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DIET OF THE NORTHERN PACIFIC RATTLESNAKE, *CROTALUS VIRIDIS OREGANUS*, IN BRITISH COLUMBIA

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ABSTRACT: The diet of a population of the Northern Pacific rattlesnake (*Crotalus viridis oreganus*) in southern British Columbia was determined by palpation of stomach contents and fecal material. Over a 3 yr period, 221 samples were obtained from 4227 captures of rattlesnake (captures and recaptures combined). Rattlesnakes were active between late March and early October. Heaviest feeding (17% of snakes with food or fecal material) occurred during June–August. Prey consisted of rodents (91% by occurrence, nine species), shrews (5%, one species), and birds (4%, four species). Neonates and small juveniles preyed on the smallest mammals whereas adults fed on larger prey and a greater diversity of species. Gravid females greatly restricted their summer movements and usually did not feed during gestation or after parturition. Body weight stability and higher survival of gravid females (compared to non-gravid females) suggest that their sedentary lifestyle minimizes weight loss during gestation and lessens the risks to predation.

Key words: Serpentes; Viperidae; *Crotalus viridis*; Diets; Gravid females; British Columbia

In a recent review, Mushinsky (1987) emphasized that the evaluation of hypotheses concerning snake foraging ecology will require an understanding of relationships such as between prey size and snake size, energetic requirements and foraging frequency, and prey availability and diet composition. For many species, the detailed information needed to examine these relationships is lacking. Presumably, this stems from a basic difficulty of obtaining a reasonably large sample of snakes of both sexes, and from different age and reproductive classes, that contain recently ingested prey.

Food habits, even of frequently investigated snake species, may be poorly known. For example, despite numerous field studies of the western rattlesnake, *Crotalus viridis* (Diller and Wallace, 1984; Duvall et al., 1985; Fitch, 1949; Fitch and Glading, 1947; Fitch and Twining, 1946; Gannon, 1980; Parker and Brown, 1974; Preston, 1964; Sehman, 1977), detailed descriptions of the diet are available only for one population in California (Fitch, 1949; Fitch and Glading, 1947; Fitch and Twining, 1946). Incidental observations of cannibalism and scavenging have been re-

ported (Gloyd, 1933; Lillywhite, 1982), and much has been learned recently about foraging and feeding behavior of *C. viridis* (Chiszar and Scudder, 1980; Duvall et al., 1985). Still, relatively little is known about how diet varies among individuals or populations of this wide-ranging species.

The present study describes diet composition (prey size and diversity) and seasonal feeding patterns in a population of the Northern Pacific rattlesnake (*C. v. oreganus*) in British Columbia. Differences in diets of neonates, juveniles, and adults are related to biological factors such as size of snakes, activity patterns, and reproductive condition. Geographic variation in diet is examined by comparison of this northern population with a conspecific southern population.

METHODS AND MATERIALS

Food habits of a population of *C. v. oreganus* in south-central British Columbia were examined in a 3 yr mark–recapture study (1981–1983). A description of the study area and sampling methods is provided by Macartney and Gregory (1988). A total of 1697 individual rattlesnakes from 24 communal hibernacula was marked, and 2530 recaptures were obtained. At each capture, a rattlesnake was palpated and its stomach contents were gently maneuvered

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into the buccal cavity for identification. In the first year of the study (1981), all stomach contents were removed and preserved. Because it was felt that meal deprivation could affect growth and survival, in 1982 and 1983 mammalian prey were identified by characteristics of the tail, hind feet, and pelage, and the prey item was returned to the snake's stomach. The entire stomach contents were removed only when identification by this method was uncertain in the field or when several prey items had been ingested. Taxonomic keys used to identify mammalian prey were Cowan and Guiguet (1965) and Maser and Storm (1970).

Fecal material in the colon was noted for rattlesnakes sampled in 1981, but collection of fecal material to identify guard hairs did not begin until 1982. Stomach contents collected in 1981 and museum skins in the Royal British Columbia Provincial Museum (RBCPM), which were collected near the study area, provided a reference series of guard hairs. Feces were dried and prey were identified to genus with the aid of permanent slides made from these guard hairs. A key to dorsal guard hairs (Moore et al., 1974) aided in the identification of some of the material. Hairs were assumed to belong to one prey item unless the presence of more than one item or species was obvious. Identities of guard hairs were confirmed in all cases when skulls in the feces were also present. Because stomach contents were not removed from most snakes, mean zygomatic breadth was determined from measurements of museum specimens ($n = 10$ skulls, RBCPM) for each of the mammal prey species and was used as an index of body size in an analysis of the relationship between mean prey size and mean snout–vent length (SVL) of snakes. A Shannon-Wiener Index (Zar, 1984) was used to compare diet composition diversity between adult and juvenile diets, and between populations in British Columbia and California (Fitch and Twining, 1946).

