

FOOD HABITS OF THE RACER (*COLUBER CONSTRICTOR MORMON*) IN THE NORTHERN PART OF ITS RANGE.

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Dietary habits of the racer, *Coluber constrictor mormon*, were studied based on stomach and faecal contents from 26 road-killed specimens and 297 live animals collected in the field during 1992–1994 in southern British Columbia, Canada. Thirty percent of the specimens examined contained gut contents. *Coluber constrictor mormon* feeds mainly on insects (91% of prey; Acrididae > Gryllidae > Tettigoniidae > Gryllacrididae) and occasionally rodents (7.5% of prey), as well as frogs and snakes (both < 1%). There were proportionally more vertebrates in the diets during the early part of the season (April – May). Diet was related to individual attributes, such as size or sex of the snake. Thus, larger individuals – primarily females – were more likely to feed on vertebrates, although insects were not absent from the diet of larger individuals. Diet composition (mammals vs. insects only) did not depend upon the method of sampling snakes. This study adds to the growing number of dietary studies on *Coluber constrictor* that continue to provide insights into the evolutionary ecology of this widespread but poorly-known species.

Keywords: *Coluber constrictor*, feeding ecology, British Columbia, Canada, diet, food habits

INTRODUCTION

A renewed interest in the feeding ecology of snakes (Arnold, 1993; Cundall & Greene, 2000) reflects a recognition of its importance as an aid to understanding other ecological and evolutionary phenomena such as habitat use, activity periods, and movement patterns within and between populations (Greene, 1983; Rodríguez-Robles, Bell & Greene, 1999). On a larger scale, patterns of food resource utilization may explain species assemblages and provide insights into the evolution of life history traits of snakes (Brown & Parker, 1982; Rodríguez-Robles, Mulcahy & Greene, 1999).

The racer (*Coluber constrictor*) is a common and polytypic species found across continental North America, from southern Canada to Guatemala. In western USA it occurs in a wide variety of habitats (e.g. grasslands, woodlands, meadows, rocky wooded hill-sides and shrub-steppe desert), at elevations from sea level to 2150 m (Stebbins, 1985; Conant & Collins, 1991). Its wide distribution and morphological variation have resulted in 11 subspecific designations, some of which are the focus of taxonomic debate (Fitch, Brown & Parker, 1981; Greene, 1984; Corn & Bury, 1986; Collins, 1991). Detailed life history studies have been conducted in Utah (e.g. Brown, 1973; Brown & Parker, 1984) and Kansas (Fitch, 1963), and dietary information is available from Illinois (Klimstra, 1959), Utah (Brown, 1973; Brown & Parker, 1984), Kansas (Fitch, 1999), Georgia (Hamilton & Pollack, 1956), and South Carolina (Cooper, Burghardt & Brown, 2000). Together, these studies demonstrate some distinct di-

etary differences among eastern and western populations. Logically one would also predict dietary differences between northern and southern populations, possibly related to differences in length of feeding season, habitat or prey availability.

We present information on the diet of the western yellow-bellied racer, *Coluber constrictor mormon*, at the northernmost limits of its range in southern British Columbia, Canada. Our data are based on stomach and faecal samples collected from both live and road-killed specimens over three field seasons. We describe variation in the taxonomic constitution of the racer diet and relate these data to published reports from more southerly and easterly populations. We also investigate whether diet varies according to season, sex or snake size.

MATERIALS AND METHODS

This study was conducted in the extreme southern portion of the Okanagan Valley of British Columbia, Canada, from 1992 to 1994. The main study site was approximately 1.5 x 1.9 km in extent and located near the town of Osoyoos (49°02'N, 119°28'W, elevation 285m). Additional data were gathered opportunistically from road-killed snakes collected in the area surrounding the main study site. The Okanagan Valley is characterized by grassland and shrub steppe habitat with a narrow riparian zone occurring along the Okanagan river. The Okanagan Valley typically has hot, dry summers, with near desert conditions (mean annual precipitation 340 mm, mean daily min/max temperatures -5.7/-0.1°C in Jan. to 14.8/28.9°C in July; Environment Canada).

