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HABITAT SELECTION AND PREY ODOR IN THE FORAGING BEHAVIOR OF WESTERN RATTLESNAKES (CROTALUS VIRIDIS)

by

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Summary

We tested the roles of prey odor and other habitat cues in the pre-strike movement patterns of two, ecologically distinct sub-species of the western rattlesnake in naturalistic arenas. In the first experiment, rattlesnakes preferred habitat containing prey odor and cover comprised of rocks, sticks and plants. While searching, rattlesnakes methodically investigated the edges and crevices within rock, areas rodents might frequent in nature. In the second experiment, rattlesnakes investigated sticks more than rocks arranged topographically similar to sticks. In the third experiment, rattlesnakes preferred habitat that included brush foliage and used chemical prey trails in pre-strike behavior via (i) trail-following, (ii) casting search patterns and (iii) scanning search patterns. Several snakes coiled in stereotyped ambush postures that allowed them to face chemical trails while resting against rocks and foliage. These results suggest that rattlesnake foraging exhibits qualities advantageous for hunting rodent prey in addition to providing protection from predators and perhaps promoting thermoregulation.

Sub-species did not exhibit geographic variation in foraging behavior despite differences in natural history and morphology. Hence, the microevolutionary pattern suggests that generalized foraging repertoires are successful in numerous environments when coupled with locally specialized body patterns.

Keywords: *Crotalus viridis*, Viperidae, foraging behavior, habitat selection, geographical variation, snake ecology, evolution.

Introduction

Foraging behavior is believed to be of primary importance in the origin and radiation of snakes, promoting the evolution of specialized sensory systems and morphology for prey capture (Cock Buning, 1983; Greene, 1983; Pough & Groves, 1983). Yet, little is known about the behavioral repertoires of snakes owing to the secretive and stealthy nature of these animals (Carpenter, 1977; Greene, 1994), and the difficulty in analyzing their behavior due to the simultaneous presence of predatory, defensive, and thermoregulatory elements (Barlow, 1977; Drummond, 1981).

Viperids generally strike, envenomate, and release their prey, but they may hold onto prey when hunting ectotherms or mammals that are relatively small compared to the snake's body size (Chiszar & Radcliffe, 1989; Chiszar *et al.*, 1989, 1992a; Boyer *et al.*, 1995). Then they increase their tongue-flicking rate, which aids them in the detection and subsequent following of chemical trails left by their envenomated prey. This process, called Strike Induced Chemosensory Searching (SICS) (reviewed in Chiszar *et al.*, 1992a), demonstrates that foraging behavior can be partitioned into 'pre-strike' and 'post-strike' components.

Although each viperid so far examined exhibits a heightened chemosensory state after a predatory strike (Chiszar *et al.*, 1982, 1992a), the role of prey chemicals in the pre-strike environment is less well known. Vipers may wait in ambush for prey to pass nearby (Reinert *et al.*, 1984) or they may actively pursue certain prey (Tevis, 1943; Fitch, 1946; Hennessy & Owings, 1988). Choice of ambush sites by adults seems to depend on the presence of mammalian prey or their odor (Duvall & Chiszar, 1990; Duvall *et al.*, 1990). Although trail-following has usually not been reported until after a successful predatory strike (Golan *et al.*, 1982; Radcliffe *et al.*, 1986), trail-finding occurs during the pre-strike period and is a likely prerequisite to ambush

hunting. It appears, however, that trail-finding is a subtle process, easily disturbed or rarely elicited in captive rattlesnakes living in small cages (Chiszar *et al.*, 1986).

Crotaline species exhibit pronounced diversity in life cycle patterns, including habitat preferences and degree of dietary specialization. *Crotalus viridis* thus is a valuable species for comparative studies of foraging behavior because of its broad geographical range and its consequent adjustment to numerous habitats (Klauber, 1956; Chiszar *et al.*, 1992a). Moreover, foraging snakes are rarely found more than a few body lengths from refugia (reviewed in Reinert, 1993), suggesting that these environmental features interact with effects of prey cues in influencing the motor patterns and microhabitat choice of snakes.

