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# SMALL MAMMAL PREDATION AND PREY HANDLING BEHAVIOR BY THE GARTER SNAKE *THAMNOPHIS ELEGANS*

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ABSTRACT: Predation on small mammals is of common occurrence in some coastal populations of the western terrestrial garter snake (*Thamnophis elegans*). These snakes often handle mice by coiling loops of the body around the prey, much in the manner of constrictors. This coiling behavior, however, is quite variable and unstable, unlike that shown by other constricting species. There is no clear relationship between snake size and size of small mammal taken in field or laboratory. Rather, a restricted size range of mammals is eaten by a restricted size range of snakes. Coiling behavior seems to be a means of immobilizing prey rather than killing it, although death of prey sometimes occurs. Although limited anatomical evidence suggests that *T. elegans* should be more capable of handling difficult prey such as mice than are other sympatric species of garter snakes, *T. elegans* may not be very efficient at capturing small mammals in the field.

*Key words:* Reptilia; Serpentes, Colubridae; *Thamnophis;* Small mammals; Constriction; Predation

MAMMALS, especially rodents, are eaten by many species of snakes. Snakes feeding on such active, potentially dangerous prey usually subdue the prey by envenomation, by constriction, or by simply holding it down with the weight of the body. Green and Burghardt (1978) suggested that constriction has evolved as a means of handling large prey, and Willard (1977) implied that many colubrids are more likely to constrict larger than smaller prey. Presumably, similar statements could be made concerning the other methods of prey handling mentioned above. In contrast to such feeding modes, garter snakes (*Thamnophis*) usually just seize their prey and swallow it alive. As might be expected, garter snakes feed upon mammals only rarely. Such predation seems to have been recorded for only three species of *Thamnophis*: *T. radix* (Hart, 1979), *T. sirtalis* (Anderson, 1977; Carpenter, 1952; Fitch, 1965; Hamilton, 1951; White and Kolb, 1974), and *T. elegans* (Anderson, 1977; Campbell 1969; Fitch, 1941; Fleharty, 1967; Fox, 1951, 1952; Gregory, 1978; Tanner, 1949; White and Kolb, 1974). The records of mammals in the diets of *T. radix* and *T. sirtalis* appear to represent occasional food items rather than major dietary components. Some populations of the western terrestrial garter snake (*T. elegans*), however, feed fairly heavily on small mammals. Such is the case for *T. elegans* on Vancouver Island, Canada; small mammals, especially voles (*Microtus*), form the third most important component of the diet in many populations of this snake on Vancouver Island (Gregory, 1978). In addition, this species has been observed to make considerable use of its body when handling small mammals (but not other prey) in the field (S. Mitchell, pers. com.) and laboratory (Gregory, pers. obser.). The snakes frequently coiled around the prey in the manner of constrictors and sometimes actually killed the prey. Although Peterson (1978) has briefly described constricting behavior in *T. elegans*, our first objective in this paper is to report our own observations on such behavior. Specific questions we address are: (1) What is the relationship between size of snake and size of rodent eaten? Expectations might be that larger snakes eat larger mice and/or a greater range of prey sizes. (2) Is the use of coiling behavior a function of relative sizes of snake and mouse or is this behavior just shown by a few individual snakes? (3) Do these garter snakes often kill their prey using coiling behavior and if so, how?

## Materials and Methods

We obtained as many field-collected stomach samples containing small mammals as possible from populations of *T. elegans* on Vancouver Island. Most were preserved samples of stomach contents reported in Gregory (1978) or collected by us, but we also examined preserved stomach samples loaned to us by Neil Dawe of Qualicum Beach, British Columbia. We eliminated all partly digested samples and used only intact prey items in our analysis. We initially measured maximum cross-sectional diameter and volume of each intact prey specimen but found these two measures to be highly correlated (Spearman's rank correlation, $r_s = .76$, $n = 11$), so we used only prey volume in subsequent analysis. We also measured body length (tip of snout to base of tail) of each prey specimen for purposes of comparison with body sizes presented in Burt and Grossenheider (1964). The relationship of prey volume to snout–vent length (SVL) of the corresponding snakes was examined graphically.

