

Feeding Habits of the Pacific Rattlesnake

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DURING 1938 and 1939 we had an opportunity to study the feeding habits of the Pacific rattlesnake, *Crotalus viridis oreganus* (Holbrook), at the San Joaquin Experimental Range near O'Neals, Madera County, California. Other wildlife and range management studies in progress at the same time supplied information on populations and seasonal behavior of many plant and animal species. As part of a general program for wildlife studies on range lands of the Sierra Nevada foothills, this work was directed by Mr. Everett E. Horn, Biologist, of the U. S. Fish and Wildlife Service, in collaboration with the California Forest and Range Experiment Station. Jesse W. Nelson, Ben Glading, Charles A. Kaley, Freeman Swenson, and Raymond Sharp cooperated in securing data. Gathering of field data and examining of stomachs were done by Fitch; Twining aided in preparation of the manuscript and analyzed most of the scatological material, some of which was analyzed by John E. Chattin.

The animal life of the region is typical of the Upper Sonoran Life Zone in the blue oak and digger pine belt on the west flank of the Sierra Nevada. Eleven of the sixteen rodent and lagomorph species known to occur on the area were recorded in the food of the snakes. All these species vary in abundance on different parts of the Range, and are subject to fluctuations in numbers seasonally and over longer periods. The pocket gopher (*Thomomys bottae*) is the most generally abundant species, and may occur in populations up to twenty or more per acre over extensive areas. The ground squirrel (*Citellus beecheyi*), kangaroo rat (*Dipodomys heermanni*), woodrat (*Neotoma fuscipes*), white-footed mouse (*Peromyscus maniculatus*), rock mouse (*Peromyscus truei*), brush mouse (*Peromyscus boylii*), San Joaquin pocket mouse (*Perognathus inornatus*), and cottontail (*Sylvilagus auduboni*) generally are present in populations of one to many per acre. The meadow mouse (*Microtus californicus*), and the California pocket mouse (*Perognathus californicus*), are scarcer and more localized.

Those species not recorded among the food items are all relatively scarce, and the adult gray squirrel (*Sciurus griseus*), and jackrabbit are too large to be eaten by the Pacific rattler. The house mouse (*Mus musculus*) is here confined to the vicinity of buildings, where it is relatively safe from snakes. The harvest mouse (*Reithrodontomys megalotis*) is probably preyed upon but we obtained no records. The species is rare and localized here. The chipmunk (*Eutamias merriami*) was not recorded among the prey, and it is also one of the less common rodents.

Several kinds of lizards were recorded in the snakes' diet. The brown-shouldered lizard (*Uta stansburiana*), is the most abundant vertebrate species on the area, and the fence lizard (*Sceloporus occidentalis*) and whip-tail (*Cnemidophorus tessellatus*) also are common. The alligator lizard (*Gerrhonotus multicarinatus*) and the horned toad (*Phrynosoma blainvillii*) are much less common, and neither was found among the food items. The spadefoot toad is abundant, and it is the only one of the seven amphibian species occurring locally that was preyed upon. It remains inactive

below ground throughout the summer and hence is readily available to the snakes only in spring.

In several instances actual field observations were made on the hunting and feeding behavior of rattlesnakes. Only four records of predation on birds were obtained. The two kinds of birds recorded among the prey items, the brown towhee (*Pipilo fuscus*), and California quail (*Lophortyx californica*), are both ground-living species frequenting thick cover where snakes are often concealed. On one occasion a flushed covey of quail consisting of parent birds and nearly grown young lit in thick brush, and immediately loud distress calls and fluttering were heard. The observer hurried to the spot and found a quail struggling feebly, anchored down by a large rattlesnake whose fangs were deeply imbedded high on one side of the quail's breast. In a few seconds the quail's head drooped and its breathing became convulsive; in four minutes its movements ceased and it appeared to be dead. Three and a half minutes later the snake released it and began nosing over the limp body, occasionally opening its mouth to grasp the quail hesitantly. These actions continued for about sixteen minutes; the snake was continually shifting its coils and moving over and around its prey, until finally it seized the head and began swallowing, backing away as it did so, and dragging the bird, which was thus kept stretched out full length with a minimum diameter to be swallowed. After six minutes of swallowing the head and neck had been engulfed, but the snake was having some difficulty in getting over the bend of the wing. The quail had been dragged in a circuitous course to a distance of about three feet, and half way back again. At this stage the observer interrupted by catching the snake. On another occasion a large rattlesnake was found beside a towhee which had been bitten in the leg and then partially swallowed. Retention of the hold at the time a bite is delivered may be characteristic in dealing with birds, which would fly and escape if released, but all rodents seen to be bitten were immediately released by the snakes, which waited for death of the prey before tracking it down. A rodent held by the snake might retaliate with a bite and inflict serious injury.

