THE FOOD HABITS AND FEEDING BEHAVIOR OF NEW WORLD CORAL SNAKES

by

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ABSTRACT

This thesis considers the food habits and feeding behavior of New World venomous coral snakes, with emphasis on Micrurus fulvius, a species that is found in the southeastern United States and northern Mexico. Literature records and the stomach contents of preserved specimens demonstrate that M. fulvius of all sizes are specialized tertiary consumers. In Texas, they feed mostly on several species of small, secretive colubrid snakes and on skinks of the genera Eumeces and Leiolopisma. Other kinds of lizards and the young of large colubrid and viperid snakes make up the remainder of their prey. Geographic and seasonal variations in the diet reflect the distribution and availability of particular prey species. The data from other parts of the range do not show differences from the pattern observed in Texas.

A preliminary ethogram for Micrurus fulvius includes 26 action patterns and two orienting movements, and many of these elements are used in feeding behavior. Coral snakes use stereotyped searching movements to find food in litter and to follow prey trails. Visual and chemical stimuli elicit attack, and the prey is held until it is immobilized by the venom. Pre-ingestion movements are inhibited by the prey's struggles and directed by scale overlap. Swallowing is head first, and includes movements of the entire head of the coral snake as well as individual jaw elements. The feeding behavior is interpreted as being intermediate between a simple colubrid method and the highly specialized viperid type.

Data are presented on the food habits of 26 other New World elapids. They are known to eat onycophorans, eels, caecilians, amphisbaenians, lizards, and snakes. The feeding behavior of Micruroides euryxanthus, Micrurus corallinus, and M. distans is similar to that of M. fulvius. Micrurus frontalis and

perhaps *M. lemniscatus* bite, release, and relocate prey prior to swallowing, but the reason for this apparent innovation is unknown.

Morphological, behavioral, and ecological similarities between Old and New World coral snakes may reflect the phylogeny and zoogeography of the snakes or represent convergence and equivalence. It is suggested that sympatry among New World species might be uncommon or accompanied by size differences.

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INTRODUCTION

Snakes are elongate, legless reptiles that probably evolved from lizards in the Cretaceous (Frazetta, 1970). Today they are prominent predators in many terrestrial communities, and exhibit some peculiar morphological and behavioral modifications for this role. Perhaps most importantly, snakes possess an extremely flexible jaw apparatus that permits the ingestion of large prey items without the assistance of limbs or mastication (Gans, 1961). They also rely heavily on the chemical senses for finding and recognizing food (Burghardt, 1970; Gehlbach, et al., 1971), and several groups have specialized venom injection mechanisms for immobilizing their prey (Gans and Elliott, 1968). Thus, the food habits of snakes should be of interest from ecological and evolutionary points of view.

Unfortunately, much of the available information on food habits consists only of lists of prey items. There is rarely a hint of why particular individuals or populations eat certain prey. Studies are needed that deal with snakes as predators in terms of Charles Elton's "food niche" (Elton, 1927), or in more modern jargon, their "trophic role" (Lein, 1972)--to learn not only what a particular species eats, but also how and why. Such investigations could contribute valuable information for broader considerations of functional morphology, community structure, and zoogeography (cf. Arnold, 1972; Frazetta, 1970; Milstead, 1972; Rabb and Marx, 1973).

This thesis examines the trophic roles of some New World venomous coral snakes, members of the cosmopolitan family Elapidae. There were four objectives: (1) To provide an ecological characterization of the food habits of one species, *Micrurus fulvius*, with emphasis on one segment of its range. (2) To describe the feeding behavior of *M. fulvius* from a broad, ethological point of view, and thereby gain evidence of factors affecting the diet of this species. (3) To assemble data on the food habits and feeding behavior of other New World coral snakes. (4) To evaluate the results in terms of the zoogeography of elapids and the feeding behavior of other snakes.

METHODS

The stomachs of preserved coral snakes were opened with a ventral incision and the orientation of each prey item in the gut was recorded (see Appendix for a list of specimens that contained prey). The identity and approximate size of each item was determined when possible, often on the basis of a tail or a tail and posterior part of a body. This was done by comparison with published information or reference specimens. Fecal samples were obtained from two live coral snakes before they fed in captivity, treated with Fitch's (1960) detergent rinse technique, and stored in alcohol.

Fifteen live *Micrurus fulvius* were donated by biologists at several Texas colleges, and one was purchased from a collector. Two *Micruroides euryxanthus* were received from the Arizona-Sonora Desert Museum. Three of the *M. fulvius* and one *M. euryxanthus* fed readily in captivity and were used for behavioral observations. Another *M. fulvius* and a *M. distans* were studied in their exhibit cages at the Dallas Zoo. My captives were individually housed in glass terraria that measured 32x32x62 cm or 27x32x52 cm. Each cage had a gravel substrate covered with leaf litter, a water bowl, and at least one large piece of bark for cover. Water was sprinkled over the leaves two or three times each week. The snakes were kept in a dark room that usually had a temperature of 22-24°C, but occasionally rose to 30°C. A one hundred watt bulb on top of the perforated metal cover of each tank raised the temperature at one end to *ca.* 24-26°C. These lights were automatically turned on for 10 hours each day. Live snakes were moved on a stiff wire hook when necessary but never handled directly. Observations were timed with stop watches and recorded on tape or with a 35 mm camera and electronic flash.

Captive coral snakes were fed live or dead prey of the following species: *Anolis carolinensis*, *Eumeces brevilineatus*, *E. fasciatus*, *Leiolopisma laterale*, *Coluber constrictor*, *Diadophis punctatus*, *Elaphe obsoleta*, *Heterodon platyrhinos*, *Natrix erythrogaster*, *N. rhombifera*, *Opheodrys aestivus*, *Sonora episcopa*, *Storeria dekayi*, *Tantilla gracilis*, *T. nigriceps*, *Thamnophis proximus*, *Tropidoclonion lineatum*, and *Virginia striatula*.

Experiments on the direction of prey ingestion utilized "body pieces" and "skin reversed" specimens. Body pieces of snakes were segments 10-15 cm long and 4-7 mm wide from a blue racer (*Coluber constrictor*), a rough green snake (*Opheodrys aestivus*), and a western ribbon snake (*Thamnophis proximus*). Body pieces of five-lined skinks (*Eumeces fasciatus*) were prepared by removing the head, legs, and tail of dead animals. All specimens were frozen in water, and the pieces were allowed to reach room temperature before use. Skin reversed snakes were made by cutting the skin of a dead specimen a few millimeters in front of the anus and in back of the head. The skin was then carefully removed, rinsed with water, and slipped back over the snake so that the anterior end of the skin was at the posterior end of the body. The tails were removed. Rough green snakes, small blue racers, a rough earth snake (*Virginia striatula*), and small water snakes (*Natrix sp.*) were used. Only the anterior portions of green snakes were used, because of their length relative to coral snakes. Body pieces and skin reversed specimens were presented to coral snakes with metal forceps, so that they were on the ground and perpendicular to an approaching snake.

Trail following behavior was studied with a modified version of the arena used by Gehlbach, *et al.* (1971). It consisted of an 80x80 cm piece of white duck cloth (28 strands/cm^2) in a plastic swimming pool. An octagonal trail lane with segments 20 cm on an outer side and 1 cm wide was marked on the cloth with indelible ink. Prior to an experiment a potential prey item was confined to the trail lane by a portable 8 cm high cardboard alley and allowed to crawl around for a specified period. Then the prey animal and the cardboard alley were removed. Next a coral snake was placed in the center of the arena for three minutes in a one gallon plastic jar with the bottom removed. It was released by lifting the jar. The behavior of the snake was observed under a sixty watt red light positioned so that it very dimly lit the arena. Observations were made from outside the pool in the dark. The cloth arenas were machine washed, rinsed, and dried after each test.

An attempt was made to test the response of newly hatched coral snakes to prey extracts, using techniques developed by Burghardt (1970). Surface wash extracts were prepared by placing mealworms, newborn mice, a ground snake (*Sonora episcopa*), or earthworms in a beaker of distilled water at 60°C for three minutes. The prey to water ratio was 3g/10ml. Extracts were stored frozen and warmed to room temperature before use. For testing, a sterile cotton swab was dipped in a vial of extract and then slowly moved to within 5 mm of the snout of a snake. Repeated attempts with each extract failed because of the extreme nervousness of the coral snakes. They consistently responded by frantically avoiding the swabs.