During the active season (April–Oct.) snakes were captured using eight funnel traps or by hand. In total 297 live snakes were examined for stomach or faecal

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contents by palpation. Road-killed snakes ($n=26$) were dissected and gut contents examined. Snakes were weighed, measured for snout-vent length (SVL) and sexed by everting the hemipenes or by probing (Gregory, 1983; Schaefer, 1934). For some animals (primarily road-kills, $n=22$ of 26) sex could not be confidently determined and these were subsequently left out of sex-related analyses. Similarly, some heavily damaged animals ($n=19$ of 26) were not measured for SVL.

Insects were identified to family where possible, following Bland & Jaques (1978). A reference collection was used to assist identifications. Quantification and identification of prey items were conservative in that insect head capsules were counted to ensure that prey items were not over-represented. If a unique prey item was identified by a body part other than a head, it was scored as a single item. Faecal samples that contained mammalian hair were assumed to be the remains of a single prey item (hair was not analysed to determine species).

Prey items are reported by frequency of occurrence (stomachs containing the item divided by the total number of stomachs containing food). The large number of near completely digested insects in the diet precluded measures of prey volume. Values given are sample means \pm SD and significance was assessed at the $\alpha=0.05$ level.

RESULTS

A total of 323 racers were examined for stomach or faecal material, 98 of which contained prey items (60 of stomach samples, 38 of fecal samples). Road-kill (DOR) samples made up a small portion of the records (26, of which 13 contained food). Of the 79 snakes captured in traps, 28 (35%) contained prey.

Diet consisted primarily of orthopterans, but representatives of three vertebrate classes (Amphibia, Reptilia and Mammalia) were also identified. We iden-

tified four orthopteran families: Acrididae (grasshoppers) were the dominant food item, followed by Gryllidae (crickets), Tettigoniidae (longhorned grasshoppers) and Gryllacrididae (Jerusalem crickets) (Table 1). We were unable to identify a number of miscellaneous orthopteran parts found in stomach or faecal contents. Evidence of unidentified orthopterans usually consisted of wing parts or body segments that may have been the result of unsuccessful prey capture or that may have passed through the digestive tract at different speeds from the rest of the prey (Gunzburger, 1999). The predominant type of vertebrate prey was rodents (Table 1). Two anuran amphibians (*Pseudacris regilla*) and a tail portion of a garter snake (*Thamnophis* sp.) were also identified. Plant matter occurred in 7% of guts, and was probably ingested accidentally while feeding. Multiple prey taxa were identified in 17 snakes (6 stomach records, 11 faecal records), excluding records featuring unidentified taxa (Table 2).

Prey items were categorized into 'vertebrates' and 'insects' for the purpose of testing whether there were sexual differences in prey frequency. No significant difference in frequency of these prey groups by sex was detected. There were fewer than half as many vertebrates in male guts (6 of 37; 4 rodents, 2 frogs) as in female guts (14 of 39: all rodents; $\chi^2=2.83$, $df=1$, $P>0.09$). When the smaller vertebrates (i.e. frogs) were removed from the analysis, this dietary difference between the sexes was significant ($\chi^2=4.85$, $df=1$, $P<0.05$). The presence of mammalian prey was restricted to larger snakes (>55.0 cm SVL), with the exception of one male snake (SVL=38.5 cm) that had one rodent in its stomach. The snake may have been attracted to the rodent in the trap in which it was captured and this may therefore represent an opportunistic feeding event. Nonetheless, a significant difference in SVL was observed between snakes with only insects in their diet ($n=53$, mean SVL=54.5 \pm 10.4) and those containing mammals and insects ($n=18$, mean

TABLE 1. Prey items identified in gut contents of *Coluber constrictor mormon*. Frequency refers to the number of times prey items were found in snakes ($n=98$). Figures in parentheses refer to the number of snake guts that contained particular prey items.