On two different occasions the actual striking of a squirrel by a rattlesnake was seen in the field. In one observation, recorded by Raymond Sharp, the squirrel jumped from an overhanging flat rock and was struck by a snake which had been lying coiled beneath. The squirrel was hit in the left shoulder, and ran about erratically bumping into objects in its path, then lay down with its sides jerking convulsively and its eyes shut. Four minutes later when the observer approached, it escaped into a burrow entrance, reeling about and falling on its side as it moved. Another instance was observed when a young squirrel running to its burrow in alarm, passed near a large rattlesnake, which lashed out and struck it broadside, and was jerked out full length before it could disengage its fangs. The squirrel squealed and scurried into its hole but probably it died soon afterwards.

Many animals bitten by rattlesnakes are not eaten by them, and the snakes are much less inclined to rattle in the presence of small animals than in the presence of man or large animals which might trample them, causing death or injury. Rather, when approached by a rodent, the snake is apt to strike without warning. The bitten animal may be too large to be swal-

lowed, or it may run too far for the snake to follow or may die in some inaccessible place, or the snake may not be sufficiently hungry even to attempt trailing it. The number of prey animals killed in this way but not used perhaps exceeds the number actually eaten.

In a number of instances rattlesnakes seen hunting in the vicinity of burrow systems where there were litters of small and inexperienced young ground squirrels were believed to have bitten several within a short time. One such occasion illustrating in detail the behavior of squirrels and snake toward each other was recorded on June 10, 1938, when the observer's attention was attracted by the shrill distress squeal of a squirrel, which then appeared, reeling about unsteadily on a burrow mound, holding its head sidewise, and pawing the right side of its face. This was at 6:57 P.M. Another small squirrel, probably of the same litter, but uninjured, came up beside the first one, and appearing very nervous, sat on the summit of the mound with its hair fluffed out, and twice within five minutes it gave long, vibrating chirps. The first squirrel became more quiet, sitting in a hunched position, but occasionally it toppled over sidewise or backwards, righting itself unsteadily each time until it had moved down to the lower edge of the mound. The uninjured squirrel moved slowly and cautiously off the mound, and away through the grass to another burrow. It stopped and chirped, looking into the hole, and then entered hesitantly. At 7:05 P.M., a third squirrel was noticed behaving like the first one and apparently similarly injured; it was crawling feebly and unsteadily under the edge of a boulder, about twenty feet from the mound where the other two were first seen. At 7:10 P.M., a three-foot rattlesnake emerged from the burrow and crawled slowly over the mound where the young squirrels had been. Obviously in search of prey, it was darting out its tongue continually, nosing over the ground from side to side apparently trying to pick up a scent. It moved over and around the mound, passing within a foot of the afflicted squirrel, which was still sitting in the same hunched position, but apparently the snake did not notice it. The squirrel had become lethargic, and did not notice the snake either. An adult squirrel had been perched on a rock about thirty feet away, giving the low musical chirps used by mother squirrels to warn their small and inexperienced young of approaching danger. This adult came hesitantly toward the place where the young had been, encircling the rock outcrop where the burrows were, and moving around the base of a boulder, it suddenly came face to face with the rattlesnake at a distance of about two feet. The squirrel emitted a sharp chirp and flicked its tail, and its hair fluffed out. The snake's body was extended so the squirrel was well beyond its striking range. For a moment it lay motionless, watching the squirrel, then it began to crawl slowly forward with its head and the anterior part of its body drawn back ready to strike. It seemed to be trying to get within reach but the squirrel edged away warily. The squirrel was aggressive, however, and would jump back, then take several quick steps toward the snake. Once it approached within a foot of the snake's head, and once scurried away in sudden fright, but quickly returned. It continually faced the snake and kept flicking its tail sidewise and giving low, vibrating chirps. The snake, without making any sudden movement,