RESULTS

Foraging Period

When rattlesnakes emerged from hibernacula between late March and late May, their stomachs were empty and only fluid or hardened lumps of uric acid could be palpated from their cloacae. Snakes containing stomach contents during April and May had dispersed from their dens. As sampling during the emergence period occurred mainly at hibernacula rather than surrounding areas, the data may underestimate the proportion of snakes with food in the early spring (Table 1). The occurrence of stomach contents and fecal material was highest (17%) in snakes captured during June, July, and August. In September and early October, stomach contents were palpated mainly from rattlesnakes captured prior to their return to hibernacula. Fecal material was present in many individuals that had newly arrived at hibernacula. I found fresh and dried rattlesnake scats around most hibernaculum entrances in the autumn, suggesting that rattlesnakes defecated prior to hibernation.

Diet Composition

Ten mammalian and four avian prey species were identified from stomach contents and fecal material of 79 juvenile and 124 adult *C. v. oreganus* (Table 2). Fecal material collected from 18 rattlesnakes lacked guard hairs and could not be identified. Two species of *Microtus*, *M. montanus* and *M. pennsylvanicus*, were identified but no attempt was made to distinguish between these species of voles using guard hairs, tail, or hind feet, and all records of *Microtus* were pooled.

Stomach contents or fecal material from an individual rattlesnake nearly always represented a single prey item and a single prey species. Exceptions were three adult voles (stomach of adult male), a shrew and a vole (stomach of adult female), and an unidentified bird and a deer mouse (feces of adult male).

Sorex, *Peromyscus*, and *Microtus* made up 92.5% of the juvenile diet. Stomach contents revealed that snakes <450 mm SVL (neonates to 2 yr old) selected mainly *Sorex* and juvenile *Peromyscus* and *Microtus*. A greater diversity of prey was eaten by adults, although 60.5% of their diet consisted of the same two species (*Peromyscus* and *Microtus*) as occurred in the

TABLE 1.—Percent of *C. v. oreganus* with stomach contents or fecal material in each month of the active season, based on the total number of captures and recaptures of snakes between spring 1981 and spring 1983.

Month	No. snakes examined*	No. snakes with food	% with food
March	42	0	0.0
April	1059	2	0.2
May	956	20	2.1
June	112	19	17.0
July	202	36	17.8
August	342	56	16.4
September	945	75	7.9
October	569	13	2.3
Total	4227	221	5.2

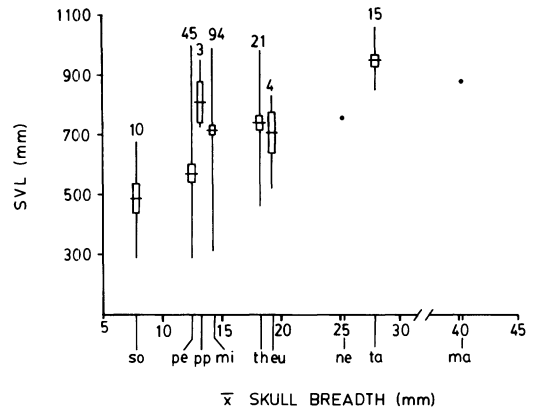* Some snakes were examined more than once each month.

FIG. 1.—Relationship between mean prey size (zygomatic breadth) and mean SVL of *C. v. oreganus* that fed on individual mammal prey species. Horizontal bar = mean SVL; vertical bar = SVL range; rectangle = 1 SE; sample size given above. Abbreviations for prey species are: so = *Sorex cinereus*, pe = *Peromyscus maniculatus*, pp = *Perognathus parvus*, mi = *Microtus* sp., th = *Thomomys talpoides*, eu = *Eutamias amoenus*, ne = *Neotoma cinerea*, ta = *Tamiasciurus hudsonicus*, ma = *Marmota flaviventris*.

juvenile diet (Table 2). Larger rodents (*Thomomys, Eutamias, Neotoma, Tamiasciurus,* and *Marmota*) and birds made up the balance of the adult diet. Avian prey identified from stomach contents were a common bushtit (*Psaltriparus minimus*), a European starling (*Sturnus vulgaris*), a dark-eyed junco (*Junco hyemalis*), and a rufous-sided towhee (*Pipilo erythrophthalmus*).