We investigated this matter experimentally with two sub-species of *Crotalus viridis*, using semi-naturalistic arenas for behavioral observations (Lorenz, 1950). We used *C. v. viridis* from dry scrub habitat in Colorado and *C. v. oreganus* from a Mediterranean habitat in central California. Our first experiment assessed whether prey odor, cover, or a combination of the two creates a more preferred habitat for *C. viridis*. The second and third experiments elucidated possible roles of vegetative cover in the choice of ambush sites.

Experiment I. The role of prey odor and cover in the choice of habitat

Methods

Subjects were eight adult prairie rattlesnakes, *Crotalus viridis viridis*, ranging in snout-vent length from 50-60 cm. All had been in captivity and feeding on rodents for at least six months. Snakes resided individually in 95-liter glass terraria with wire screen tops, newsprint floor coverings and water dishes. The photoperiod was 12L:12D. Air temperature was 26° ± 1°C. Snakes almost always accepted weanling rat prey each week. We conducted individual trials prior to feeding the snakes.

The semi-naturalistic arenas were in two 3 × 3-m rooms. A sand/pebble mixture approximately 3-cm deep covered the floors of each room. The rooms were divided schematically into four quadrants (Fig. 1). Each quadrant received one of four unique treatments: cover, rodent odor, both cover and rodent odor, or a control with neither cover nor odor. Sandstone rubble placed within the two cover quadrants created a matrix of crevices that simulated potential refugia. We also placed dried sticks, plastic cactus, and bushes in the cover treatments. Soiled bedding from weanling rat cages placed within 0.2-liter plastic containers was the source of prey odor. The containers were placed in the sand/pebble mixture or in the rubble so that the lip of the container was level with the ground surface. Spatial arrangement of treatments varied between trials.
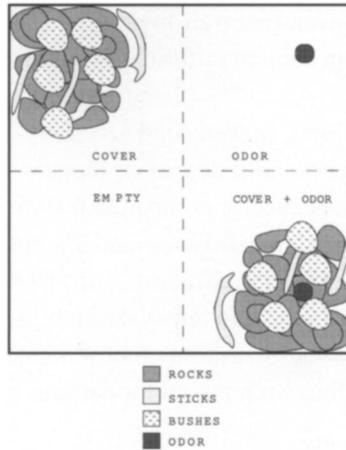
Fig. 1.   Schematic of arena design for Experiment 1. Dashed lines denote quadrants. Each
          quadrant is titled and includes a graphical representation of its contents.

During each trial, we presented each of two rattlesnakes with all four treatments simulta-
neously, by placing them in the center of the two arenas at the point where all four quadrants
converged. We began observations in one arena and recorded the snake's location every 15
seconds over a five-min period. We then switched to the second arena and completed a 5-min
block of observations. During the two hour observation period, we continued to alternate be-
tween the two arenas every five minutes. Thus, we completed twenty-four consecutive time
block rotations with 12 5-min observation periods per arena. We also recorded qualitative ob-
servations of snake searching behavior throughout the time blocks in addition to the location
data. At the end of two hours, we recorded the position of the snake. Five snakes remained in
the arenas over night and we noted the location of the rattlesnakes the following morning.

Results

A one-way analysis of variance disclosed an unequal amount of time spent
in the four quadrants during the two hour observation sessions ($F_{3,21} =$
10.6, $p < 0.0001$). Snakes favored the cover-with-odor combination over
the treatments containing rocks, odor and the control (see Fig. 2). This
was confirmed by Dunnett's Method for pairwise multiple comparisons
($p < 0.05$). After two hours, 7 of 8 snakes inhabited quadrants with cover
(four in cover with odor and three in cover without odor). All five snakes
that remained in arenas overnight resided in covered regions the following
morning (three in cover with odor and two in cover without odor).