followed it up over the sloping rock surface, but was not in a position to strike effectively. The squirrel, backing away up over the boulder, appeared to be exercising excellent judgment in keeping just beyond striking range; its movements were tense and cautious, and its attention was concentrated on the snake, so that for many minutes it failed to notice the observer. Finally it took alarm and ran to another rock outcrop. The snake crawled around to the burrow where it had emerged and disappeared. The uninjured young squirrel meanwhile had reappeared from the burrow it had entered, and moving in a hesitant, nervous fashion, flicking its tail and fluffing its fur, and chirping, it came to the injured squirrel and nosed it. Squirrel activity elsewhere had long since ceased, as darkness was rapidly setting in. At 7:25 it had left the vicinity of the home burrow and was hiding beneath a rock twenty feet away, chirping at intervals; at last it came out again, and at 7:37 it disappeared into the burrow, but with apparent reluctance. At 7:40 it was almost too dark to see; the observer approached the injured squirrel and found it hunched against the base of the boulder with its eyes half closed, but suddenly it aroused itself and escaped into the burrow entrance. The snake could not be found. On the following day no squirrels were out in the vicinity of this burrow. The snake was not found either, but its tracks indicated that its movements had been much more extensive than those actually observed.

On another occasion, an unusually large rattlesnake seen coiled in a burrow entrance beside a dying young squirrel, appeared to have its body already distended with food. Still another encounter was observed when one of the writers was directed to a place where earlier in the day a young squirrel had been seen in the road, showing evidence of snake bite and evidently dying. This squirrel could not be located again, but two others in the vicinity ran to a rock outcrop, and one was moving erratically, seeming to be injured. The second, running among brush and rocks, was struck by a rattlesnake lying concealed there, and it died under a nearby boulder a few minutes later.

As the squirrel burrows are favorite hiding places for rattlesnakes, the squirrels are in constant danger of being bitten underground or in the burrow entrances. Although squirrels are alert and watchful for lurking snakes, accidents are frequent, and are most apt to happen when the squirrels are frightened to their burrows by some other danger and momentarily are off guard. Several such incidents were seen. Two young squirrels scared into the same hole when the observer approached popped out and back in again several times within a few seconds, and gave shrill squeals while underground. Then a small rattlesnake emerged from the hole, rattling and attempting to escape. Another time a large squirrel frightened into an apparently deserted burrow burst out again backwards and ran to another hole. Then a snake was heard rattling down in the burrow the squirrel had left.

Thirteen animals bitten by rattlesnakes were found dead in the field. Once a snake was caught in the act of swallowing a ground squirrel; in three instances the snake involved was lying beside the prey, another snake was seen to trail a kangaroo rat lying dead in the road, and after finding it dragged it for several yards to the shade of a bush and swallowed it. Two

other times snakes were located within a few feet of the freshly killed prey, which probably would have been found and eaten. Four ground squirrels and a meadow mouse all had been pierced in the thoracic or abdominal cavities by the bite; a brown towhee had been bitten in the leg. The other four prey animals had evidently been dead for some time and would not have been found by the snakes. Of these last prey animals, two ground squirrels and a kangaroo rat had only subcutaneous bites and probably died slowly; in another kangaroo rat the bite had penetrated the thoracic cavity, so death must have been almost immediate. Two other dead squirrels were found which had been swallowed and disgorged. On one occasion a squirrel and a rattlesnake were caught together in a box trap. When found the squirrel had been bitten in the thigh and axilla and it died in an hour and forty-five minutes.