Statistical procedures follow Simpson, *et al*. (1960). Nomenclature is based on Peters and Donoso-Barros (1970), Peters and Orejas-Miranda (1970), Raun and Gehlbach (1972), and Smith and Taylor (1966).

THE FOOD HABITS OF *MICRURUS FULVIUS*

Literature on the food habits of coral snakes in Texas dates from 1860, when the frontier naturalist Benno Matthes examined the stomachs of four specimens. Curtis (1952), Kennedy (1964), Malloy (1971), Minton (1949), Mitchell (1903), Ruick (1948), Schmidt (1932), and Strecker (1908) have subsequently mentioned prey eaten by free-living snakes. These records and the stomach analysis of museum specimens (combined in Table 1) demonstrate that Texas coral snakes of all sizes are specialized tertiary consumers. Small, secretive snakes and scincid lizards make up the bulk of their diet.

Forty-seven of the 117 prey items (40.2%) were colubrid or leptotyphlopid snakes of the genera *Diadophis*, *Leptotyphlops*, *Sonora*, *Storeria*, *Tantilla*, *Tropidoclonion*, and *Virginia*. At least some of the unidentified snakes probably also belong to these genera. These snakes are secretive species, normally found in litter or beneath logs or rocks (Clark, 1964; Kassing, 1961; Ramsey, 1953; Wright and Wright, 1957). *Diadophis*, *Sonora*, *Tropidoclonion*, and *Virginia* usually have snout-vent lengths of 200-400 mm and weigh 3-10 g (Conant, 1958; Greene, unpublished). *Leptotyphlops* and *Tantilla* tend to be shorter and more slender, and to weigh less. Six coral snakes had eaten green snakes, *Opheodrys aestivus*; these are relatively long snakes (total length normally up to 800 mm) but no thicker than an adult *Tropidoclonion*.

Seven skinks of the genus *Eumeces* make up 6.0% of the total sample. The *E. fasciatus* were females or subadult males, and probably weighed 5-7 g (Fitch, 1954). Adult *E. brevilineatus* are shorter than *E. fasciatus* and probably weigh somewhat less. Sixteen ground skinks, *Leiolopisma laterale*, comprise 13.7% of the prey items, but probably make only a small contribution to total prey biomass. Adult *L. laterale* have snout-vent lengths of 40-60 mm and weigh a gram or slightly more, and only four records of this species represent confirmed ingestion of an entire skink. In 12 cases only the tail was found. Six had clearly been autotomized, and five others looked as if they had been also. It seems likely that in most cases the skink escaped, and observations that support this conclusion are presented in the section on feeding behavior.

Most of the other prey were young or subadult individuals of large terrestrial or aquatic snakes (Agkistrodon, Elaphe, Lampropeltis, Natrix, Salvadora), fence lizards (Sceloporus sp.), and other coral snakes. On some occasions Micrurus fulvius eats colubrids that are proportionately quite large (Matthes, 1860; Mitchell, 1903), but such meals are obviously infrequent and can even be fatal for the coral snake (Neill, 1968). Amphibians and mammals are only rarely eaten, if at all; the single items in each of these classes might have been secondarily ingested.

Even very small coral snakes eat skinks and small colubrid snakes. Seven specimens from Texas with snout-vent lengths of 250-290 mm contained three Leiolopisma laterale (tails only), scales of an unidentified skink, one Opheodrys aestivus, one Storeria dekayi, and one Virginia striatula. Campbell (in press) reported that a snake hatched in captivity began feeding on L. laterale at an age of two months.

I evaluated geographic variation in food habits by grouping the records for Texas in four subsamples (Table 1; see the Appendix for a list of counties and specimens in each group). "East Texas" includes material from an area of mixed deciduous and pine forests. The "north-central" sample is from the tall grass praire-forest ecotone. The "central Texas" group includes snakes from the forested hill country of the Edwards Plateau and from the eastern edge of the Chihuahuan Desert. "South Texas" snakes are from the semiarid thorn scrub and subtropical forest region (see Gould, 1962, and Tharp, 1952, for vegetation regions). The results indicate that there are no important geographic changes in the food niche of Texas coral snakes. Each geographic subsample includes small, secretive colubrid snakes, skinks, and the young of larger snakes. Differences among the four areas reflect the distribution of certain prey species, rather than a shift in the size and class of prey taken. Thus, coral snakes prey on *Virginia* and *Storeria* in east Texas, on these species and *Tropidoclonion lineatum* in north-central Texas, and on *Sonora*, *Storeria*, and *Tantilla* in the more xeric western and southern parts of the state. There does appear to be a change in the utilization of skinks, however, with predation on these lizards more frequent in the more mesic eastern forests. This is probably because there are more species of skinks found in east Texas (Raun and Gehlbach, 1972).

There may be seasonal variation in the food habits of Texas coral snakes. Collecting dates are available for 69 specimens that contained prey, and the monthly distribution of 91 prey items (Table 2) suggests that skinks and juveniles of large snakes (*Agkistrodon*, *Elaphe*) are more frequently eaten in the spring and fall.

Information for 29 *Micrurus fulvius* from elsewhere in the species range is presented in Table 3, based on preserved specimens, unpublished observations by M. A. Nickerson and R. A. Thomas, and literature records (Chance, 1970; Clark, 1949; Hay, 1893; Loveridge, 1938, 1944; Martin, 1958; Myers, 1965; Neill, 1968; Schmidt, 1932; Telford, 1952). Like Texas snakes, they had fed on snakes and lizards. Small, secretive colubrids of the genera *Diadophis*, *Ficimia*, *Storeria*, *Tantilla*, *Tropidodipsas*, and *Virginia* accounted for 46.5% of the sample. Most of the remaining food items were anguid and scincid lizards and other colubrid snakes. The only mammal was represented by a few hairs in a Tamaulipas specimen, and was perhaps secondarily ingested.

Other _Micrurus_ _fulvius_ make up 3.1% of the total of 160 prey items from throughout the species range, but the reason for cannibalism is unknown. Curtis (1952) suggested that two males from Angelina County, Texas had attempted to swallow a _Storeria_ _dekayi_ from opposite ends, and that the smaller coral snake was then eaten by the larger one. This seems unlikely, because it implies that two free-living coral snakes found a single food item almost simultaneously and, more importantly, because it would mean that one of them attempted to swallow the brown snake tail first. Ardrey (1970) misquoted Loveridge's (1944) account of cannibalism and then suggested it is an example of the inability to control aggressive social behavior--a far-flung speculation at best. There is no evidence for size or sex as an explanation, since five cases involved the following combinations of predator and victim: two adult males had eaten other adult males, one adult male had eaten a juvenile male, one adult male had eaten a gravid female, and one adult female had eaten another adult female.

Table 1. Occurence of prey items in the stomachs of Texas coral snakes, *Micrurus fulvius*. Abbreviations refer to specimens from east Texas (E), north-central Texas (N), central Texas (C), south Texas (S), and no specific locality (U). Number of coral snakes containing prey is in parentheses.

Prey Species	U (10)	E (43)	N (13)	C (14)	S (16)	Total (96)
Unidentified frog					1	1
Unidentified reptile		1				1
Unidentified lizard	1					1
Sceloporus sp.				1		1
Sceloporus undulatus		1				1
Unidentified skink				1	1	2
Eumeces brevilineatus				1		1
Eumeces fasciatus	1	5				6
Leiolopisma laterale	1	13		1	1	16
Cnemidophorus gularis				1		1
Unidentified snake	4	5		2	3	14
Agkistrodon contortrix		2				2
Diadophis punctatus				1		1
Elaphe obsoleta	1	2				3

Table 1, continued.

Prey Species	U	E	N	C	S	Total
Lampropeltis calligaster			1			1
Lampropeltis getulus	1		1			2
Leptotyphlops dulcis					1	1
Masticophis flagellum	2					2
Micrurus fulvius		2				2
Natrix sp.			1			1
Natrix rhombifera		1				1
Opheodrys aestivus		5			1	6
Salvadora grahamiae				1		1
Sonora episcopa				3	3	6
Sonora episcopa or *Tantilla sp.*			1		1	2
Tantilla sp.					4	4
Tantilla gracilis		2				2
Tantilla atriceps				1		1
Thamnophis sp.	1					1
Thamnophis marcianus					2	2

Table 1, continued.