In the laboratory we individually housed 20 randomly collected specimens of *T. elegans* in small wooden cages measuring 30 × 26 × 26 cm. The cages were kept in an isolated room at 22–23 C and at about 8 h light per day. The substrate in the cages was sawdust or sheets of newspaper, and fresh water was constantly available. The snakes were of various sizes ranging from 250–610 mm SVL. All snakes were not used simultaneously; most were involved in the study at various times from mid-May to the end of December 1978. SVL's of snakes were measured infrequently during the study in order to minimize handling and disturbance; inspection of the data indicated that the small amount of growth taking place during the experiment did not affect our overall conclusions.

The prey we fed to the snakes were laboratory mice (*Mus musculus*) of various colors. Natural prey were too difficult to catch or raise in large numbers and we had already discovered that *T. elegans* would readily accept laboratory mice. We assumed that the basic characteristics of such mice as prey would be similar to those of wild mice, although laboratory mice reach a smaller maximum size than do local voles. At various intervals each snake was offered a randomly chosen mouse. These mice ranged in size from newborn to adult. Usually at least a week intervened between successive offerings of mice to a snake although we sometimes gave a feeding snake a second mouse or presented a smaller mouse to a snake which had previously been offered a relatively large mouse.

When a mouse was presented to a snake we watched to see if the snake would immediately strike at and/or catch it. If the snake immediately captured the mouse we made general observations of the method used to handle the mouse but we did not quantify such behavior. We also tried to ascertain whether or not the snake killed the mouse before eating it (i.e., by watching the mouse for breathing movements, kicking, etc.). Otherwise we did not stay continuously in the room with the snakes so they were allowed to feed with minimal disturbance. We rechecked the cage at irregular intervals to observe whether or not the mouse was eaten and, if possible, general features of the capture and eating process. If the mouse was not captured in an hour the experimental run was terminated. Again we examined the relationship between predator size and prey size for prey that were eaten.

All statistical tests were Spearman's rank correlation analyses with $\alpha = 0.05$.

## Results

We were able to obtain only 11 intact specimens of small mammals from field

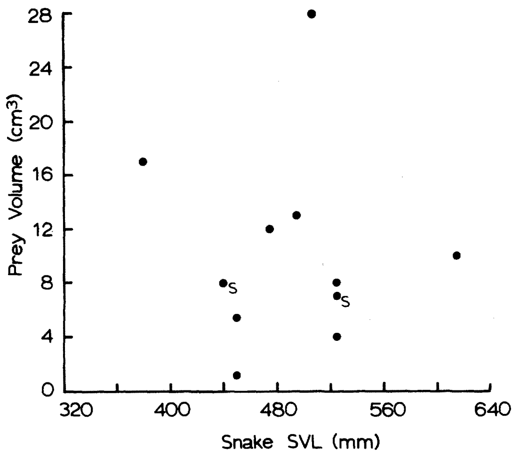


FIG. 1.—Relationship between size of snake and size of prey for field-caught snakes containing intact small mammals. Two prey were shrews (indicated by S) and the other nine prey were voles. $n$ = 11.

collected stomach samples. Of the specimens used, 9 were Townsend voles (*Microtus townsendi*) and 2 were vagrant shrews (*Sorex vagrans*). These are the only mammals known to be eaten by snakes on Vancouver Island. As general body form was not greatly dissimilar, we lumped these two prey types into one sample. No correlation was observed between prey volume and snake SVL (Fig. 1; $r_s$ = .14, $n$ = 11). The largest *Microtus* eaten was 7.8 cm long which is well short of the maximum length of 12–14.4 cm given for *M. townsendi* by Burt and Grossenheider (1964). However, one partly digested specimen of *Microtus* in our samples measured 13 cm in length, so more data might reveal a greater range of prey sizes taken.

