on the average number of tongue flicks, and propensity to adopt the ambush posture. Data from the blank control blocks are not presented in Table 1 because snakes were unresponsive to them (no ambush postures were ever exhibited toward control blocks, and the  $\bar{x} \pm SE$  number of tongue flicks toward them was  $19 \pm 7$ ).

Snakes showed a significant increase in TFAM toward rat chemical extracts after being fed a large rat (Wilcoxon signed ranks test:  $T = 3$ ,  $N = 12$ ,  $p = 0.005$ ) (Fig. 1). Snakes also showed an increase in TFAM after being fed a small rat, but the difference was not significant (Wilcoxon signed ranks test:  $T = 20$ ,  $N = 12$ ,  $p = 0.27$ ). Snakes fed large rats showed a greater increase in TFAM after feeding experience than snakes fed small rats (change in TFAM was  $122 \pm 18$  for snakes fed large rats, and  $32 \pm 18$  for snakes fed small rats; Mann–Whitney U-test,  $W = 188$ ,  $N = 12$ ,  $p = 0.03$ ).

*Table 1:* Behavioral responses of captive-raised timber rattlesnakes to chemical trails before and after feeding experience

Trail	N	Feeding experience	Tongue flicks	Ambush posture occurs (%)
Rat	12	No, small rat	$72 \pm 8$	25
Rat	12	Yes, small rat	$83 \pm 10$	50
Rat	12	No, large rat	$55 \pm 9$	8
Rat	12	Yes, large rat	$98 \pm 10$	92
Woodchuck	12	No, small mouse	$73 \pm 8$	25
Woodchuck	12	Yes, small mouse	$60 \pm 8$	17
Woodchuck	12	No, large mouse	$75 \pm 9$	8
Woodchuck	12	Yes, large mouse	$84 \pm 8$	42
Fish	24	No	$41 \pm 8$	25
Fish	24	Yes	$52 \pm 9$	8

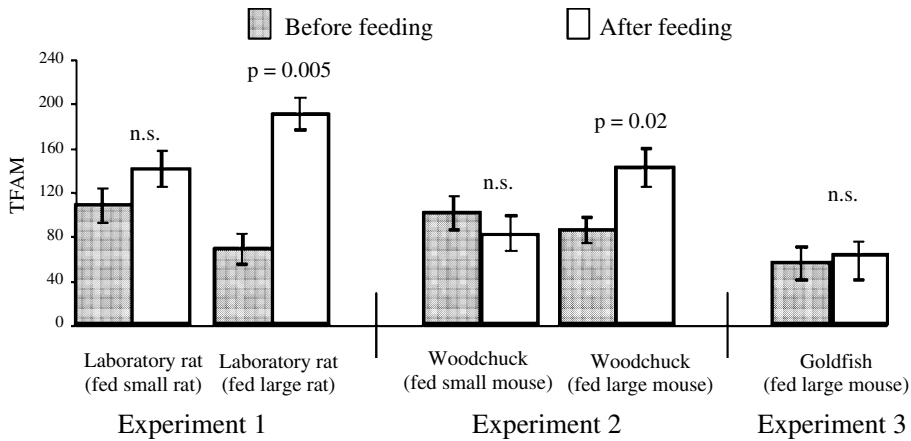


Fig. 1: Tongue flick ambush (TFAM) scores of timber rattlesnakes in response to chemical trails of various prey items. Responses are shown both before and after snakes were given feeding experience with food items containing prey chemical cues on their integument. Two-tailed p-values are for Wilcoxon signed rank tests. Error bars represent  $\pm 1$  SE

## Experiment 2: Recognition of Mammalian Chemical Cues on Prey Integument

### Methods

Following the first experiment, snakes were tested for their responses to methanol extracts from a non-prey mammal – a woodchuck (*Marmota monax*). Snakes were then placed back in their cages and fed a laboratory mouse that had been treated with woodchuck extract. Mice were killed by carbon dioxide inhalation and 1 ml of woodchuck extract was daubed onto their fur with a paper towel. The treated mouse was then placed in the snake cage for 4 h, after which any uneaten mice were removed. Snakes were again randomly assigned to either a small food (5–7 g mouse) or a large food (40–45 g mouse) treatment. Approx. 30 d later (after being replaced in clean cages and fed untreated pre-killed laboratory mice), all individuals were retested for their response to woodchuck methanol extract ( $\bar{x} \pm SD = 36 \pm 4$  d between retesting).