Prey Species	U	E	N	C	S	Total
Tropidoclonion lineatum			4			4
Virginia striatula		6	8	1	1	16
Virginia valeriae				1		1
Virginia striatula or Storeria dekayi		4				4
Storeria dekayi		4			1	5
Unidentified rodent	1					1
Total prey items	13	53	16	15	20	117

Table 2. Seasonal incidence of different kinds of prey in the stomachs of coral snakes, *Micrurus fulvius*, from Texas. Numbers of coral snakes in parentheses.

Month	Skinks	Other Lizards (*Sceloporus*)	Unidentified Snakes	Small Colubrid Snakes	Young of Large Snakes
March (2)	3				
April (20)	6	1	2	13	1
May (7)	2		1	4	1
June (2)	1		1		
July (5)	1		2	3	
August (6)			1	3	2
September (4)			3	2	
October (14)	4	1	2	7	3
November (5)	2			3	
December (4)	2			4	

Table 3. Occurence of prey items in the stomachs of coral snakes, _Micrurus fulvius_, from the southeastern United States and northern Mexico. Abbreviations refer to specimens from South Carolina (S), Florida (F), Louisiana (L), and the state of Tamaulipas, Mexico (M). Number of coral snakes containing prey is in parentheses.

Prey Species	S (1)	F (16)	L (8)	M (4)	Total (39)
Ophisaurus sp.		2			2
Leiolopisma laterale			1		1
Eumeces fasciatus			3		3
Unidentified snake		1			1
Coluber constrictor		4			4
Diadophis punctatus		3	2		5
Elaphe guttata		1			1
Farancia abacura		3			3
Ficimia olivacea				1	1
Lampropeltis getulus			1		1
Opheodrys aestivus		2			2
Storeria dekayi		1	3		4
Storeria dekayi or _Virginia striatula_			2		2

Table 3, continued.

Prey Species	S	F	L	M	Total
Storeria occipitomaculata			1		1
Tantilla sp.		3			3
Tantilla gracilis			1		1
Tantilla rubra				1	1
Tropidodipsas sartorii				1	1
Virginia valeriae	1		1		2
Micrurus fulvius		3			3
Unidentified mammal				1	1
Total prey items	1	23	15	4	43

SNAKES AND ETHOGRAMS

Ethological studies have classically included an inventory of behavior patterns, called an ethogram. Detailed ethograms have now been prepared for many animals, especially various invertebrates, fishes, birds, and mammals, and these have served as foundations for intensive causal analyses and extensive comparative studies (Eibl-Eibesfeldt, 1970; Hinde, 1970). Two studies which illustrate the usefulness of this approach are Daanje's (1950) discussion of displays derived from locomotor intention movements of birds, and Eisenberg's (1968) survey of the behavior of the rodent genus *Peromyscus*.

Brattstrom (1971) presented an ethogram for the Australian bearded dragon, *Amphibolurus barbatus*, and reviewed the meager literature on other lizards. Perhaps no comparable study of a snake has been published because these "legless tetrapods" seem poorly suited for analysis in terms of postures and sequences of movements. Instead, descriptions of snake behavior typically consist of isolated observations on free-living animals (Wright and Wright, 1957), detailed studies on the functional morphology of locomotion or prey ingestion (Frazetta, 1966; Gans, 1952, 1970), or experimental investigations of the stimuli used in feeding or courtship (Burghardt, 1970). While each of these approaches has merit, I believe that the ethogram offers a unifying perspective for understanding the behavior of snakes.

Enough information is now available to prepare a partial ethogram for *Micrurus fulvius*. I have tentatively identified 26 action patterns and two orienting movements used by this species, based on published descriptions of defensive behavior and observations on captive snakes. These motor patterns are briefly surveyed here as a background for the discussion of feeding behavior and to illustrate the feasibility of using ethograms.

Orienting Movements

1. Pointing (Thurow, ms)--a positive orienting movement, in which the head and a few centimeters of the body are held slightly above the substrate and directed up, down, laterally, or forward.

2. Head withdrawal--a negative orienting movement, in which the head is pulled back toward the snake's coils.

Action Patterns

1. Coiling with head down--the snake's head is on the substrate or resting on a part of its body.

2. Coiling with head up--the snake's neck rests on a coil and its head is extended horizontally or raised slightly.

3. Crawling slowly--the snake moves by lateral undulations (Gans, 1970), with the body arranged in a series of sine waves of approximately equal amplitude and length.

4. Crawling rapidly--the snake's body is more extended than in (3), so that the lateral body curves are no so deep and are fewer in number.

5. Tongue-flicking--probably consists of a "cluster" of movements, including protrusion, vertical and horizontal excursions, and retraction (Ulinski, 1972).

6. Poking--the snake briefly inserts its head beneath objects or into cracks and crevices. Poking appears to differ from pointing in that it is a random searching activity ("appetitive behavior"), rather than a taxis. Alternatively, it might be an orienting movement to some environmental stimulus, such as contrast (e.g., shadows beneath leaves or holes) or odor.

7. Biting--the snake seizes an object in its jaws and, usually, makes movments which imbed the fangs.

8. Jaw movements--a complex of actions which includes protraction and retraction of the tooth bearing bones (McDowell, 1970).

9. Prey dragging--a prey item is held in the jaws and pulled forward or backward a few centimeters.

10. Rolling--the snake turns about its long axis.

11. Head rubbing--the snake rubs the sides of its head on the substrate.

12. Snout pushing--the snake presses its snout against the substrate or an object.

13. Lateral bending--the anterior or posterior part of the body is contracted in a series of half loops.

14. Head elevating--the head is raised a few centimeters from the substrate, and directed either up or parallel to the ground. This occurs as the tail of a prey animal is swallowed and, unlike pointing, is not a response to external stimuli.

15. Yawning--the jaws are opened to varying degrees and for varying lengths of time.

16. Drinking movements--the lower jaws and labial surfaces move slightly.

17. Tail lifting--the anterior portion of the tail is lifted rigidly near the anus, and the posterior part hangs limply to either side.

18. Tail raising--the tail is elevated, usually from a point anterior to the anus.

19. Tail curling--the tail is curled back and forth in the shape of a question mark (low intensity) or in a tight loop (high intensity).

20. Tail waving--the tail is either curled or not, and is moved back and forth from a point slightly anterior or posterior to the anus.

21. Body flattening--the posterior part of the body is flattened.

22. Body snapping--a loop of the snake's body is snapped back and forth through a vertical arc, or jerked from side to side in a horizontal plane.

23. Head hiding--the head is covered with a body coil.

24. Cloacal discharge--the contents of the cloaca are expelled.

25. Prey regurgitation.

26. Immobility--the snake is limp and immobile.

Commentary

Several aspects of this scheme require comment. Some action patterns occur in several different contexts (e.g., tongue flick clusters) or repeatedly in one type of behavior (e.g., jaw movements during swallowing). In some instances two or more may have been confused as one, and this is probably the case with jaw movements. In others, I might have given an unjustified distinction to two patterns, or to the results of two or more patterns. This might be true of head hiding, which perhaps only reflects the outcome of combining head withdrawal with coiling or body snapping.

Some patterns remain to be observed, especially those that function in social and thermoregulatory behavior. I observed coral snakes that had fed recently to coil for several days under leaves beneath a lamp, and perhaps they were basking. Protruding the head from beneath cover ("coiling with head up") might be another basking posture. Grijs (1898) claimed that his specimen flattened its body when sunning, but I have not seen such behavior. Coral snake social behavior probably includes some postures known for other snakes as well as some specific to this species, but combat, courtship, and copulatory behavior remain unknown. Werler (1951) mentioned a mating between captive *Micrurus fulvius*, but he did not give details. Campbell (in press) suggested that female coral snakes brood their eggs, and this behavior might utilize postures also used in thermoregulation or defense or both.

This brief and preliminary survey demonstrates that the feeding and defensive behavior of Micrurus fulvius can be described in terms of movements and postures. These motor patterns are released by specific stimuli and occur in functional groupings (Table 3) that are probably adaptive in the natural environment (see Gehlbach, 1972; Greene and Pyburn, 1973; Greene, in press; and the "Discussion" section of this thesis).