Nevertheless, these results were not greatly different from those obtained in the laboratory. Although a great variety of sizes of mice were offered to snakes in the laboratory (range = 1.55–36.37 g), the largest mice taken were approximately half-grown (Fig. 2). Unsuccessful strikes or series of strikes were occasionally made at larger mice (Fig. 2). The rank correlation between snake size and size of mouse eaten was not significant ($r_s$ =

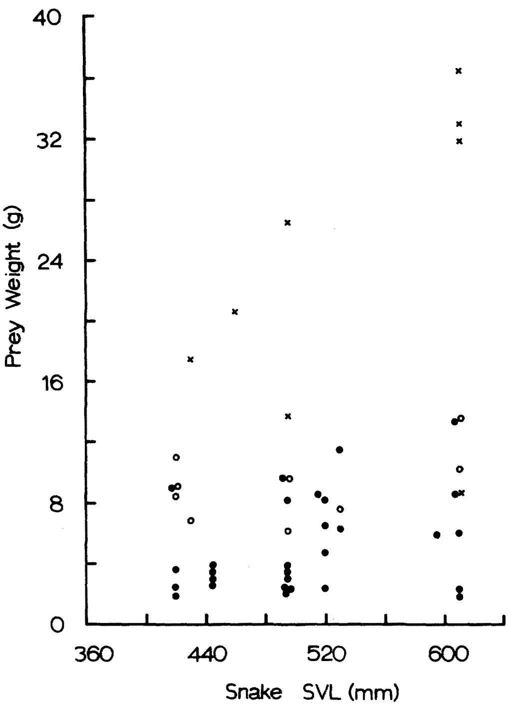


FIG. 2.—Relationship between size of snake and size of prey for snakes fed laboratory mice. X's represent unsuccessful attempts to capture mice. Successful feedings ($n$ = 38) are divided into 2 categories: open circles indicate coiling behavior observed; closed circles indicate no coiling behavior observed.

.17, $n$ = 38) and there was little suggestion that larger snakes ate a greater range of prey sizes. There was also no tendency for individual snakes to eat larger mice as the experiment progressed. Similar results were obtained when we substituted snake head width (measured with a vernier caliper at the level of the posterior margin of the postparietal head shields) for SVL. This was not surprising since head width and SVL are highly correlated ($r_s$ = .99, $n$ = 10). As the specific gravity of small mammals is probably near unity, the sizes of such prey taken in the laboratory and field were more or less equivalent with the exception of two fairly large prey eaten in the field (compare Figs. 1 and 2).

Mice were frequently taken immediately or within a few minutes of being put in the cage, but the time to attack varied considerably (up to 55 minutes on rare occasions). Coiling behavior was observed in only nine instances and was usually on relatively large prey (Fig. 2), but no clear relationship between prey-predator size ratios and coiling behavior emerged. However, we may have missed this behavior in some instances because of our method of observation. Nevertheless, this low incidence of coiling behavior also precluded any conclusion about whether or not such behavior was a trait of certain individuals. In two instances snakes were unsuccessful in their attempts to coil around active prey, but eventually ate the mice anyway. Some snakes refused to eat at all, but three of these were small snakes and were probably incapable of handling most mice offered them. When mice were refused by snakes it was not possible to distinguish between lack of interest in mice as food or simple lack of hunger. Snakes often showed initial interest in a mouse (tongue flicks, etc.) but appeared reluctant to attack, especially if the mouse was large and/or active. Snakes sometimes even appeared to avoid mice under such circumstances.

Snakes were somewhat variable in the manner in which they captured mice, although mice were frequently seized just behind the head in the shoulder region. This often seemed to immobilize the mouse. If the mouse was relatively large there was usually considerable struggling and the snake appeared to experience considerable difficulty in getting a loop of its body over or around the mouse. Sometimes the mouse was lost and recaught, but recapture seemed to be more a function of the confines of the cage than of any particular skill or speed on the part of the snake. The number of attempts made by snakes to capture a mouse was usually small, but one snake made 15 attempts before finally securing a particular mouse. Although our observations were limited there appeared to be much variation in the way snakes made use of the body in coiling behavior. Sometimes the body was neatly coiled in a few tight loops around the mouse, but sometimes the coils were simply a tangled disarray. In addition, the coiling configuration tended to be unstable as the movement of the mouse often caused the snake to uncoil and recoil several times. This behavior does not appear to fit readily into any known pattern of constriction in snakes (Greene and Burghardt, 1978; Willard, 1977). However, videotape analysis of the behavior might reveal more details. Most often, even when the snake had used its body to restrain the mouse, the mouse was swallowed alive although often inactive, possibly because of exhaustion. Sometimes a mouse was apparently dead when swallowed, especially if its head had been held in the snake's mouth while struggling.