### Results

All snakes offered either large mice or small mice consumed them within the 4 h period. Snakes showed an increase in TFAM toward woodchuck chemical extracts after being fed a large mouse treated with woodchuck extract (Wilcoxon signed rank test:  $T = 9$ ,  $N = 12$ ,  $p = 0.02$ ). Snakes that were fed a small mouse treated with woodchuck extract showed no increase in TFAM following feeding experience (Wilcoxon signed rank test:  $T = 20$ ,  $N = 12$ ,  $p = 0.5$ ) (Fig. 1). Snakes fed large mice treated with woodchuck extract showed a greater increase in TFAM after feeding experience than snakes fed small mice treated with woodchuck extract (change in TFAM was  $57 \pm 16$  for snakes fed large mice,

and  $-18 \pm 22$  for snakes fed small mice; Mann–Whitney U-test:  $W = 114$ ,  $N = 12$ ,  $p = 0.04$ ).

### **Experiment 3: Recognition of Non-Mammalian Chemical Cues**

#### **Methods**

Following Expt 2, all snakes were tested for their response to methanol extracts from goldfish, a non-prey, non-mammalian species. Snakes were then replaced in their cages and fed a laboratory mouse that had been treated with goldfish extract. Mice were killed by carbon dioxide inhalation and 1 ml of goldfish extract was daubed onto their fur with a paper towel. The treated mouse was then placed in the snake cage for 4 h, after which any uneaten mice were removed. All 24 snakes received a large (40–45 g) mouse. Approx. 30 d later (after being replaced in clean cages and fed untreated pre-killed laboratory mice), all individuals were retested for their response to goldfish methanol extract ( $\bar{x} \pm SD = 38 \pm 6$  d between retesting).

#### **Results**

All snakes ate the large mouse treated with goldfish extract offered to them. The snakes showed no difference in responsiveness toward goldfish chemical extracts after their initial feeding experience (Wilcoxon signed rank test:  $T = 73$ ,  $N = 24$ ,  $p = 0.2$ ) (Fig. 1).

#### **Discussion**

Timber rattlesnakes are able to use past predatory experiences to modify their foraging behavior and choose ambush locations where profitable prey may be encountered. This finding is in agreement with studies on actively foraging snakes (reviewed in Burghardt 1990). In general, these studies show that feeding experience with prey increases the responsiveness of snakes to chemical cues from that prey. This is true even of species that have genetically based prey preferences (Arnold 1981), demonstrating that experience modifies innate preferences. The ability to chemically identify prey through learning and experience is taxonomically diverse (Langley 1983; Daniel & Bayer 1987; Menzel 1990; Vet et al. 1995; Nams 1997), and is probably a common ability among chemically oriented predators.

None of the three species used to make chemical trails in these experiments are natural prey items of timber rattlesnakes (Clark 2002), and only the woodchuck is sympatric. Timber rattlesnakes are more likely to exhibit ambush behavior in response to chemical trails from sympatric prey than to non-sympatric rodents, but do still show some tendency to respond to non-sympatric rodents (Clark 2004). The results of the current study show that snakes also retain some plasticity in this response that allows them to incorporate new prey species into their diet.



Timber rattlesnakes were more responsive toward woodchuck trails after feeding on a large mouse treated with woodchuck extract, but did not increase their responsiveness to fish trails after feeding on a mouse treated with fish extract (Fig. 1). Timber rattlesnakes are specialists on small mammals (Clark 2002), and do not feed on fish in the wild. Previous experiments indicate that *C. horridus* shows an innate predisposition for small-mammal chemical trails (Clark 2004). These results show that snakes are also predisposed toward learning rodent integumentary cues over those from fish. Organisms often exhibit a predisposition to learn in a manner consistent with their natural environment (Garcia et al. 1955; Pietrewicz & Richards 1985; Daniel & Bayer 1987; Halloy & Burghardt 1990). It is likely that most predators that specialize on a certain type of food will selectively learn ecologically relevant tasks.

Timber rattlesnakes showed increased responsiveness to prey chemical extracts both after feeding on an untreated prey item (rat), and on a familiar prey item that had been artificially treated with the methanol integumentary extract from another species (mouse treated with woodchuck extract) (Fig. 1). Therefore, the chemical cues present in the integumentary extract can be used to find ambush sites where that prey is likely to be encountered again. The chemical composition of these integumentary extracts is currently unknown, but preliminary studies indicate that they are a complex mixture of high- and low-molecular weight components (R. W. Clark, unpubl. data), similar to garter snake chemoattractants that have been isolated from earthworms and frogs (Burghardt et al. 1988; Wang et al. 1993; Wattiez et al. 1994).