Table 4. Partial ethogram for the eastern coral snake, *Micrurus fulvius*. Motor patterns in parentheses. See text for details.

I. Maintenance Behavior

    A. Thermoregulation (unknown).

    B. Drinking (poking, tongue-flicking, drinking movements).

    C. Feeding.

        1. Encountering and recognizing prey (coiling with head up, crawling slowly, crawling rapidly, pointing, tongue-flicking, poking).

        2. Immobilizing prey (biting, prey dragging).

        3. Pre-ingestion maneuvers (jaw movements, snout pushing).

        4. Swallowing (jaw movements, rolling, head rubbing, snout pushing, lateral bending, head elevating).

        5. Post-ingestion behavior (tongue-flicking, head rubbing, head elevating, yawning, crawling slowly, poking, pointing).

    D. Elimination (tail lifting, lateral bending, crawling slowly).

II. Antipredator Behavior

    A. Concealment (coiling with head up or down).

    B. Flight (crawling rapidly, tail waving).

    C. Warning or intimidation.

        1. Tail display (tail raising, tail curling, tail waving, body flattening, head withdrawal, head hiding).

        2. Erratic behavior (body flattening, body snapping, cloacal discharge, prey regurgitation, biting).

        3. Death feigning (immobility).

Table 4, continued.

III. Social Behavior

A. Courtship (unknown).

B. Copulation (unknown).

C. Other intraspecific behavior, e.g., brooding or combat (unknown).

FEEDING BEHAVIOR OF MICRURUS FULVIUS

The description that follows incorporates published accounts (Clark, 1949; Ditmars, 1907, 1912; Grijs, 1898) and my observations on four specimens from widely separated localities in Texas (Table 5). Feeding behavior is discussed in groups of motor patterns to permit comparisons with other snakes.

Encountering Prey

Methods of encountering prey should be included in a discussion of feeding behavior, because snakes use species-specific, presumably adaptive postures and strategies for obtaining food. Prey can be located by random searching, trail following, or "sitting and waiting" (Pianka, 1966), and each of these techniques might be enhanced by behavioral or morphological specializations. For example, random searching and trail following utilize stereotyped poking behavior and highly selective receptor systems (e.g., facial pits, Jacobson's Organ). "Sitting and waiting" is probably more efficient when accompanied by camouflage (Fitch, 1960) or caudal luring (Greene and Campbell, 1972).

Coral snakes probably initiate searching behavior in response to a complex of internal factors (cf. Hinde, 1970). When one of my snakes had not fed for several days, it crawled slowly over the substrate and poked its head in and out of the leaf litter. This involved repeated forward and lateral head movements, and was accompanied by frequent tongue flick clusters. At times a snake crawled slowly beneath a large leaf or small piece of bark and soon emerged from the opposite side, still moving its head from side to side and flicking its tongue. When a coral snake was searching, any movement of an object in the terrarium elicited pointing and, if it was not a large object, approach behavior. When an acceptable prey item caused the approach, it was seized and eaten. Unsuccessful attempts to capture prey were followed by more searching behavior.

F. R. Gehlbach (pers. comm.) observed similar random crawling and poking movements by two free-living coral snakes on the Santa Ana Wildlife Refuge, one of which I later used for behavioral studies. Neill (1951) described what was perhaps random foraging behavior by a coral snake in Clay County, Florida. The snake crawled rapidly, moved its head from side to side, and poked its head into the surface litter. Neill also stated that the snake's tail made "constant rapid, probing motions" in the leaves, and that at times "the hind part of the creature was thrown nearly as far forward as the head." He observed similar behavior in a captive snake, and suggested that the head and tail movements served to flush small reptiles and amphibians from cover. These observations suggest that crawling and poking in ground litter are motor patterns normally used by coral snakes to locate potential prey items. However, neither Gehlbach nor I have observed use of the tail in foraging, and I doubt that it is normal behavior, at least for Texas coral snakes. I have noticed that the threshold for tail waving, an important component of coral snake defensive behavior, is very low in this species, and perhaps the snake observed by Neill was responding to tactile or vibrational stimuli.

Several species of small snakes deposit chemical trails that serve as attractant pheromones (Burghardt, 1970; Gehlbach, _et al._, 1971), and there are indications that these trails release searching and trail following behavior by coral snakes. On one occasion two small _Virginia striatula_ were kept in a jar of wet moss for several days before the snakes and moss were put in a coral snake's cage. The coral snake was searching in the leaves and encountered the moss. It moved its head back and forth over the moss for approximately five minutes and frequently flicked its tongue. Then it crawled across the cage, generally following the route taken by one of the earth snakes. The coral snake soon found the prey in a corner and ate it. During staged encounters with ground skinks, a coral snake frequently paused for several seconds in the exact spot where a skink had recently rested and pointed and tongue-flicked before searching again.

Experiments with coral snakes on cloth arenas provide additional evidence that they respond to prey trails. For two trials with each of two coral snakes, a small colubrid snake (adult Storeria dekayi or Virginia striatula) was allowed to crawl around the alley one time. In each case the coral snakes crawled away from the central release point, paused briefly and pointed at the trail, and moved off the cloth. A second block of trials used trails laid by a small snake or a skink (adult female Eumeces fasciatus) making four circuits of the octagon in five minutes. One coral snake responded to two snake trails with pointing and then escape behavior but followed a skink trail for one complete circuit and two additional turns on the octagon. The other coral snake followed trails laid by S. dekayi (two trials) and V. striatula (one trial) for one complete circuit, seven lane segments, and three lane segments, respectively. It followed two lane segments of a skink trail before crawling off of the cloth. These observations suggest that known prey species can deposit trails which are perceived and followed by coral snakes. Additional experiments using more coral snakes, more prey species, and more trials are required before comparisons with the extensive study by Gehlbach, et al. (1971) are warranted.

Trail following behavior was stereotyped and similar to that described by Gehlbach, et al. (1971) for blind snakes, Leptotyphlops dulcis. A coral snake crawled slowly from the release site, pointed and flicked its tongue at the trail, then turned 90° and began following it. The snake's head remained elevated while it crawled, and there were frequent tongue-flick clusters. At each corner it overshot 2-4 cm, paused, pointed and tongue-flicked at the cloth, moved its head from side to side, turned back onto the trail, and resumed crawling. If a wire was jiggled on the cloth in front of a snake, it pointed and then approached rapidly.

There is no evidence that free-living coral snakes use a "sit and wait" strategy to ambush prey, but observations on captives suggest that they might. My snakes were frequently seen coiled with head raised and protruding from beneath the edge of a piece of bark or pile of leaves. Such snakes responded to nearby movements by pointing, tongue-flicking, and approaching.

Recognizing Prey

Recognition of prey probably begins as soon as a coral snake points toward a stimulus, and incorporates visual and chemical cues. Captives approached any small movement, such as a wire jiggled in the leaves or a finger moved against the glass from outside of the terrarium. Larger moving objects, such as a hand or a piece of bark, usually elicited pointing and then rapid head withdrawal and crawling. This was especially likely if the object was moved suddenly.

Approach is accompanied by tongue-flick clusters, which evidently receive the necessary stimuli for seizing or avoiding a potential prey item. Coral snakes quickly approached to within 2 cm of large coleopteran larvae, cricket frogs (*Acris crepitans*), and newborn mice, but then withdrew without seizing them. Small live water snakes (*Natrix sp.*) were also approached and rejected, especially if they had discharged the cloacal sac contents. However, rapid prey movements seemed to result in a quicker attack and to override aversive chemical cues. Usually dead *Natrix* were refused when stationary or pulled slowly but were attacked when pulled more rapidly.

A coral snake continues to receive input from the prey after it is seized, probably via either oral sensory papillae (Burns, 1969; Greene, unpublished) or the Jacobson's Organ (cf. Burghardt, 1970). This is indicated by 10 incomplete feeding sequences (Table 5) in which a prey item was grasped and immediately released, or maneuvered for a short time and then released.