## Discussion

A direct relationship between prey size and predator size has been noted for several kinds of animals (e.g., Hespenheide, 1975; Labanick, 1976). Such relationships may be important in determining the outcome of competition between different sized predators (Wilson, 1975). In snakes, because of their ability to handle relatively large prey, it might be expected that the predator-prey size relationship would be less pronounced. Studies of feeding habits of garter snakes on Vancouver Island, however, generally indicate a fairly close relationship between snake size and prey size, for a rather wide diversity of prey such as slugs, earthworms, amphibians, and fish (Gregory, unpubl. data). A striking exception to this generalization appears to be when the prey are small mammals, as supported by both field and laboratory data in this study. This result was unexpected as mice might be considered difficult (and dangerous) prey for garter snakes to handle and therefore be more likely to lead to a strong relationship between predator and prey sizes.

In this study the smallest snake which took a mouse was 420 mm SVL and no snake took a mouse heavier than 13.6 g, although attempts were occasionally made at mice as heavy as about 36 g. Carpenter (1952) indicated that *T. sirtalis* over 400 mm long were more likely to eat *Microtus* than were small snakes. White and Kolb (1974) found that *Microtus* were eaten only by garter snakes (*T. elegans* and *T. sirtalis*) of 460 mm SVL and greater. Other authors are not specific about the relationship between snake size and size of mammalian prey, although Fitch (1965) suggested that rodents were not available prey for younger (smaller) *T. sirtalis*. Hamilton (1951) and White and Kolb (1974) indicated that only subadult and smaller *Microtus* were taken by garter snakes. Our data are in agreement with these observations. Thus, it appears that a limited size range of small mammals is available to a limited size range of garter snakes. This probably accounts for the fact that mammals are the least frequently taken of the three major dietary items of *T. elegans* on Vancouver Island (Gregory, 1978) and explains the lack of a statistically significant correlation between snake size and prey size.

Among mammals recorded in the diets of garter snakes, voles (*Microtus*) have been the most frequently noted (Anderson, 1977; Carpenter, 1952; Fitch, 1941, 1965; Fox, 1951, 1952; Gregory, 1978; Hamilton, 1951; Tanner, 1949; White and Kolb, 1974). Several other mammals have been reported, however, including rabbits (Fitch, 1941), shrews (Fitch, 1941; Fleharty, 1967; Gregory, 1978; Hamilton, 1951), harvest mice (Fitch, 1965), chipmunks (Fleharty, 1967; Hamilton, 1951), and deer mice (Anderson, 1977; Campbell, 1969; Fitch, 1941, 1965; Fox, 1952; Tanner, 1949). We assume that these records (all for *T. elegans* and/or *T. sirtalis*) do not reflect preferences of snakes for different species of mammals, but are simply due to relative prey availabilities and body sizes. We have not noticed any reluctance by Vancouver Island *T. elegans* kept in the laboratory to eat *Mus musculus* or *Peromyscus maniculatus*, neither of which has been reported in the natural diet of *T. elegans* on Vancouver Island (Gregory, 1978). Likewise, Fox (1952) found that *T. elegans* readily feed on newborn rats and mice in captivity. Carpenter (1952), however, was unable to induce *T. sirtalis* to feed on small mammals in captivity even though *Microtus* were occasionally recorded in the natural diet. We also have had no success in inducing *T. sirtalis* from Vancouver Island to eat mice in captivity, although we have made few attempts. We have only two records of small mammals in the diet of this species on Vancouver Island (Gregory, pers. obser.). Of garter snakes on Vancouver Island, only *T. elegans* preys significantly on small mammals. It is interesting to speculate as to why *T. elegans* on Vancouver Island feeds almost exclusively on *Microtus* even though *Peromyscus* are abundant. Campbell (1969) found *T. elegans* preying on both young and adult *Peromyscus* on Mittlenatch Island off the east coast of Vancouver Island. *Peromyscus,* however, is the only rodent species occurring on Mittlenatch Island (Campbell, pers. com.). *Microtus* are probably more available in the open meadow habitats which *T. elegans* seems to favor on Vancouver Island (Gregory, 1978) and *Microtus* are probably easier to catch than the more active *Peromyscus*. In addition, *Microtus* is frequently active in the daylight as are snakes. *Peromyscus,* however, is nocturnal (Burt and Grossenheider, 1964).