Stomach contents were dissected from dead snakes and palped from live ones. Undoubtedly in the live snakes many well digested prey items that might have been revealed by dissection were overlooked because too much digested to be forced up by manipulation. Hence the ratio of snakes containing food among those examined was low—only 79 of the total number of 521. Seasonal distribution of feeding records was as follows: March, 3 (out of 36 examined); April, 22 (of 123); May, 26 (of 140); June, 14 (of 88); July, 10 (of 31); August, 2 (of 41); September, none (of 34); October, 1 (of 21); November, 1 (of 7). Snakes that have secured a meal in spring probably are able to subsist on it throughout the summer without feeding again, and still remain in good condition. Although less than one-fourth of the snakes recorded were adult females, this group includes 33 of the 79 that contained food. The feeding records for adult females were distributed seasonally as follows: March 1, April 12, May 15, June 5. During March, April, May and June, large adult females were found in a ratio of slightly less than two males to one female, but in July, August, September, and October, 34 males were found to only two females.

Evidently during the period of their pregnancy females remain in seclusion underground, and they must subsist largely on food taken in the spring during the breeding season. Among the snakes yielding food records, the high proportion of adult females in spring seems to indicate that they are then especially active in hunting.

Likewise nearly all feeding records for adult males were in April and May, although occasional adult males were found during the summer months. Feeding records for young were more evenly distributed seasonally than were those of adults, with nearly as many records for July (6) as for May (7) and June (7).

Small snakes, less than a year old, with head and body lengths less than eighteen inches and without more than three rattles had eaten one of the eight pocket gophers, one of the five kangaroo rats, six of the nine pocket mice, seven of the ten *Peromyscus*, two of the four fence lizards, both of the whiptails, the three brown-shouldered lizards, and both of the spadefoot toads.

Rabbits, ground squirrels, woodrats and quail are the main food of the large snakes. Gophers, kangaroo rats, meadow mice, larger lizards, and mice

are eaten mainly by middle-sized individuals, which likewise may occasionally take a small squirrel or rabbit, or any of the food items taken by the small snakes. Mice, small lizards, and spadefoot toads comprise the food of the smallest ones during the period when growth is most rapid. Size of prey is thus roughly proportional to size of the snake; in twenty recorded instances in which both the snake and its food were weighed, the prey was, on the average, 39.9 per cent of the snake's weight. The relatively largest prey item weighed 123 per cent of the weight of the snake that had eaten it. The prey item of relatively smallest size amounted to only $3\frac{1}{2}$ per cent of the snake's weight.

All of the ground squirrels among the food items recorded, were immature individuals of the season's brood, and all were taken in April (9 records), May (10 records), June (3 records) and July (1 record). Though only young ground squirrels during the first few weeks after their emergence above ground are taken, they comprise about one-third of all food items recorded—more than twice the toll taken from any other species. "Mice," including six different species, about equalled the number of squirrels taken. All of the 23 squirrels were taken by adult snakes (head and body lengths of more than two feet). Nine of the ten rabbits taken and 20 of the 23 squirrels were eaten by large adult snakes with head and body lengths of more than 28 inches. Squirrels and rabbits thus comprised approximately 75 per cent of the items taken by snakes of this largest size group, which also ate gophers, woodrats, kangaroo rats, pocket mice, white-footed mice, and quail.

Of the 79 snakes that had food in their stomachs (or were found with their freshly killed prey), only four had more than a single food item. Two of these four contained young cottontails; in each instance the snake had found the helpless litter in the nest. Another contained a fence lizard and a pocket mouse, and a third had eaten two adult meadow mice.

Conditions favoring a high population of rattlesnakes probably could exist only in a habitat affording an abundance of several different prey species, which would provide adequate food sources for snakes of every size. Abundance of small rodents and lizards favors successful development of the smaller snakes. The area of the Experimental Range has relatively high populations of rat and squirrel-sized rodents, providing a food source for the larger snakes. But, compared with many other areas in the western states, its populations of lizards and mouse-sized rodents are low. Though several species are present, none is particularly abundant, and all are subject to marked fluctuations in numbers. Thus small rattlesnakes on this area are less well supplied with food than are adults, and a critical stage in the life cycle may occur during the first few months of life. During the late summer many young have been found in emaciated condition and we suspect that a high proportion of each season's brood dies before reaching the age of a year, partly through lack of sufficient food. Half-grown snakes with four, five, or six rattles are scarce as compared with adults or small young.