Capturing and Immobilizing Prey

Coral snakes have relatively small eyes (Marx and Rabb, 1972) and apparently cannot strike very accurately. Live *Leiolopisma laterale* proved difficult for them to seize, probably because of the coral snakes' relatively poor sight and the skinks' small size and erratic escape behavior (Lewis, 1951). Also, ground skinks seemed to perceive an approaching coral snake at a distance of several centimeters and often slipped away unseen. During 11 attempts on these lizards by a coral snake, I observed eight misses, two tail autotomies (skinks escaped), and one capture. These were during staged confrontations on a 32x62 cm substrate of gravel and scattered leaves, and the only capture occurred when the snake trapped a skink in a corner. Small prey snakes presented a slower and more elongate target, and were captured without difficulty; each of 23 attempts was successful. Approach was usually slow if the prey snake was moving slowly, and rapid if it crawled away quickly. In some cases a coral snake crawled parallel to a moving snake, flicked its tongue several times, and then seized the prey by turning its head sharply to the side and down.

Clark (1949) and Ditmars (1907) stated that *Micrurus fulvius* immobilizes its prey with venom before swallowing, but Ditmars (1912) remarked that the venom was of little value in subduing "cold blooded" animals. My observations indicate that this species typically holds prey at the point of seizure until paralysis and then begins pre-ingestion maneuvers (see below). Slight movements of the prey were sometimes seen even as the tail was swallowed, suggesting that it is immobilized but not immediately killed by the venom. Coral snakes usually dragged their prey a few centimeters backward or forward before pausing, seemingly in response to its struggles. This tended to untangle a small, writhing snake, and it might also imbed the fangs more deeply. During envenomation, the temporal region of the coral snakes sometimes appeared shriveled; this was probably caused by contraction of the _Muscularis superficialis_, which has been shown to force venom out of the main venom gland in another elapid, _Bungarus caeruleus_ (Rosenberg, 1967).

In two instances a coral snake bit and quickly released an adult female _Eumeces fasciatus_ that struggled violently. One of the skinks was immediately recaptured. The other lizard crawled slowly for several centimeters and went under a piece of bark. It was soon followed by the coral snake and regrasped. Both skinks subsequently made only feeble movements and were eventually eaten.

Pre-ingestion Maneuvers

Coral snakes normally do not release prey prior to swallowing it. Pre-ingestion maneuvers are probably evoked by tactile and/or chemical cues (cf. Nalleau, 1966; Thurow, ms) and inhibited by prey movements. If prey movements inhibit the coral snake, the time between seizure and the onset of pre-ingestion maneuvers should be longer with live prey than with dead prey. The mean times with live and dead prey differ significantly with each of two coral snakes (Table 6; t test, $p<.001$). The hypothesis was also tested by considering the time between the last prey movement and the onset of pre-ingestion maneuvers for live prey. If prey movements inhibit the snake, this latency should be similar to that for dead prey. These times were very similar for snake No. 5 ($.5<p<.6$) but differed significantly for snake No. 4 ($p<.001$). I interpret the variation in all times and the results of the last comparison as caused by individual differences in the coral snakes and the use of several different sizes and species of prey for feeding trials.

The direction of prey ingestion was determined for 81 food items in 71 Texas coral snakes. Fifty-nine snakes, nine skinks, eight skink tails, and three other lizards had been swallowed from the anterior end. One skink (a small Eumeces fasciatus) had been swallowed tail first, and one skink tail had been swallowed from the posterior end. Captive coral snakes grasped live snakes and unaltered dead snakes at various points along the body and, with one exception, swallowed them head first. The head and tail of such elongate prey are often hidden in leaf litter or under some other cover, and thus probably could not provide visual cues to the location of either end. Similarly, location of the initial bite, taper of the body, movements of the head or tail, and chemical differences between the head and tail of the prey might not affect the direction of ingestion. An obvious and uniform directional feature on the body of a snake is scale overlap, and the results of three body piece and 20 skin reversed trials (Table 5) suggest that scale overlap influences the direction of prey ingestion by coral snakes. In every case swallowing began at the head end of the skin, despite the fact that in some skin reversed trials the prey snake was initially seized quite close to the real anterior end. Seven body piece trials with skinks are also consistent with this conclusion; in each case swallowing began at the anterior end. Although these results do not specifically exclude a directional chemical gradient, its presence seems unlikely because coral snakes correctly determined the anterior end of pieces of snakes. If a chemical cue did influence the direction of ingestion, it had to exist as a uniform and rather steep gradient along the entire body of a prey snake.

Coral snakes used alternate jaw movements to shift along the prey's body and over its head prior to swallowing. In one instance a small stick in the mouth of a coral snake prevented it from shifting over a snake's snout to begin swallowing. The coral snake released the prey, removed the stick by jaw movements and rubbing its head on the substrate, regrasped the prey by the snout, and swallowed it. In all other feeding sequences the prey was not released before it was swallowed.

Swallowing

After the prey's head has been shifted down the throat, it is swallowed by repeated series of alternating jaw movements. These are separated by brief pauses and accompanied by lateral movements of the entire head. According to McDowell (1970), *Micrurus* belongs to a group of elapids in which "the palatine is erected along with the maxilla during maximum protraction of the palate." This presumably occurs when a coral snake's head is rotated back and forth across a prey snake's long axis during swallowing movements. I could not observe the action of the palatine bones in live coral snakes, but frequently saw the maxillary teeth imbedded following protraction.

During swallowing coral snakes sometimes roll over, apparently using the prey's inertia to acheive better contact between the coral snake's teeth and the prey's skin. As swallowing nears completion, lateral bends serve to move the prey further into the gut. When the prey's tail was swallowed, the coral snake usually raised its head almost vertically and two to ten centimeters from the substrate. Sometimes it attempted to maneuver the tail by head rubbing or snout pushing.

Post-ingestion Behavior

Swallowing was always followed by tongue-flick clusters, and sometimes by yawns. These usually occurred prior to lowering the head, and were followed by searching behavior. Occasionally a snake rubbed its head on the substrate after swallowing was completed. After feeding, coral snakes always responded to small movements by pointing, tongue flicking, and approaching. If another prey item was offered it was seized and eaten.

Table 5. Summary of feeding observations on captive coral snakes. Numbers in parentheses indicate incomplete sequences in which the prey was not swallowed. Abbreviations refer to weight in g (WT), estimated total length in mm (TL), body piece lizards (BL), dead lizards (DL), live lizards (LL), body piece snakes (BS), skin reversed snakes (RS), dead snakes (DS), and live snakes (LS).

Species, Source	Sex	WT	TL	BL	DL	LL	BS	RS	DS	LS
1. *Micruroides euryxanthus* Arizona, Pima County	f	4.8	367							1(1)
2. *Micrurus distans* Mexico, Sonora, 2.2 mi W Alamos	f	43.0	670						3	1
3. *Micrurus fulvius* Texas, Dallas County	f	20.0	525						3	2
4. *Micrurus fulvius* Texas, Nacogdoches County, near Melrose	m	37.2	675	4	1	1		5(3)	1	8
5. *Micrurus fulvius* Texas, Hidalgo County, Santa Ana Refuge	m	56.0	850	3	1(1)	3	3	6(6)	10	13
6. *Micrurus fulvius* Texas, Nacogdoches County	m	29.6	600			1				

Table 6. Pre-ingestion latencies for coral snakes, *Micrurus fulvius*, dealing with live and dead prey. Snake numbers refer to Table 5. Ranges, means, standard deviations, and sample sizes are given.

Latency	Snake No. 4	Snake No. 5
Time between seizure and onset of pre-ingestion maneuvers (live prey)	290-595 ($\bar{x}=434.2\pm132.5$) N=6	70-940 ($\bar{x}=400.9\pm334.9$) N=8
Time between seizure and onset of pre-ingestion maneuvers (dead prey)	0-85 ($\bar{x}=28.6\pm32.3$) N=10	0-290 ($\bar{x}=73.7\pm86.5$) N=10
Time between last prey body movement and onset of pre-ingestion maneuvers	63-190 ($\bar{x}=99.2\pm52.6$) N=5	0-152 ($\bar{x}=71.8\pm73.3$) N=4

FOOD HABITS AND FEEDING BEHAVIOR OF OTHER NEW WORLD ELAPIDS

Leptomicrurus narducci

A snake from Turula, Ecuador and two from Iquitos, Peru each contained the tail of an unidentified microteid lizard (AMNH 35962, 53752, 55020; see Appendix for a list of museum abbreviations used in this section). At least two of the tails had been swallowed from the anterior end, and one of them appeared to have been autotomized.