| Prey Type | Frequency | | | Total | % of total number of prey |
|--------------------|------------------|--------------------|--------------|-----------|---------------------------|
| | Males ($n=37$) | Females ($n=39$) | Undetermined | | |
| <i>Insects</i> | | | | | |
| Acrididae | 29 (18) | 40 (16) | 26 (11) | 95 (45) | 35.6 |
| Gryllidae | 10 (6) | 31 (9) | 27 (9) | 68 (24) | 25.5 |
| Tettigoniidae | 2 (2) | 2 (1) | 1 (1) | 5 (4) | 1.9 |
| Gryllacrididae | 10 (6) | 31 (9) | 27 (9) | 68 (24) | 25.5 |
| Unidentified | 4 (4) | 3 (3) | 1 (1) | 8 (8) | 3.0 |
| <i>Vertebrates</i> | | | | | |
| Rodents | 3 (3) | 16 (14) | 1 (1) | 20 (18) | 7.5 |
| Frogs | 2 (2) | 0 (0) | 0 (0) | 2 (2) | 0.7 |
| Snakes | 0 (0) | 0 (0) | 1 (1) | 1 (1) | 0.3 |
| Totals | 60 (41) | 123 (52) | 84 (33) | 267 (126) | 100 |

TABLE 2. Gut contents of *Coluber constrictor mormon* with more than one prey taxon. Sex: male (M), female (F), unknown (U). Sample refers to stomach (s) or faecal (f). Figures in parentheses following prey taxa refer to the number of individual prey items in that sample.

| Sex | SVL (cm) | Sample | Taxa |
|-----|----------|--------|--|
| F | 48.0 | f | Acrididae (1), Gryllidae (1) |
| F | 74.0 | f | Acrididae (4), mammal (2) |
| F | 61.0 | f | Acrididae (1), mammal (1) |
| F | 61.0 | f | Gryllacrididae (1),Gryllidae (1), Acrididae (1) |
| F | 71.6 | f | Acrididae (1), Gryllidae (3) |
| F | 73.0 | s | mammal (1), Acrididae (2) |
| M | 60.0 | s | Acrididae (3), mammal (1) |
| M | 45.0 | s | Acrididae (2), Gryllacrididae (1) |
| M | 45.0 | f | Acrididae (1), Tettigonidae (1) |
| M | 55.0 | s | Acrididae (1), Tettigonidae (1) |
| U | 48.5 | f | Acrididae (1), Gryllidae (1) |
| U | 49.0 | s | Gyllacrididae (1), Gryllidae (1) |
| U | U | f | <i>Thamnophis</i> (1), Gryllidae (3), Tettigonidae (1) |
| U | U | f | Gryllidae (1), Acrididae (1) |
| U | U | f | Acrididae (1), Gryllidae (8) |
| U | U | f | Gryllidae (7), Acrididae (2) |
| U | U | s | Acrididae (2), Gryllidae (1) |

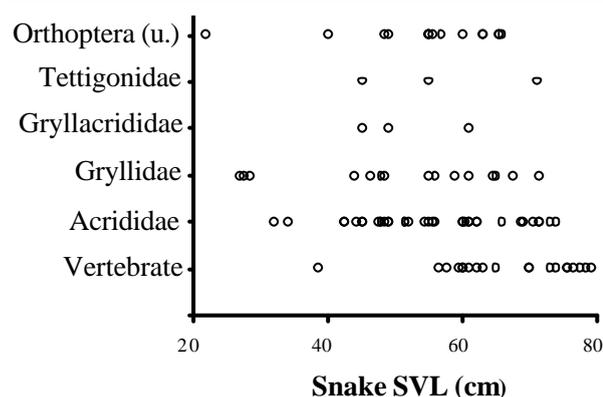


FIG. 1. Relationship between prey category (Vertebrates, Acrididae, Gryllidae, Gryllacrididae, Tettigonidae, and unidentified Orthoptera) and body size (SVL) of *Coluber constrictor mormon* (n=76).