There was a significant correlation between mean zygomatic breadth and mean SVL of snakes ($r = 0.83$, $P = 0.005$, $n = 9$, Spearman rank correlation, Fig. 1). There was no sex-related difference in prey preference for the four common prey taxa (*Sorex, Peromyscus, Microtus,* and *Thomomys, $\chi^2 = 3.26$, $P > 0.35$, df = 3). All red squirrels and the one juvenile yellow-bellied marmot were preyed on by large male rattlesnakes (>850 mm SVL).

Gravid females usually did not travel farther than 50–100 m from their dens and typically stayed near one or two cover objects during the entire active season. Of 362 captures of gravid females, only eight (2.2%), captured during spring and early summer, had stomach contents or fecal material. Females remained active near dens for periods of 1 day to 2 wk following

TABLE 2.—Percent occurrence of species of mammalian prey in the diets of 79 juvenile and 203 adult *C. v. oreganus* in British Columbia. Distinction between juvenile and adult SVL is based on size of smallest sexually mature female in the population. See text for a list of avian prey species. Shannon-Wiener Diversity Index (*J*) is calculated on the basis of 10 categories (9 species of mammals plus all bird species combined).

Prey species	Juveniles <650 mm SVL	Adults ≥650 mm SVL	Combined
Cinereus shrew (*Sorex cinereus*)	11.5	0.8	4.9
Deer mouse (*Peromyscus maniculatus*)	40.5	10.5	22.1
Great Basin pocket mouse (*Perognathus parvus*)	0.0	2.4	1.5
Montane and meadow vole (*Microtus montanus* and *M. pennsylvanicus*)	40.5	50.0	46.3
Northern pocket gopher (*Thomomys talpoides*)	5.1	13.7	10.3
Northwestern chipmunk (*Eutamias amoenus*)	1.2	2.4	2.0
Bushy-tailed wood rat (*Neotoma cinerea*)	0.0	0.8	0.5
Red squirrel (*Tamiasciurus hudsonicus*)	0.0	12.1	7.3
Yellow-bellied marmot (*Marmota flaviventris*)	0.0	0.8	0.5
Total mammalian prey	98.8	93.5	95.6
Total avian prey	1.2	6.5	4.4
Dietary diversity (*J*)	0.538	0.689	0.693

parturition in the last half of September, but they rarely fed prior to hibernation. The only postpartum female containing prey had given birth in early September and was captured a short distance from a den in late September.

The mean interval between birth and completion of the first moult was 24 days (SE = 1.1, range 11–40 days, $n = 37$). Neonates entered hibernation 1–7 days after completing their first moult. Of approximately 160 neonates examined at hibernacula in autumn, none had stomach contents or fecal material.

DISCUSSION

Previous studies of the food habits of *C. viridis* indicate a strong preference for mammalian prey (Fitch and Glading, 1947; Fitch and Twining, 1946; Klauber, 1972). Seven species of mammals, including five genera taken by *C. v. oreganus* in British Columbia (*Microtus, Peromyscus, Thomomys, Neotoma,* and *Perognathus*), made up 86% of the diet of California *C. v. oreganus* (Fitch and Twining, 1946). Other prey included birds (3%), small lizards (10%), and amphibians (1%). The diet of *C. v. oreganus* in south-central British Columbia has a similar composition, in terms of the range of prey size; however, dietary diversity is greater in California populations mainly because of the occurrence of ectotherms ($J = 0.83$, calculated for the entire population from data presented in Table 1 in Fitch and Twining, 1946). Additional prey species have been recorded in the diet of *C. v. oreganus* in British Columbia, including muskrat (*Ondrata zibethica*), white-crowned sparrow (*Zonotrichia leucophrys*), vesper sparrow (*Pooecetes gramineus*), savannah sparrow (*Passerculus sandwichensis*), and blue grouse (*Dendragapus obscurus*) (A. C. Mackie, unpublished observations).

Neonate *C. v. oreganus* in British Columbia do not feed prior to overwintering and therefore must rely on yolk reserves until the following spring or summer when they obtain their first meal. I found several rattlesnakes that weighed less at 1 yr of age than they had at birth and had not grown in SVL. These undernourished snakes generally did not survive their second winter in hibernation (Macartney, 1985). Similarly, Fitch and Twining (1946) observed emaciated yearlings in late summer and suspected that some neonates have difficulty obtaining food. Thus, starvation may contribute significantly to mortality of neonate rattlesnakes in their first active season in both populations.