Rattlesnakes investigating quadrants that contained cover exhibited me-
thodical searching behavior. When first entering areas with cover, the snakes
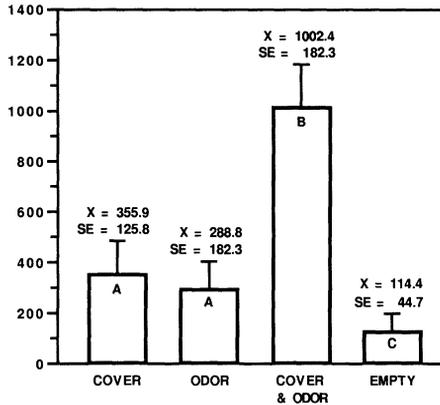
Fig. 2.   Time spent in each quadrant (mean ± SE). Bars with a common letter are not significantly different $p > 0.05$.

tongue-flicked and slowly scanned the rock-ground intersections, usually searching the entire periphery around these cover sections. Snakes often switched back and reinvestigated previously scanned areas before proceeding. Once snakes entered the rock piles, they routinely investigated rock crevices greater than 5 cm diameter. The snakes anchored themselves with the lower third of their bodies and penetrated the crevices. If able, they completely entered the crevice and remained within for 30-60 seconds.

As snakes reached containers of rodent odor, the rate of tongue flicks increased. Snakes often submerged their heads into the containers repeatedly and followed this with visual scanning of the environment. Rattlesnakes that coiled up next to the containers usually yawned several times. Two snakes that did not coil inserted the posterior portion of their body into nearby crevices as Chiszar et al. (1992b) describe. Both coiled and uncoiled rattlesnakes usually rested their necks in a sigmoidal curve that is believed to be a stereotyped ambush posture for the family Viperidae (Iglehart & Chiszar, 1977). One snake dug itself into the sand of an odor treatment in a manner similar to the resting crater of a sidewinder rattlesnake, *Crotalus cerastes* (Klauber, 1956). This animal also rested its head and neck in a sigmoidal conformation, but oriented its head in an upward plane so that the background ambient air formed a backdrop for its infrared receptive field (Theodoratus et al., 1997).

Rattlesnakes investigated plants and large sticks within the cover quadrants. Several snakes extended themselves up the stalks of plants, while one

individual crawled up a cactus. These snakes usually sat stationary under-neath or beside the plants before continuing searching behavior. Rattlesnakes thoroughly investigated large sticks placed in cover sections. When snakes searched a quadrant, they often moved along the lengths of sticks if they were available. It was our subjective impression that snakes investigated sticks more than they investigated rocks.

Experiment II. The role of sticks in habitat choice

Methods

We designed Experiment II to elucidate further which factors comprising cover were preferred by western rattlesnakes. Based on our observations of snakes investigating wood in Experiment I, we hypothesized snakes would spend more time searching sticks than a control. We added rodent odor to all treatments in this experiment because Experiment I suggested prey odor helped stimulate snake searching behavior. Our interest was inspired by *Crotalus horridus*, which frequently rests in ambush next to fallen limbs and logs (Reinert *et al.*, 1984; Brown & Greenberg, 1992).

Subjects for Experiments II and III were eight adult northern pacific rattlesnakes, *Crotalus viridis oreganus*, ranging in snout-vent length from 50-80 cm. All had been in captivity and feeding on rodents for at least four months prior to the study. Snakes resided individually in 38-liter glass terraria, containing redwood chip bedding and a glass vessel filled with water. The photoperiod was 12L:12D. Room temperature fluctuated between an extreme high of 32°C and a low of 18°C. Magnesium heat tape underneath one end of the cages provided opportunities for thermoregulation. We ran trials at least seven days after the snakes had eaten.