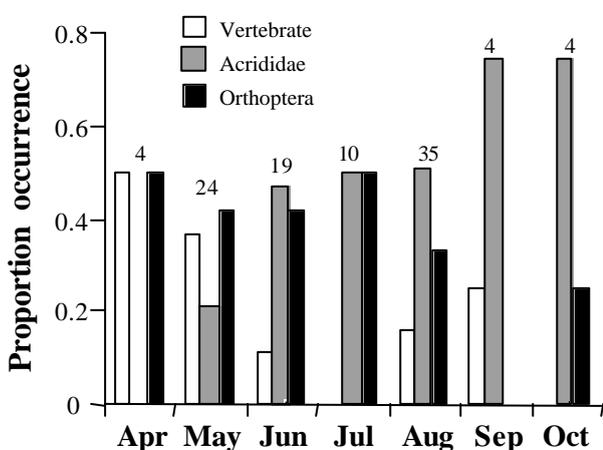


FIG. 2. Relative occurrence of prey (Vertebrate, Acrididae, other Orthoptera) by month (all years combined). Data shown as proportion occurrence. Numbers above months represent the number of snake guts that particular prey categories occurred in (n=68). Excluded are snake guts with unidentified Orthoptera.

SVL=67.3±10.9; one-tailed $t=4.46$, $df = 30$, $P<0.001$. Six of the 28 snakes caught in traps contained mammals, while 12 of the 70 snakes caught by hand contained mammals. Thus the incidence of mammals in the diet was not significantly related to method of capture ($\chi^2=0.22$, $df=1$, $P>0.5$).

Two other trends are worth noting. First, it appears that larger snakes did not make a definitive switch from insect to vertebrate prey (Fig. 1, Table 2), although the largest six snakes in our study (range= 75.5–79.0 SVL, all female) contained only rodents. Second, there was a seasonal variation in diet composition, the proportion of mammals and other vertebrate prey decreasing in gut contents through the feeding season with a concomitant increase in acridids and other insect taxa (Fig. 2).

Anecdotal observations of foraging racers suggest that foraging behaviour may favour the detection and capture of specific prey species. A foraging racer was observed to place the side of its head against a grass stem and then slowly raise it up the stem while still maintaining contact with the stem. The snake raised its head approximately 25 cm before proceeding to a new stem. His behaviour was continued and eventually resulted in the detection and pursuit of a grasshopper that had been disturbed from a stem. It is well documented that *Coluber constrictor* are visual predators (e.g. Herzog & Burghardt, 1974, Cooper *et al.*, 2000), and such fixed behaviours as described here may be efficient when prey concentrations are high, as is often the case with Acrididae.

DISCUSSION

Our study supports the generalization that *Coluber constrictor mormon* rely largely on insect prey, although larger vertebrate prey are also taken (Fitch, 1963; Brown, 1973, Cooper *et al.*, 2000). Brown's

(1973) study in Utah offers the only thorough examination of the diet of *C. c. mormon*. Brown (1973) examined 411 snakes, retrieving stomach contents from 101 (24%), a slightly smaller proportion than reported here (30%). In both Brown's study and ours, acridid grasshoppers made up the bulk of the diet, being proportionately more important in Utah (76%) than in British Columbia (45%). Gryllacrididae were also more prevalent in racer diets in Utah (26% vs. 3%), whereas Gryllidae were more prominent in British Columbia (4% vs 24%). Brown (1973) found that noctuid moths occurred in 11% of stomachs, but moth prey items were not detected in our study. Most interesting is the greater proportion of mammals in the diet of British Columbia racers as compared to those in Utah (19% vs. 3%). Amphibians and reptiles were also recorded in British Columbia racer diets; these ectotherms were not observed as prey in Brown's (1973) Utah population, although snakes and birds were infrequent prey items in other studies (Brown & Parker, 1982; Cooper *et al.*, 2000). The interpretation of these differences remains equivocal as neither study measured relative prey availability. Furthermore, caution must be used when interpreting these results, as we found a definite seasonal variation in the diet of racers (Fig. 2), whereas Brown's (1973) study was restricted to September and October.