Although ectotherms constitute a minor part in the overall diet of *C. v. oreganus* in California, they are the principal prey of small (<500 SVL) rattlesnakes (Fitch and Twining, 1946; Mackessy, 1988). Lizards and amphibians (*Elgaria coerulea, Ambystoma macrodactylum, Hyla regilla, Spea intermontana,* and *Rana pretiosa*) were present on my study sites, but apparently they had patchy distributions and low population densities (personal observation). An absence of ectotherms in the diet of juvenile rattlesnakes in British Columbia may be attributed in part to the scarcity of these prey species in this region. Alternatively, rattlesnakes may be exhibiting a differential preference for endothermic prey, because red-sided garter snakes (*Thamnophis sirtalis*) at these study sites feed heavily on amphibians (personal observation). In either case, neonate rattlesnakes, by virtue of their small size (270 mm SVL), apparently utilize a very restricted prey base consisting mainly of shrews and juvenile deer mice and voles.

Diets of juveniles and adults show considerable overlap. The greater prey diversity in the adult diet appears to be due mainly to the inclusion in their diet of rodent and bird species that would be too large for most juvenile rattlesnakes to swallow. Thus ontogenetic changes in diet are less dramatic than the major transition from ectotherm to endotherm prey that seems to occur in California (Fitch and Twining, 1946; Mackessy, 1988).

Adult males and non-gravid females make extensive summer movements and have home ranges that are up to 40 times larger than those of gravid females (Macartney et al., 1988). Lengthy periods of inactivity and fasting are behavior patterns characteristic of gravid females in other species of viperid snakes (Fitch, 1960;

Fitch and Glading, 1947; Keenlyne, 1972; Prestt, 1971; Reinert and Kodrich, 1982; Viitanen, 1967). In British Columbia, female *C. v. oreganus* reproduce at irregular intervals (Macartney and Gregory, 1988). Non-gravid females accumulate large body fat reserves during the year(s) prior to reproduction and, despite this fasting, gravid females lose only 6% of their body mass during gestation (Macartney and Gregory, 1988). Fat reserves appear to be adequate for body maintenance and embryogenesis, and summer foraging may not be required (a few gravid females, however, did feed in early summer). Presumably, inactivity minimizes weight loss in gravid females during the prolonged period of aphagia.

Fasting by gravid females could be a consequence of inactivity, because a female's chances of encountering prey are greatly reduced if she stays in a localized area all summer. Alternatively, lack of feeding may be due to low prey availability in areas near hibernacula, although I did not determine prey availability in the field that would be needed to support this hypothesis. However, gravid female *Sistrurus catenatus* will not accept food until after parturition, suggesting that appetite is completely suppressed during gestation in that species (Keenlyne and Beer, 1973). Offering food to gravid female *C. viridis* in captivity would help clarify whether fasting is self-imposed or a function of local prey availability.

Females also may limit their movements and restrict their surface activity during pregnancy if these behaviors reduce the risk to predation. Gestating females are likely to be at greater risk than adult males and non-gravid females, because their increased abdominal bulkiness, especially in late pregnancy, may reduce their locomotory performance and their ability to escape from predators. Reduced locomotory performance during pregnancy has been demonstrated for viviparous snakes (Seigel et al., 1987) and viviparous lizards (Bauwens and Thoen, 1981; Shine, 1980). A hypothesis that a sedentary and cryptic lifestyle lessens predation is supported indirectly by a greater annual survival of gravid females (88%) compared with non-gravid females (72%) (Macartney, 1985). By adopting behavior patterns that minimize energetic demands and reduce exposure to predators, female rattlesnakes are able to offset the potential costs of aphagia and reduced locomotory ability during pregnancy.

Rattlesnakes return to dens throughout September and early October and remain active on the surface for a few days to several weeks prior to hibernating. Gregory (1982) suggested that fasting may be required to clear the digestive tract to prevent putrefaction of gut contents during hibernation. Accumulations of fresh and dried scats around entrances of dens and the observation that most snakes were devoid of stomach contents or fecal material by late autumn lend support for this idea. Variation among individuals in how long surface activity lasts prior to entering the dens could be explained by temporal variation in autumn feeding and defecating.

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