Micruroides euryxanthus

Free-living Sonoran coral snakes are known to eat blind snakes, *Leptotyphlops humilis* (Vitt and Hulse, ms; Woodin, 1953), and Parker (1972) mentioned this species as a potential predator on banded geckoes (*Coleonyx variegatus*). Captives have eaten lizards and snakes of the following species: *Anniella pulchra*, *Cnemidophorus sp.*, *Chilomeniscus cinctus*, *Chionactis occipitalis*, *Diadophis punctatus*, *Hypsiglena ochrorhyncha*, *Leptotyphlops humilis*, *Sonora semiannulata*, *Tantilla sp.*, *T. nigriceps*, and *T. atriceps* (Gates, 1960; Linder, 1962; Lowe, 1948; Vitt and Hulse, ms; Vorhies, 1929; Woodin, 1953; see below). Vitt and Hulse (ms) reported that captives refused *Cnemidophorus tigris*, *C. velox*, *Coleonyx variegatus*, *Sceloporus undulatus*, *Urosaurus ornatus*, *Uta stansburiana*, *Xantusia vigilis*, *Arizona elegans*, *Phyllorhynchus browni*, *P. decurtatus*, *Rhinocheilus lecontei*, and *Thamnophis cyrtopsis*. Vitt and Hulse concluded on the basis of some simple choice experiments with five coral snakes that blind snakes are a preferred food item. Fowlie (1965) stated that this species "lives on insect larvae or other small snakes," but there is no evidence that it eats invertebrates.

The feeding behavior of *Micruroides euryxanthus* has been described briefly by Linder (1962), Vorhies (1929), and Woodin (1953), and in somewhat greater detail by Vitt and Hulse (ms). Linder (1962) and Vorhies (1929) claimed to have observed constriction by M. euryxanthus, and both authors emphasized the apparent ineffectiveness of the venom on prey snakes (Sonora and Tantilla). Vitt and Hulse (ms) reported that captives responded to acceptable prey items with increased tongue flicking and then bit them across the body. Usually the prey was not released before the coral snake maneuvered to the head for swallowing. Blind snakes were usually bitten near the head and other (larger) snakes near the tail, and Vitt and Hulse (ms) noted that envenomation seemed most effective on Leptotyphlops.

I observed the feeding behavior of a snake from Arizona (Table 5). The coral snake grasped a dead adult Tantilla gracilis, moved quickly to the head, made a few jaw movements, and released it. One week later I offered it a live T. nigriceps (1.2 g, total length 152 mm). The coral snake grabbed the Tantilla at midbody with a quick lateral bite as it crawled past. Both snakes writhed and wrapped about each other, and the coral snake rolled about its long axis. The coral snake's head did not move from the initial bite site during these struggles. By 7.42 minutes the Tantilla was still, and the coral snake made a single jaw movement at 10.08 minutes. From 10.50 to 12.00 minutes the coral snake crawled slowly backward into a corner, dragging the limp Tantilla. The coral snake began maneuvering toward the prey's head at 12.50 minutes, and a reddish wet spot could be seen at the original bite site. The head was reached and swallowing began at 17.58 minutes. Ingestion involved lateral movements of the coral snake's head and, during the final stages, lateral bending of the coral snake's body. Swallowing lasted 17.75 minutes. Afterward the coral snake crawled slowly, flicking its tongue, and quickly approached forceps moved in the gravel substrate.

Additional studies of this species are needed, but it is evident that prey is grasped, held, maneuvered without releasing it, and swallowed head first. The venom is effective against at least some prey species (*Leptotyphlops* and *Tantilla*). It seems likely that Linder (1962) and Vorhies (1929) misinterpreted tangled, writhing masses of predator and prey as constriction on the part of *Micruroides*, since neither Vitt and Hulse (ms) nor I observed it in our specimens.

Micrurus sp.

There are several general statements on the food habits of Neotropical coral snakes. They are reported to eat small snakes, lizards, and salamanders in Chiapas, Mexico (Alvarez del Toro, 1960); small rodents, lizards, and small snakes in Nicaragua (Villa, 1962); small subterranean snakes in Colombia (Medem, 1968); and *Elapomorphus tricolor*, a small, secretive colubrid snake, in Argentina (Abalos, *et al*., 1964). South American members of the genus are reported to eat amphisbaenians (J. A. Roze, pers. comm.; Vanzolini, 1951).

Micrurus alleni

A snake from Rio Siquia, Nicaragua contained an eel, *Synbranchus marmoratus* (Gaige, et al., 1937).

Micrurus ancoralis

Boulenger (1913) reported a small, secretive colubrid snake, *Ninia atrata*, in the stomach of a specimen from the Choco region of Colombia.

Micrurus annellatus

Schmidt (1953) found a limbless microteid lizard, *Ophiognomon sp.*, in a snake from the Marcapata Valley, Peru.

Micrurus browni

A snake from Acahuitzotla, Guerrero, Mexico (TCWC 11578) had swallowed a blind snake, probably Typhlops braminus, head first. A specimen from Cerro San Felipe, Oaxaca, Mexico (UCM 40078) contained two pedipalp chelae from a scorpion of the genus Diplocentrus (Diplocentricidae, identified by Stanley C. Williams). Snakes of the genus Stenorrhina eat scorpions (Alvarez del Toro, 1960), and coral snakes are known to eat these snakes (see accounts of M. diastema and M. elegans), so it seems likely that the scorpion was not a primary prey item.

Micrurus carinicauda

Schimdt (1932) found an eel, Synbranchus marmoratus, and a microteid, Bachia cuvieri, in snakes from Venezuela (Schmidt listed both snakes as M. corallinus riisei, but Roze, 1955, referred them to this species).

Micrurus corallinus

Mertens (1927) observed a captive from Santa Catharina, Brazil. It fed on small lizards (Lacerta agilis, L. muralis, L. sicula, and L. vivipara). and usually did not release them after the initial bite. Instead, the snake held them in its jaws six to eight minutes, until they were dead, and then maneuvered to the head for swallowing.

Micrurus diastema

A snake from Oaxaca, Mexico (UCM 49376) had swallowed a Coniophanes imperialis head first. Another from Oaxaca (UCM 40082) contained four small Geophis sallei; three had been swallowed head first and one tail first. Thirteen specimens from Guatemala (UCM 23169, 23170, 34291, 34292; CM uncatalogued, nine specimens) contained two Adelphicos quadrivirgatus, one G. carinosus, one

Ninia diademata, four N. sebae, one Stenorrhina degenhardti, four unidentified snakes, and one unidentified reptile. The direction of ingestion was determined for 13 of these items, and all had been swallowed head first. The identifiable prey from Oaxaca and Guatemala are small species that live in ground litter or are burrowers.

Thirty snakes from the northeastern part of the Yucatan Peninsula contained 33 food items, mostly small, secretive snakes, as follows: 11 Sibon sanniola, six Ninia sebae, four Stenorrhina freminvillei, three Typhlops microstomus, two Tantilla canula, two Ficimia publia, two Ameiva undulata, one Elaphe phaescens, one unidentified snake, and one unidentified reptile (McCoy and Greene, unpublished). Ameiva undulata, a teid lizard, was represented by tail pieces only, which may have been autotomized. The E. phaescens was a juvenile of this large, terrestrial colubrid. Yucatan coral snakes had swallowed 29 items head first and one, a N. sebae, tail first.

Micrurus distans

I observed four feeding sequences by a captive snake (Table 5). A live Chionactis occipitalis was grasped, held until it was dead, and then swallowed head first. Twice, dead Thamnophis proximus were grasped, maneuvered, and swallowed without being released. Once a dead T. proximus was initially grabbed by the head and swallowed immediately. In each instance the coral snake pushed its snout against its body or the pebble substrate during the final stages of swallowing.

Micrurus elegans

Schimdt (1932) found a small, burrowing colubrid snake, Geophis semidoliatus, in a Mexican specimen. A gravid female from Alta Verapaz, Guatemala had eaten a juvenile Stenorrhina degenhardti (Stuart, 1948).

Micrurus ephippifer

Two snakes from Tejocotes, Oaxaca, Mexico each disgorged a colubrid snake, *Rhadinaea aemula* (C. M. Bogert, *in litt.*). Another snake from Oaxaca (AMNH 103118) contained a *Geophis dubius*. The *Geophis* and at least one of the *Rhadinaea* had been swallowed head first. A captive from Oaxaca ate a lizard, *Xantusia henshawi*, and an unidentified gecko (AMNH live book No. 1019).