Seasonal shifts in prey type are rarely examined in the snake literature (e.g. Auffenberg, 1949; Klimstra, 1959; Fitch, 1963), although such data provide important ecological information. Seasonal changes observed in the diet of British Columbia racers may reflect changes in food availability. Adult insects are at a seasonal low in the spring as few insect species overwinter. During spring, mammals may be one of the main food resources for larger racers. As the season progresses, insect numbers increase and racers may switch to this abundant food resource. In Illinois and Kansas, *Coluber constrictor flaviventris* similarly demonstrated a dietary shift from a high proportion of mammals in the spring to a higher proportion of insects in the summer (Klimstra, 1959; Fitch, 1963). Conversely, in Texas, *Coluber constrictor stejnegerianus* have been observed to shift away from insects as the season progresses (Auffenberg, 1949).

Food habits of organisms also require consideration of sex-related differences (Shine, 1991). *Coluber constrictor* is a sexually dimorphic species, with females being the larger sex (Fitch, 1963; Brown & Parker, 1984). Our data suggest that there may be a sexual difference in diet, but this difference may simply reflect a tendency for larger snakes to eat larger prey items (Mushinsky, Hebrard & Vodopich, 1982; Shine, 1991; Arnold, 1993). Our data reveal two size-related trends: first, vertebrates appeared predominantly in the diets of larger snakes; second, the range of prey taxa increased with snake size, apart from the largest snakes (Fig. 1). The six largest snakes observed in this study contained only mammals, which suggests a difference in feeding

preference when compared with smaller snakes, in which we found vertebrates, insects or both.

The racer is a diurnal, visual predator and actually prefers moving prey (Herzog & Burghardt, 1974; Cooper *et al.*, 2000). However, in one instance a rodent palpated from a racer stomach contained maggots (dipteran larvae), suggesting opportunistic ingestion of carrion, as has been shown for other colubrids (e.g. Rodriguez-Robles, Bell & Greene, 1999).

Mammals appear to be an important part of the diet of larger racers in British Columbia, but our data suggest that smaller prey species are not dropped from the diet of larger individuals. Predation on orthopteran insects may be beneficial if their relatively low individual energy content is offset by high abundance, thus making location and capture economically efficient. This would help to explain apparent seasonal shifts in *Coluber constrictor* diet composition as well as continued predation on insects by larger snakes.

ACKNOWLEDGMENTS

We thank P. Gregory and L. Friis for providing the opportunity to conduct this research; K. Kissner, R. Saumure and H. Waye for their help in the field and thoughtful discussion. Comments from two anonymous reviewers greatly improved this paper. Permits for this research were issued by the B. C. Ministry of Environment and the University of Victoria Animal Care Committee. Research was partially funded by the World Wildlife Fund Canada, Canadian Wildlife Service, British Columbia Ministry of Environment, University of Victoria and the Victoria Natural History Society, and an NSERC operating grant to P. Gregory.

REFERENCES

- Arnold, S. J. (1993). Foraging theory and prey-size-predator-size relations in snakes. In *Snakes: ecology and behavior*, 87-115. Seigel, R. A., and Collins, J. T. (Eds). New York: McGraw-Hill.
- Auffenberg, W. (1949). The racer, *Coluber constrictor stejnegerianus* in Texas. *Herpetologica* **5**, 53-58.
- Bland, R. G. & Jaques, H. E. (1978). *How to know the insects*. Dubuque, Iowa: Wm. C. Brown Company Publishers.
- Brown, W. S. (1973). Ecology of the racer, *Coluber constrictor mormon* (Serpentes, Colubridae), in a cold temperate desert in northern Utah. unpublished PhD. dissertation, Univ. of Utah, Salt Lake City.
- Brown, W. S. & Parker, W. S. (1982). Niche dimensions and resource partitioning in a Great Basin desert snake community. In *Herpetological communities: a symposium of the Society of the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977*, 59-81. Scott, Jr., N. J. (ed). Wildlife Research Report, U.S. Fish and Wildlife Service.
- Brown, W. S. & Parker, W. S. (1984). Growth, reproduction and demography of the racer, *Coluber constrictor mormon*, in northern Utah. In *Vertebrate Ecology and Systematics—A Tribute to Henry S. Fitch*,