A semi-naturalistic arena was constructed within a 2.5 × 2.5-m room. A sand/pebble mixture of approximately 5 cm covered the floors of each room. We placed cover objects at equal distances from an imaginary plane that divided the room into two halves such that objects were symmetrically opposite from one another on both sides of the plane. Thus, we created mirror images on each side of the arena (Fig. 3). Sticks were placed on one side of the room; the control treatment was created by constructing a symmetrical shadow of sticks with rocks on the other side of the room. Rock shadows corresponded to the location, length, and thickness of the sticks of the experimental treatment. Thus, the amount of relief was quantitatively similar in the two halves of the arena. We also created two control trials where the arena contained identical sections of either both sticks or rock shadows. Rodent odor was added to the treatments by placing equal amounts of soiled bedding from *Mus musculus* cages on each side of the arena. We collected fresh soiled bedding each trial day. The position of the odor containers was alternated between each trial, but they were placed symmetrically apart from one another on their corresponding side of the room.

Snakes were placed in the middle of the room at the initiation of the trial and allowed to range freely through the arena for thirty minutes. The trials began once the snakes started searching the arena. Position was scored based on the location of the rattlesnake's head in proximity to sticks and rock shadows. Qualitative data describing how the animals searched
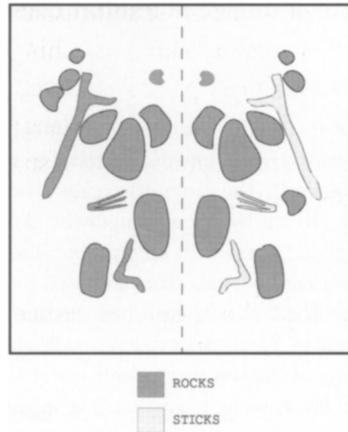
Fig. 3.   Schematic of arena design for Experiment 2. Dashed line denotes mid-line. Rock shadows are shaded.

the room were also recorded. We timed the movements of the rattlesnakes from an adjoining room via a remote video camera. The trials were also videotaped so that other observers could corroborate scoring trials.

Results

Analysis with t-tests for paired comparisons revealed that rattlesnakes investigated sticks ($\overline{x} = 317.1 \pm 115.7$ s) more than rock shadows ($\overline{x} = 145.8 \pm 62$ sec) ($t = 2.92$, df $= 7$, $p < 0.05$). However, we found no statistical difference in time spent investigating arena sections when both sections contained sticks ($t = 1.28$, df $= 7$, $p > 0.05$) or rock shadows ($t = 0.83$, df $= 7$, $p > 0.05$).

Six rattlesnakes assumed stereotyped ambush postures in protected habitat after thoroughly investigating the area. Four of these snakes swerved their necks around 180°, allowing them to watch their tails as they coiled up into ambush posture with rectilinear locomotion. After resting in ambush, five rattlesnakes extended their necks out in a peering posture and subtly scanned the proximity. One snake facing an odor cup repeated the following series of actions three times: peering out from its ambush posture, scanning side to side, reorienting toward the prey odor, retracting its neck into a sigmasoidal curve, yawning, and reassuming its ambush posture.

Experiment III. The role of foliage in habitat choice

Methods

We designed this experiment to identify the role of bush foliage in habitat selection of rattlesnakes. The eight *Crotalus viridis oreganus* used for this study were maintained identically to those of Experiment II. The room was again divided into halves. We laid two narrow sheets of clear plastic (10 cm by 2.5 m) lengthwise down the center of each arena half. We then covered each plastic sheet with sand/pebble flooring. We created prey trails by running mice up and down narrow trails that ran down the center of both halves. We placed a 20-cm tall board on each side of the plastic pathway surface while running rodents to guarantee they remained on course. We ran four rodents back and forth on each pathway four times, to mimic rodent runways of the sort that rodents use repeatedly in the wild (citations listed in Reinert *et al.*, 1984). Rocks were again placed symmetrically opposite one another on each side of the room. In addition, bushes (approximately 45-60 cm tall) were added to one side of the room to create the plant treatment. Thus, only one side of the room had a marked vertical component (Fig. 4). The plants were switched to the opposite side of the room between trials. We created a new pathway for each trial.