Micrurus frontalis

This species has been reported to eat snakes (Prado, 1945) and to be cannibalistic in captivity (Abalos, *et al.*, 1964). Azevedo (1961) examined one that had eaten two colubrid snakes, *Sibynomorphus mikanii*.

Lankes (1928) and Mertens (1956) have published observations on the feeding behavior of captives from Argentina and Brazil, respectively. Both captives ate small lizards of the genus *Lacerta*, and each was observed to regularly bite, release, and then relocate its prey before swallowing took place. Lankes (1928) stated that his snake seemed to follow the trail of a dying lizard, and that it never failed to find its prey.

Micrurus hemprichi

Beebe (1946) reported that insect remains, a small snake, and two lizards ("probably *Anolis*") were found in three snakes from Kartabo, British Guiana that Schimdt (1953) referred to this species. I agree with Schmidt (1953) that the insects were probably secondarily ingested, because there is no other evidence that coral snakes eat insects and because they do eat insect predators, such as lizards.

Dixon and Soini (ms) found two onycophorans, *Peripatus sp.*, in the stomach of a Peruvian snake. A specimen from Ecuador (AMNH 28816) contained three unidentified onycophorans, each 60-65 mm long, and another snake (AMNH 52713) contained an unidentified onycophoran *ca.* 90 mm long.

Micrurus hippocrepis

Four snakes from Middlesex, British Honduras (UCM 25710, 25885, 25886, 30887) contained three Ninia sebae and unidentified snake scales. The N. sebae had been swallowed head first.

Micrurus ibiboboca

Amaral (1933) reported that this species eats lizards and snakes and is a cannibal.

Micrurus isozonus

A captive ate Coluber constrictor, Natrix sipedon, Storeria dekayi, and Thamnophis sirtalis (AMNH live book No. 817).

Micrurus langsdorffi

A snake from Iquitos, Peru (AMNH 54089) had swallowed an unidentified blind snake head first.

Micrurus latifasciatus

Landy, et al. (1966) reported a Geophis nasalis in the stomach of a snake from Volcan Tacana, Chiapas, Mexico. Two others from the same locality (UCM 45822, 45824) had each swallowed an unidentified snake head first. A large female (snout-vent length 1035 mm) from Depto. Esquintla, Guatemala (AMNH 49975) had swallowed a caecilian, Dermophis mexicanus, head first. The caecilian was 310 mm long and ca. 16 mm in diameter.

Micrurus lemniscatus

The following prey items have been found in this species: 17 eels, Synbranchus marmoratus (Beebe, 1946); one amphisbaenian, Leposternon polystegum (Boulenger, 1885); 1 microteid lizard, Bachia sp.(Urich, in Mole, 1898); two blind snakes, Typhlops reticulatus (Dixon and Soini, ms); three young M. lemniscatus (Wehekind, 1955); and a M. psyches (Wehekind, 1955). Mole (1898) reported that this species "often disgorged ground snakes" (Atractus trilineatus), and that captives ate other snakes.

Mole and Urich (1894) and Mole (1898) described the feeding behavior of a captive from Trinidad. In one case the snake released its prey after biting and in two instances it did not. They observed that the venom of this species rapidly killed small snakes, that prey was swallowed head first by rapid lateral head movements, and that ingestion was sometimes followed by yawning. Lankes (1938) observed a snake that always released prey after biting and then relocated it. The coral snake used searching behavior that included crawling slowly, moving its head jerkily from side to side, and pausing briefly at times. Eventually the prey was found and swallowed.

Micrurus limbatus

The feces of a snake from the Sierra de Tuxtla, Veracruz, Mexico (UTA R3686) contained unidentified snake scales.

Micrurus mipartitus

Schmidt (1932) found the tail of an unidentified snake in a Venezuelan specimen. Another snake from Venezuela (CM 7290) contained scales of an unidentified amphisbaenian.

Test, et al. (1966) observed apparent foraging behavior by three snakes at Rancho Grande, Venezuela. Each of the snakes was crawling slowly in forest litter, and one "poked its head repeatedly into the accumulated litter at the base of a tree, as though foraging."

Micrurus nigrocinctus

Four snakes from Volcan Tacana, Chiapas, Mexico had eaten one unidentified scincid lizard tail, one unidentified snake, one Geophis nasalis, and one Ninia sebae (Landy, et al., 1966; UCM 45829-45831). Another snake from Chiapas (CM 51754) contained unidentified snake scales. The food items in four snakes from Guatemala included one unidentified macroteid lizard, two reptile eggs, one Geophis sp., and N. sebae (Schmidt, 1932; AMNH 99964, 99969, 99971). Three specimens from Honduras had swallowed two N. sebae and an unidentified snake (Schmidt, 1932). Two snakes from Nicaragua contained a juvenile iguana, Ctenosaura similis, and a Geophis dunni (Schmidt, 1932). Picado (1931) stated that this species eats snakes in Costa Rica, and a specimen from that country had swallowed a Coniophanes sp. (Schmidt, 1932). Five Panamanian snakes contained one caecilian; two anomalepid blind snakes, Anomalipis mexicanus and Helminthopis sp.; a skink, Mabuya sp.; and another coral snake (Schmidt, 1932; Smith and Grant, 1958; Swanson, 1945).

Schmidt and Smith (1943) reported that a specimen from Chiapas, Mexico was found crawling rapidly in bushes about ten feet above the ground, and they speculated that it might have been searching for small frogs. Picado (1931) stated that captives in Costa Rica bit their prey several times and usually swallowed it head first.

Micrurus psyches

The data for this species are based on Trinidad snakes, referred to in much of the literature as M. corallinus riisei or M. circinalis (Roze, 1967). Mole and Urich (1894) and Mole (1898) reported that it feeds on ground snakes, Atractus trilineatus. They observed that the venom did not have much effect on these little snakes, and that prey is swallowed head first, apparently without being released prior to ingestion. Wehekind (1955) stated that it feeds on "ground snakes and young snakes" and is cannibalistic. V. C. Quesnel (*in litt.*) mentioned a captive that disgorged an *A. trilineatus*.

Micrurus spixi

Snakes from Peru each contained a single prey item: one *Atractus* sp., one *A. collaris*, one *Dipsas* sp., one *Leimadophis pygmaeus*, one *L. reginae*, one unidentified snake, and one unidentified caecilian (Dixon and Soini, ms; Schmidt, 1932; AMNH 23373, 23390). A specimen from Bolivia (CM 2828) had eaten an unidentified teid lizard.

Micrurus surinamensis

A snake from Iquitos, Peru (AMNH 54538) had swallowed an eel, probably *Synbranchus marmoratus*, head first.

DISCUSSION

The Trophic Role of *Micrurus fulvius*

A complex of behavioral and ecological factors interact to determine the prey items regularly consumed by *Micrurus fulvius*. Certain fossorial or subfossorial snakes are especially vulnerable to the coral snake feeding strategy because of their small adult size, ineffective defensive behavior, and preferred microhabitat. This vulnerability is reflected in their prevalence, in terms of both frequency and biomass, as stomach items. These same factors probably account for predation on skinks of the genera *Eumeces* and *Leiolopisma*. However, it appears that skinks are not as vulnerable as small snakes, because of their small total length, agility, and capacity for tail autotomy.

Small iguanid lizards of the genera *Anolis* and *Sceloporus* are abundant in some parts of the range of *Micrurus fulvius* and are accepted as food by captives, but are not an important part of the normal diet (Tables 1 and 3). This is probably because these lizards are largely arboreal (Smith, 1946) and thus are not often encountered by foraging coral snakes. The young of large, terrestrial snakes are also eaten by captive *M. fulvius*, but predation on juvenile snakes is restricted by their seasonal availability in temperate climates (Tables 1 and 2; Fitch, 1970).