- 13–40. Seigel, R. A., Hunt, L. E., Knight, J. L., Malaret, L. and Zuschlag N. L. (Eds). Lawrence: Special Publication No. 10. Museum of Natural History, University of Kansas.
- Collins, J. T. (1991). A new taxonomic arrangement for some North American amphibians and reptiles. *Herpetological Review* **22**, 42–43.
- Conant, R. & Collins, J. T. (1991). *A field guide to reptiles and amphibians of eastern and central North America*. Boston: Houghton Mifflin Company.
- Cooper, Jr. W. E., Burghardt, G. M. & Brown, W. S. (2000). Behavioural responses by hatchling racers (*Coluber constrictor*) from two geographically distinct populations to chemical stimuli from potential prey and predators. *Amphibia-Reptilia* **21**, 103–115.
- Corn, P. S. & Bury, R. B. (1986). Morphological variation and zoogeography of racers (*Coluber constrictor*) in the central Rocky Mountains. *Herpetologica* **42**, 258–264.
- Cundall, D. & Greene, H. W. (2000) Feeding in snakes. In *Feeding: Form, function, and evolution in tetrapod vertebrates*, 293–332. Schwenk, K. (ed). San Diego: Academic Press.
- Fitch, H. S. (1963). Natural history of the racer *Coluber constrictor*. *Univ. of Kansas Publications of the Museum of Natural History* **15**, 351–468.
- Fitch, H. S. (1999). *A Kansas snake community: Composition and changes over 50 years*. Melbourne: Krieger Publishing Company.
- Fitch, H. S., Brown, W. S. & Parker, W. S. (1981). *Coluber mormon*, a species distinct from *C. constrictor*. *Transactions of the Kansas Academy of Science* **84**, 196–203.
- Greene, H. W. (1983). Dietary correlates of the origin and radiation of snakes. *American Zoologist* **23**, 431–441.
- Greene, H. W. (1984). Taxonomic status of the western racer, *Coluber constrictor mormon*. *Journal of Herpetology* **18**, 210–211.
- Gregory, P. T. (1983). Identification of sex of small snakes in the field. *Herpetological Review* **14**, 42–43.
- Gunzburger, M. S. (1999). Diet of the Red Hills Salamander *Phaeognathus hubrichti*. *Copeia* **1999**, 523–525.
- Hamilton, W. J. Jr. & Pollack, M. (1956). The food of some colubrid snakes from Fort Benning, Georgia. *Ecology* **37**, 519–526.
- Herzog, H. A. J. & Burghardt, G. M. (1974). Prey movement and predatory behavior of juvenile western yellow-bellied racers, *Coluber constrictor mormon*. *Herpetologica* **30**, 285–289.
- Klimstra, W. D. (1959). Foods of the racer, *Coluber constrictor*, in southern Illinois. *Copeia* **1959**, 210–214.
- Mushinsky, H. R., Hebrard, J. J. & Vodopich, D. S. (1982). Ontogeny of water snake foraging ecology. *Ecology* **63**, 1624–1629.
- Rodriguez-Robles, J. A., Bell, C. J. & Greene, H.W. (1999). Food habits of the glossy snake, *Arizona elegans*, with comparisons to the diet of sympatric long-nosed snakes, *Rhinocheilus lecontei*. *Journal of Herpetology* **33**, 87–92.
- Rodriguez-Robles, J. A., Mulcahy, D. G. & Greene, H.W. (1999). Feeding ecology of the desert nightsnake, *Hypsiglena torquata* (Colubridae). *Copeia* **1999**, 93–100.
- Schaefer, W. H. (1934). Diagnosis of sex in snakes. *Copeia* **1934**, 181.
- Shine, R. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* **138**, 103–122.
- Stebbins, R. C. (1985). *A field guide to western reptiles and amphibians*. Boston: Houghton Mifflin Company.

Accepted: 7.6.01