At the beginning of each trial, snakes were placed in the center of the room. Rattlesnakes were allowed to move freely through the room for two hours while being videotaped. We scored the amount of time that each snake spent on each side of the arena. We also summed the duration of time spent investigating prey trails for each side of the arena if they lasted at least five seconds and spanned at least one third of the trail. Finally, we timed how long snakes were situated next to sticks. In addition, qualitative observations were noted such as whether rattlesnakes coiled in ambush postures, climbed vegetation, etc.
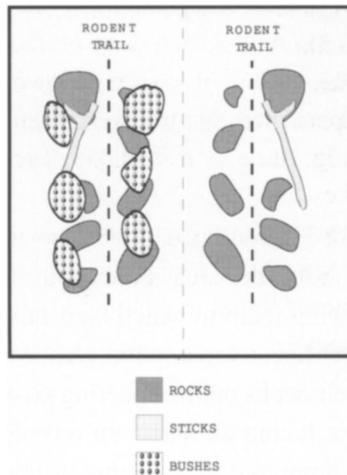

Fig. 4.   Schematic of arena design for Experiment 3. Light-dashed line denotes mid-line.
Bold-dashed lines denote rodent odor trails as titled.

Results

Paired *t*-tests disclosed snakes spent significantly more time on the arena half containing vegetation ($\bar{x}$ = 4843.9 ± 287.6 sec) than on the non-vegetation side ($\bar{x}$ = 2247.1 ± 286.3 sec) over the two-hour trials (t = 4.32, df = 7, $p < 0.05$). *Crotalus viridis oreganus* investigated and followed rodent trails significantly longer with vegetation present ($\bar{x}$ = 555.6 ± 53.7 sec) than without vegetation ($\bar{x}$ = 183.6 ± 41.9 sec) (t = 7.40, df = 7, $p < 0.05$). A *t*-test failed to find a significant difference between the time that rattlesnakes situated themselves next to sticks with vegetation ($\bar{x}$ = 417.8 ± 87.9 sec) versus no vegetation ($\bar{x}$ = 217.8 ± 51.9 sec) (t = 2.24, df = 7, $p > 0.05$).

All eight rattlesnakes entered first the arena half with plants at the start of each trial. Seven of eight snakes followed rodent trails in entirety by moving their heads side to side over the width of the trail while searching. Pronounced tongue-flicking was observed despite our inability to tabulate accurately the number of flicks. Rattlesnakes routinely swerved off trails and searched adjoining rocks, vegetation and sticks. Of particular interest was the time spent investigating rock crevices. Two large adult snakes climbed up vegetation. Snakes crawled alongside and on top of sticks while searching within the inner portions of the arena. All eight snakes held their rattles upright while moving and no rattling was heard except at the initiation of trials when snakes were placed into the arena.

Three of the four rattlesnakes that coiled in stereotyped ambush postures during the trials did so within the arena halves containing vegetation. Before coiling, each of the snakes thoroughly investigated the area including rodent pathways. All four snakes faced the trail while coiling, with the posterior part of the coil against vegetation or sticks. After assuming ambush postures for some time, the snakes extended their necks out in peering postures as described in the result section from Experiment II. The only difference was that rattlesnakes briefly scanned a portion of the rodent trail while tongue-flicking. This behavior never lasted more than 20 sec before the rattlesnakes resumed their ambush postures.