The Feeding Behavior of *Micrurus fulvius*

Many nonvenomous colubrid snakes rely on a weight advantage and the ability to simply grasp and swallow prey. Others use constriction to bring about death by suffocation. The most specialized feeding method is used by viperids, which have hollow folding fangs and are able to inject venom by a quick stabbing bite. Viperids frequently release and then relocate prey before swallowing it, permitting the immobilization of relatively large prey with minimal danger and energy expenditure (Bellairs, 1969; Gans, 1961; Gans and Elliott, 1968). Micrurus fulvius uses a variation on the simple colubrid pattern; the prey is held and paralyzed with venom. The adaptive significance of this behavior is clear: as in viperids, it insures the immobilization of prey with minimal energy costs for the predator, and allows pre-ingestion maneuvers to procede without the risk of a struggling animal escaping. The prey killing technique of this species may represent a step in the development of the more advanced viperid pattern, and an important innovation is occasionally seen. Coral snakes can release prey and resume maneuvers at the same point in the behavioral chain when prey struggles violently, or when some difficulty is encountered in the pre-ingestion phase.

Head-first prey ingestion is the norm in coral snakes, and several factors probably make this behavior advantageous. My observations on king cobras, Ophiophagus hannah, suggest that elapid snakes, with relatively inflexible jaw mechanisms, have difficulty manipulating the thin tail of a prey snake to initiate swallowing (Greene, unpublished). By reducing the time required for this maneuver, head first ingestion lowers the cost for a given energy gain. Also, a reduction in the total time spent dealing with prey minimizes a period of increased vulnerability to predation. Head-first ingestion is the best way to swallow other snakes, because it precludes difficulty with a prey's sharp, recurved teeth. This difficulty was observed in one trial with a skin reversed prey snake; the coral snake was unable to continue swallowing or to regurgitate without assistance.

The Food Habits and Feeding Behavior of Other Coral Snakes

The data for Neotropical coral snakes (pp. 43-50) suggest that they also feed on small vertebrate members of the litter fauna. Micrurus diastema from the semiarid Yucatan Peninsula resembles _M. fulvius_ in that it preys almost entirely on small snakes. Tropical species from more mesic areas have broader niches that include other elongate prey, such as eels and caecilians. Predation on eels probably indicates terrestrial activity on the part of these teleosts, rather than aquatic foraging by coral snakes (Roze, 1955). The occurrence of onycophorans in three _M. hemprichi_ from Ecuador and Peru is more surprising. It will be interesting to learn if these peculiar, fusiform invertebrates are regularly preyed upon, and how coral snakes cope with their defensive tactic of shooting an enemy with quick-drying mucous (Kaestner, 1968).

Information is available on the feeding behavior of _Micruroides euryxanthus_ and six species of Neotropical _Micrurus_ (pp. 41-50). _Micrurus frontalis_, _M. lemniscatus_, and _M. mipartitus_ use lateral poking movements to locate prey. _Micruroides euryxanthus_, _Micrurus corallinus_, _M. distans_, and _M. psyches_ grasp and hold prey until it is immobilized. _Micrurus frontalis_ and perhaps _M. lemniscatus_ bite, release, and relocate prey prior to swallowing, but observations on _M. fulvius_ (see above) suggest that the activity and size of the prey might have caused this apparent difference in the behavior of some species. It is also possible that the release of prey by some tropical coral snakes is a result of attempted predation on amphisbaenians. These elongate, limbless, burrowing reptiles could be potentially important prey, but they have powerful jaws which are used for defense. I observed a captive Moroccan amphisbaenian, _Trogonophis wiegmanni_, fatally injure a smooth snake, _Coronella austriaca_, approximately three times its length and probably twice its weight. Predatory behavior which minimizes contact with live amphisbaenians would therefore be advantageous.

This preliminary survey of the food niches of New World elapids has implications for their origin and zoogeography. The Old World species that are morphologically most similar, at least superficially, are the Oriental coral snakes of the genera Calliophis and Maticora. Like the New World species, they are brightly colored, secretive snakes that have defensive tail displays and feed on small snakes and lizards (Campden-Main, 1970; Cantor, 1847; Greene, in press; Leviton, 1964; Liat, 1956, 1965; Smith, 1943; Taylor, 1965; Tweedie, 1961). If Leptomicrurus, Micruroides, and Micrurus do represent minor variations on a single trophic role--predation on small, elongate, terrestrial vertebrates--it may well have been established in a common ancestral stock. Alternatively, the Old and New World coral snakes may be convergent in several respects, and represent striking ecological equivalents. These speculations and the recent suggestion that the present disribution of elapids results from Pangaean fragmentation (Rabb and Marx, 1973) emphasize the need for in depth morphological studies of the family.

A second suggestion of the food niche survey is that the fundamental niches (Hutchison, 1965) of New World coral snakes may be so similar that syntopic situations will be infrequent, as a result of competitive exclusion, or will have resulted in size differences via character displacement (cf. MacArthur, 1972). Sympatry is evidently uncommon in much of Mexico and northern Central America (Roze, 1967), and in one case where it occurs (Micrurus distans and M. laticollaris in Michoacan) there appear to be differences in microhabitat between the two species (Duellman, 1961). Size differences could reduce niche overlap and permit coexistence, because bigger coral snakes can eat larger prey than smaller ones. Sympatric pairs that differ in size include Micruroides euryxanthus and Micrurus distans in southern Sinaloa, Mexico (Hardy and McDiarmid, 1969); M. latifasciatus and M. nigrocinctus in Chiapas, Mexico and Guatemala (Landy, et al., 1966; Stuart, 1963); and M. lemniscatus and _M_. _psyches_ on Trinidad (Mole, 1898). A third possibility is that appropriate prey are so common in the tropics that food is not in short supply. These hypotheses can be tested when more data are available on the systematics and ecology of tropical coral snakes.

APPENDIX

Museum Abbreviations

The American Museum of Natural History (AMNH). Bryce C. Brown, private collection (BCB). Carnegie Museum (CM). Fort Worth Museum of Science and History (FWMSH). Milwaukee Public Museum (MPM). S. F. Austin State University (SFA). Sam Houston State University (SHSU). Strecker Museum (SM). Texas A & I University Museum (TAIM). Texas Cooperative Wildlife Collection, Texas A & M University (TCWC). Texas Natural History Collection, Texas Memorial Museum (TNHC). The University of Colorado Museum (UCM). The University of Texas at Arlington Collection of Vertebrates (UTA).

Specimens Examined (*Micrurus fulvius*)

Texas (no specific locality)

SHSU 1880, SM 6074, TCWC 30539.

Texas (east)

Angelina County (UTA R1454). Austin County (SM 6743) Brazoria County (SHSU 2567). Brazos County (TCWC 534). Cherokee County (TCWC 19063). Harris County (SM 4468, TCWC 33510). Houston County (TCWC 5213, UTA R1216). Jasper County (UTA R2599). Jefferson County (TCWC 33513). Liberty County (BCB 6268, SM 6751). Matagorda County (TAIM 2599). Montgomery County (UTA R1019, 2600). Nacogdoches County (SFA 1644, 1875, 2045, 2288, 3023, 3114, 3141, 3229, 3360, 3411). Newton County (TNHC 17550). Orange County (TCWC 3292). Rusk County (SM 10106). San Jacinto County (SM 8183). Shelby County (915, 1704, 2993). Walker County (SHSU 66, 98, 188, 2121, 2122, TCWC 257).

Texas (north-central)

Bell County (FWMSH 4115, SM 5550, 6694). Dallas County (AMNH 71009, FWMSH 3650, UTA R1200). Lamar County (SFA 873). Limestone County (BCB 11030). McClennon County (3870, 4346).

Texas (central)

Atascosa County (CM 8460). Bexar County (SM 1143). Edwards County (BCB 8846). Hays County (TAIM 481). Kerr County (TAIM 490, 1031, 1332, 1332.1). Kimble County (SHSU 4525). Mason County (TCWC 31212). Travis County (SM 10101). ValVerde County (TNHC 31107).

Texas (south)

Cameron County (AMNH 45097). Dimmit County (TAIM 1166). Goliad County (TNHC 24557). Hidalgo County (FWMSH 2611). Kennedy County (TCWC 260). Live Oak County (TNHC 24446). Nueces County (TAIM 1949). Refugio County (TCWC 605). San Patricio County (SM, uncatalogued).

Southeastern United States and Northern Mexico

Florida (CM 19841, 36761, 46794, MPM 4955, TCWC 33503). Louisiana (CM 41544, 44184). Tamaulipas (FWMSH 3649).

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