Although rodent eating is not unique to *T. elegans* among garter snakes, it seems to be a well developed behavior in this species. The use of the body in handling mice is almost certainly not true constriction as the snake rarely seems to kill the mouse and never does so quickly. The configuration of coils is also not predictable or stable as it is in most constrictors (Greene and Burghardt, 1978; Willard, 1977). The use of loops of the body by *T. elegans* is probably more a means of restraining an active prey than killing it. A restraining function for coiling was also indicated for the striped swamp snake (*Regina alleni*) by Franz (1977) and for the smooth snake (*Coronella austriaca*) by Smith (1973). Willard (1977), however, includes *Coronella* in a study of constricting snakes; Spellerberg (1977) describes coiling behavior in *Coronella*, but does not mention constriction. Nevertheless, it seems clear that coiling around a prey does not necessarily indicate true constriction. Possibly such behavior is used mainly when the prey struggles. Peterson (1978) reached similar conclusions about the function of coiling behavior in *T. elegans*, although his description suggested a much more predictable behavior pattern than indicated here.

Interestingly, Cowan and Hick (1951) have compared the cranial myology of the three species of garter snakes in our study area. They found that in *T. elegans* and *T. sirtalis* the posterior intermandibularis muscle (pars posterior) was larger and better defined than in *T. ordinoides* and they related this difference to the fact that both *T. elegans* and *T. sirtalis* tend to eat more active prey than does *T. ordinoides* (see Gregory, 1978). Cowan and Hick (1951) indicated that this muscle is especially well defined in *T. elegans* and suggested that the contraction of the intermandibularis musculature during prey handling could result in slow suffocation of the prey. This seems to be the most reasonable interpretation of the manner in which some mice were apparently killed by snakes in our experiments. Other muscular differences between *T. elegans* and other garter snakes might be worth searching for (see Ruben, 1977).

There is thus limited evidence of a correlation between anatomy and natural feeding habits of garter snakes on Vancouver Island (Gregory, 1978). Even so, we wonder how *T. elegans* capture rodent prey in the field and how often they are successful. Carpenter (1952) also questioned how rodents were taken by *T. sirtalis* in the field (specifically whether they were taken dead or alive). We suggest that these snakes may not be very efficient at capturing rodents, especially considering that captive snakes frequently make several attempts at catching a mouse before being successful and that the mouse often seems to be caught only because of the restrictive confines of the cage. In a more natural situation it seems reasonable to expect prey to escape fairly often. However, a half grown mouse probably represents a large intake of energy so it may be worthwhile for a snake to pursue such prey. The relatively low frequency of occurrence of rodents (compared to slugs and fish) in the diet of *T. elegans* on Vancouver Island (Gregory, 1978) may not reflect adequately the importance of such prey in the diet.

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# VARIATION IN THE HISPANIOLAN GIANT ANOLE *ANOLIS BARAHONAE* WITH THE DESCRIPTION OF TWO NEW SUBSPECIES

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ABSTRACT: Analysis of geographic variation in *Anolis barahonae* from the Sierra de Baoruco and Península de Barahona in the República Dominicana indicates the presence of two undescribed subspecies: one occurs along the eastern margin of the peninsula, and the other occurs at slightly higher elevations along the Dominico–Haitian border in the Dominican portion of the Massif de la Selle.

*Key words:* Reptilia; Sauria; Iguanidae; *Anolis;* Subspecies; Hispaniola

THE West Indian island of Hispaniola is inhabited by three species of giant anoles (*Anolis ricordi, Anolis baleatus, Anolis barahonae*). Of these, *A. barahonae* occurs in the Dominican Sierra de Baoruco and on the Península de Barahona, which extends from the south coast into the Caribbean Sea. The peninsula is