Discussion

The role of chemosensory mechanisms in the biology of pitvipers and other squamates is well studied (reviewed in Burghardt, 1990; Halpern, 1992;

Cooper, 1994; Schwenk, 1995). Several studies have provided convincing evidence that prey odor arouses predatory behavior (Greene, 1984; Cooper, 1994). This study highlights the importance of prey cues and cover as rattlesnakes searched quasi-natural habitat. We discovered that rattlesnakes make use of prey trails during pre-strike foraging in addition to post-strike foraging. In addition, we witnessed the coiling of rattlesnakes into ambush postures. Most importantly, rattlesnake exploratory behavior was influenced strongly by cover.

We saw hunting behavior reminiscent of published accounts on monitor lizards (Varanidae). Based on Curio's (1976) seminal work on predation, Auffenberg (1984) defined two search patterns that varanid lizards use to locate prey. No forward movement of the lizard, few tongue flicks, and a large radial angle of coverage in the terrain marked casting search patterns. Scanning search patterns occurred while the varanid was in motion, actively tongue flicking, and was marked by a decrease in angle of coverage. Varanids relied on both of these search patterns while conducting object-concentrated searches of areas that had high probabilities of containing prey.

In our study, rattlesnakes exhibited both of these search patterns in areas containing cover. Rattlesnakes conducted casting search patterns when they investigated rock crevices and sticks. They utilized scanning search patterns when they explored the perimeters around rocks. The snakes also attended to cover items much more methodically in these situations. During trials, rattlesnakes returned to rock crevices and sticks they had explored earlier in the trial. This behavior is reminiscent of object-concentrated searches. These are areas where rodent prey is more likely either to reside or venture. Our findings with rattlesnakes clearly mirror Auffenberg's observations.

Trail-investigation and the choice of ambush sites by adult, terrestrial crotalines are surely beneficial when considering the habits of their small mammalian prey. Many rodent species routinely travel on well-worn pathways between food sources and their burrows or comparable shelter (Vorhies & Taylor, 1922; Pearson, 1959, Bendell, 1961). This phenomenon has been most extensively studied within the genus *Peromyscus*. White-footed deer mice, *P. leucopus*, use habitat markers such as rocks, trees, and fallen logs to navigate (Bendell, 1961; Douglas & Reinert, 1982; Drickamer & Stuart, 1984; McMillan & Kaufman, 1995). Desert granivores also frequent habitat containing rocks and shrubs because seeds clump there in high densities (Reichman & Oberstein, 1977). We have shown that western rattlesnakes

preferentially search habitat containing these elements and thoroughly in-
vestigate prey trails.

Moreover, caching rodents use rocks, trees, and logs as reference objects
to hide and retrieve their food stores (Jacobs, 1995). Upon caching nuts,
rodents seem to return to their food reserve sites within two weeks (Jacobs
& Liman, 1991), the maximum time that male prairie rattlesnakes tend to
remain at rodent bunkers (Duvall *et al.*, 1990). In our study, rattlesnakes
searched and coiled up into ambush posture next to these elements when
prey odor was present. Thus, rattlesnake investigation of runways, rocks,
trees and logs is likely to increase hunting success.

Crotaline snakes may also assume ambush posture in front of, or near,
foliage (Reinert *et al.*, 1984). Foliage may aid snake defensive behavior
by creating an added obstacle for terrestrial predators or possibly blocking
the aerial descent of raptors. Not only would brush obscure an escaping
snake, but predators stalking from behind would be slowed down and would
probably alert the snake. This could be a critical factor especially when
predators are downwind of the snake. In our study, rattlesnakes positioned
themselves on the side of the room with plants significantly more often.

Rock outcrops provide refuge and shelter for rattlesnakes by preventing
their detection and providing a substrate for body bridging as snakes lodge
their bodies within rock crevices (Chiszar *et al.*, 1992b). Rocky outcrops also
provide shade, moisture, and burrows that can be important for thermoreg-
ulation (Brown & Lillywhite, 1992). Since viperids maintain a more con-
sistent body temperature than the fluctuating environment, these microenvi-
ronment features seem crucial during both active and inactive periods (Saint
Girons, 1978). Hence, rattlesnakes choose habitat with rocks for multiple
reasons. We interpret the interaction between these environmental entities as
behavioral decisions that benefit foraging, defense, and thermoregulation.