Although the snakes in this study were more responsive toward woodchuck extracts after feeding on a large mouse treated with woodchuck extract, no increase in responsiveness occurred among those snakes that were fed only a small mouse (Fig. 1). Additionally, only those snakes encountering large rats showed a significant increase in ambush behavior toward rat chemical extracts. The small mice may have been regarded as substandard prey items, as they are smaller than the mice these snakes are normally fed, and smaller than prey items that naturally occur in the diet of juvenile timber rattlesnakes (Clark 2002).

The failure of snakes fed small rats to show a significant increase in ambush behavior is more perplexing, as the small rats were similar in size to the large mice used in the woodchuck trials. Snakes may have used factors other than size to evaluate prey items (e.g. weanling rodents may not be as nutritionally valuable as adult prey). Another possibility is that the increased responsiveness of snakes fed large rats is a result of the longer association these snakes had with large rats while attempting to ingest them (snakes fed mice or small rats typically completed ingestion within 30 m, whereas most of the snakes fed rats could not ingest them within the allotted 4 h). This longer association with larger prey could even be the proximate mechanism used by snakes that learn to associate larger prey with more profitable ambush sites. This mechanism might explain why snakes showed a stronger behavioral change toward large rat chemical cues, although most of these individuals did not consume the large rat.

Although most of the snakes offered a large rat did not consume it in the allotted 4 h, they still showed an increase in ambush behavior toward rat chemical trails. This result is somewhat surprising because it indicates that actual consumption of prey is not necessary for the snakes to recognize integumentary chemical cues from that prey when selecting future ambush sites. However, the maximum relative prey size for viperid snakes is approx. 155–160% of body mass (Greene 1992). The large rats (which were consumed by the two largest of the 12 snakes) were probably close to the upper limit of prey size ingestible by these snakes. Although ambush-hunting snakes pay a large metabolic cost when digesting prey, the proportion of energy lost to ingestion and digestion of small and large prey is approximately equivalent (Secor & Diamond 1997; Cruz-Neto et al. 1999). Thus, the energy gained from a large prey item would make attempting to ambush such prey much more profitable than ambushing small prey, even when the value of the large prey is discounted by the probability that it may be too large to swallow.

The results of this study indicate that snakes not only take into account the chemical identity of their prey (i.e. Clark 2004), but also other factors influencing its profitability, such as size or weight, when making decisions about ambush sites. Such learning may be very important for an ambush predator. In one study, timber rattlesnakes stayed at ambush sites for an average of 7.3 h (Reinert et al. 1984). Other ambush foragers, such as bushmasters (*Lachesis muta*), may wait for up to several weeks at one hunting site (Greene 1986). Because of this considerable investment in time and opportunity, foragers will be under selection pressure to estimate whether the prey encountered at that site will be profitable enough to offset such costs. Learning to recognize chemical cues from past encounters with potential prey items is one of the ways predators can make such an estimation.

Dietary studies of snakes show that larger individuals eat absolutely larger prey (reviewed in Greene 1983; Mushinsky 1987; Shine 1991; Arnold 1993). Although this non-random predation implies active selection and rejection of prey based on size, such a pattern could result from other processes as well (reviewed in Downes 2002). To date, empirical studies have found no evidence for active selection of prey size by snakes. Instead, patterns of size-dependent predation arose from prey behavior (Downes 2002), differential predator vulnerability to prey (Webb & Shine 1993), and increased gape size (Shine 1991). However, in these studies snakes were offered prey directly. Since energy expended during prey handling and ingestion is small compared with the typical energy value of prey (Feder & Arnold 1982; Cruz-Neto et al. 1999), snakes are unlikely to pass up even small prey, once encountered. However, for an ambush predator the cost of consuming small prey is not a metabolic cost, but an opportunity cost of waiting for small prey when large preys are available. This study elucidates a behavioral mechanism by which size-dependent predation by ambush foraging snakes would result from active prey choice. As snakes grow and gain experience, their larger size will permit them to feed on larger prey, and by using past feeding experience to ambush large prey in

preference to small prey, the correlation between prey size and snake size will be strengthened.

Chemically mediated ambush site selection occurs in a wide range of predators and parasites, including snakes (Reinert et al. 1984; Duvall et al. 1990; Downes 1999; Theodoratus & Chiszar 1999), spiders (Punzo & Kakoyi 1997; Persons & Rypstra 2000), ticks (Carroll et al. 1996), fleas (Krasnov et al. 2002), snapping turtles (Punzo & Alton 2002), komodo dragons (Auffenberg 1981), and polar bears (Stirling 1988). In general, any predator or parasite with an olfactory inclination is likely to use this strategy as part of their behavioral repertoire, as chemical cues can be useful in identifying ambush sites and providing information about prey quality and probable encounter rate.

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