To our knowledge, the food habits of snakes have never been studied through examination of their fecal material, although this method has been widely applied in studying mammalian predators. Snake feces, or "scats,"

are easily identifiable, and samples obtained from caged snakes were used for comparison with those found in the field. A typical dropping consists of one or more dark-colored, elongated segments made up mainly of animal remains, accompanied by a mass of powdery white uric acid, which is often tinted with pink or green. The animal matter is so thoroughly digested that usually no bones remain. Hair is relatively unaffected, but teeth of rodents in the scats often fall to pieces when handled. Feathers and bills of birds are somewhat disintegrated but those found were sufficiently intact to be diagnostic.

TABLE I
COMPARISONS BETWEEN STOMACH AND SCATOLOGICAL EXAMINATIONS OF
Crotalus viridis oregonus

Prey items	Stomach examinations		Scatological examinations	
	Number of prey items	Percentage of total	Number of prey items	Percentage of total
<i>Citellus beecheyi</i>	23	26.44	37	41.11
<i>Thomomys bottae</i>	8	9.20	2	2.22
<i>Perognathus</i> sp.	10	11.49	2	2.22
<i>Dipodomys heermanni</i>	5	5.75	24	26.67
<i>Peromyscus</i> sp.	10	11.49	4	4.44
<i>Neotoma fuscipes</i>	1	1.15	4	4.44
<i>Microtus californicus</i>	3	3.45	1	1.11
Unidentified mouse	0	0	2	2.22
<i>Sylvilagus auduboni</i>	14	16.09	3	3.33
<i>Lophortyx californica</i>	1	1.15	1	1.11
<i>Pipilo fuscus</i>	1	1.15	1	1.11
<i>Eumeces gilberti</i>	0	0	2	2.22
<i>Uta stansburiana</i>	3	3.45	2	2.22
<i>Sceloporus occidentalis</i>	4	4.60	3	3.33
<i>Cnemidophorus tessellatus</i>	2	2.30	2	2.22
<i>Scaphiopus hammondi</i>	2	2.30	0	0
Totals	87	100	90	100

Eight other species of snakes are known to occur on the area where our scat collection was made, but of these the night snake (*Hypsiglena ochrorhyncha*), the ring-necked snake (*Diadophis amabilis*), and the king snake (*Lampropeltis getulus*), are so rare that they need hardly be considered. The California racer (*Coluber lateralis*) is also much less common than the rattlesnake, and is limited to brushy areas different from the locations where scats were gathered. The garter snakes (*Thamnophis sirtalis* and *T. ordinoides*) are common on this range, but usually stay in the vicinity of water, and amphibians comprised all of the 83 items found in 25 garter snake stomachs. The gopher snake (*Pituophis catenifer*) is found in the same habitats where rattlesnakes occur, but is less numerous, in the ratio of about one gopher snake to five rattlesnakes. Possibly a small proportion of the scats collected are those of gopher snakes.

Most of the scats were picked up in the vicinity of squirrel burrow systems and rocky outcrops, locations in which rattlesnakes are apt to be

encountered. Several droppings were found below the surface of the ground in enlarged entrances of squirrel burrows, and it is probable that many others are deposited underground out of sight.

Many of the 90 scats examined contained two different kinds of prey. Remains identified and their associations were as follows: ground squirrel alone in 37; ground squirrel with kangaroo rat, ground squirrel with woodrat, ground squirrel with fence lizard, ground squirrel with whiptail lizard, each in one; kangaroo rat alone in 18; kangaroo rat with skink, kangaroo rat with fence lizard, kangaroo rat with whiptail lizard, each in one; kangaroo rat with brown-shouldered lizard, pocket gopher alone, pocket mouse alone, each in two; cottontail alone and woodrat alone each in three; white-footed mouse alone in four; meadow mouse alone, towhee alone, quail alone, unidentified rodent with fence lizard, unidentified rodent alone, and skink alone, each in one.

Since few of the snake stomachs examined contained more than one kind of food, the frequent occurrence of two prey species in one fecal mass suggests that the scats may ordinarily include the residues of more than one meal.

Trends shown by the scatological data and the stomach data differ most in the high percentages of squirrel and kangaroo rat and the relative scarcity of mouse and rabbit remains in the droppings. Most of the scats were those of larger snakes. Small snake scats may have been often overlooked in the field because of their resemblance to those of large lizards.

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