Geographical variation

Microevolutionary patterns in behavior, morphology and life histories can
provide insight on the dynamics integral for adaptive radiations within
lineages (Schluter, 1996; Losos *et al.*, 1997; Zamudio, 1998). Geographical
variation in snake foraging behavior may be due to differences in distribution
of prey species, competitors and/or differential habitat usage (Henderson,
et al., 1987; Arnold, 1993; Reinert, 1993). Unfortunately, few laboratory

studies have explored snake predatory behavior in an ecological context (but see Drummond, 1983; Drummond & Burghardt, 1983) although ample work has addressed perceptual mechanisms and feeding responses (Burghardt, 1970; Arnold, 1977; Chiszar *et al.*, 1992a).

Garter snakes (*Thamnophis*: Colubridae) are an excellent snake lineage for comparison of geographic variation in foraging (Rossman *et al.*, 1996). *Thamnophis elegans* exhibits pronounced variation in head ecomorphology, color pattern and diet between populations in Northern California (Fitch, 1940; Fox, 1951; Arnold 1981a). Although geographic variation in diet choice seems to be heritable (Arnold, 1981b), individuals from populations with differing diets inherit the full complement of predatory repertoires (Drummond & Burghardt, 1983). Dietary variation seems to be maintained by intense selection on amphibious and aquatic prey due to extreme environmental fluctuation (Kephart & Arnold, 1982). However, color patterns seem extremely variable between populations (Fitch, 1940; Fox, 1951), due to convergent evolution to enhance camouflage and escape from predators (Jackson *et al.*, 1976; Bellemin & Stewart, 1977).

Sub-species of *Crotalus viridis* exhibit pronounced variation in color pattern, body size and diet (Klauber, 1956). Despite being tested in different arena designs, both sub-species possessed identical foraging repertoires. Adults from both sub-species feed mainly on different species assemblages of small, burrow-dwelling mammals (Fitch, 1946; Macartney, 1989; Duvall *et al.*, 1990; Wallace & Diller, 1990). Our *C. v. oreganus* originated from a population living in a lush Mediterranean habitat where snakes featured dark, trichromatic blotched patterns, while *C. v. viridis* came from a dry scrub habitat where snakes possessed dull, dichromatic blotched patterns. Color patterns of rattlesnake populations within a sub-species resemble local habitat far more than ancestry (Sweet, 1985). This suggests convergent evolution for disruptive coloration and background matching (Norris & Lowe, 1965).

Crotalus and *Thamnophis* are among the most speciose and ecologically diverse snake genera in North America (Klauber, 1956; Rossman *et al.*, 1996). Despite geographic variation in morphology, diet, and habitat, ecologically distinct populations of both *C. viridis* and *T. elegans* seem to possess full complements of foraging repertoires. Other pitvipers within the North American temperate and Neotropical lineage (including the genera

Agkistrodon, *Crotalus* and *Sistrurus*) also possess these homologous predatory repertoires, even species with generalized or derived ecology (Theodoratus, 1998). Although crypticity in many species is compromised due to the simultaneous selection for conspicuous coloration for sexual advertisement (Endler, 1978), snake body patterns evolve to enhance camouflage in local selective regimes (Camin & Ehrlich, 1958; Beatson, 1976; King & Lawson, 1997). With over 2700 species, the success of snakes as predators is indisputable (Greene, 1997). Many snake lineages possess generalized foraging repertoires that are highly effective in numerous environments when coupled with cryptic coloration that thwarts visually oriented organisms. Hence, the microevolutionary pattern suggests that homologous behavior with subsequent modification of body coloration provides a mechanism integral to the radiation of snakes.

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