Feeding Ecology of the California Mountain Kingsnake, *Lampropeltis zonata* (Colubridae)

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Based on stomach contents of museum specimens and published records (*n* = 51 prey items), *Lampropeltis zonata* eats lizards (37, 72.5%), squamate eggs (6, 11.8%), mammals (6), and birds (2, 3.9%). Juveniles feed on lizards, especially *Sceloporus* (spiny lizards) and *Eumeces* (skinks), whereas adults supplement their diet with squamate eggs and endothermic prey. Prey items are located by active foraging, usually swallowed head-first, and average 33% of snake mass. The diet of *L. zonata* overlaps substantially with that of several other species of sympatric, medium- to large-sized snakes in mesic western North American woodlands; it is narrower than that of the more widely distributed *L. getula*, and similar to that of allopatric, more closely related *L. alterna* and *L. pyromelana*.

THE discovery of patterns in the natural history of individual taxa ultimately leads to generalizations about ecological and evolutionary processes. Empirical studies of feeding, for example, underlie theoretical considerations of foraging (Hódar et al., 1996) and coevolutionary predator–prey dynamics (e.g., Brodie and Brodie, 1999; Downes and Shine, 1997). Diet data for related taxa can be analyzed in a phylogenetic context, then used to elucidate evolutionary divergence within a lineage (e.g., Lewis-Oritt et al., 2001; Schondube et al., 2001) or to estimate the trophic ecology of rare and unstudiable members of that clade (Greene, 1994). Given the immediate and broad implications of predator-prey interactions, our lack of information on trophic niche for many widespread and even common North American vertebrates calls for additional study.

The typically red, black, and yellow- or white-banded *Lampropeltis zonata* (California mountain kingsnake) is discontinuously distributed from southern Washington in the United States to northern Baja California, México; a population of black-and-white–banded snakes on South Todos Santos Island, off the Pacific Coast of Baja California, is sometimes recognized as *Lampropeltis zonata herrerae* or as a separate species, *Lampropeltis herrerae* (Zweifel, 1974; Hayes, 1975; Rodríguez-Robles et al., 1999c). *Lampropeltis zonata* typically reaches sexual maturity at a snout–vent length (SVL) of approximately 45 cm (Goldberg, 1995) and achieves an adult SVL of 50–80 cm, although one long-term captive attained 105.6 cm (McKeown and Morgan, 1996). The species usually inhabits mesic rocky canyons associated with coniferous forests and riparian woodlands, from barely above sea level on South Todos Santos Island and in Santa Cruz County, California, to elevations of approximately 2700 m in the Sierra Nevada of California (McGurty, 1988; Rodríguez-Robles et al., 1999c). California mountain kingsnakes are generally secretive and reportedly feed mainly on lizards (Zweifel, 1974; McGurty, 1988; Goldberg, 1995). No previous study has examined the feeding ecology of *L. zonata* in detail; hence, our goal here is to assess dietary variability in this species and estimate its ecological role as a predator.

MATERIALS AND METHODS

We examined 78 and 107 preserved specimens of *L. zonata* in the California Academy of Sciences, San Francisco (CAS) and Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), respectively. We checked for stomach contents through midventral incisions, avoiding only types and especially soft, brittle, or otherwise fragile specimens. We judged that in this case the relatively meager information to be gained from study of intestinal contents (e.g., it often would be impossible to determine number and size of prey) did not justify the necessary additional damage to museum specimens (cf. Saviozzi and Zuffi, 1997). Whenever possible, for each snake containing prey, we recorded SVL, minimum number of prey items, taxonomic identity of the prey, and direction of ingestion (inferred from prey orientation in the gut). We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly with paper towels. Weights and measurements of partially digested items were estimated by comparison with complete specimens from the nearest locality available in the MVZ. We conservatively regarded sets of squamate eggs, nestling mammals, and nestling birds in a snake as representing a single feeding

event and, thus, treated them as one item. We disregarded unidentifiable animal remains in two specimens (MVZ 24676 and MVZ 76765) and insects (probably from stomachs of prey lizards) in two others (MVZ 6263 and MVZ 54623).

Our dataset also incorporates published dietary records. We accounted for redundancy among literature records (e.g., Van Denburgh, 1922, with Van Denburgh, 1897; Cunningham, 1959, with Petrides, 1941) and between literature records (Grinnell and Storer, 1924; McGurty, 1988) and MVZ specimens. We excluded items that were eaten in captivity (i.e., *Thamnophis butleri* [Butler's gartersnake; Blanchard, 1921], *Eumeces skiltonianus* [western skink; Bogert, 1930], *Bipes* cf. *B. biporus* [Baja California mole lizard; CAS 138036]). Means are followed by standard deviations, and all *P*-values are two-tailed.

RESULTS

Twenty-eight *L. zonata* (SVL 24–71 cm, mean = 53.1 ± 12.7 cm, $n = 27$; mass 7–109.2 g, mean = 57.9 ± 31.4 g, $n = 24$), 15.1% of all specimens that we examined, contained 31 identifiable prey items. Adding to that sample 20 items for 19 snakes from the literature, 37 (72.5%) of 51 prey eaten by 47 *L. zonata* were lizards (i.e., squamate reptiles other than snakes and amphisbaenians), six (11.8%) were squamate eggs, six were mammals, and two (3.9%) were birds (Appendix 1); 43 (84.3%) were ectotherms and eight (15.7%) were endotherms. Of 25 items for which direction of ingestion was determined, 16 lizards and six mammals were swallowed headfirst (88%), and of the latter one was an adult, two were nestlings, and three were neonates; three neonate mammals, probably relatively small items, were eaten tail-first (12%).

Six *L. zonata* had ingested only squamate eggs, including sets of one, five, six (two records), and 10 eggs each. Thirty-three of 41 (80.5%) other *L. zonata* had recently eaten a single item. Of the eight specimens with multiple prey, four had taken two items each: two each ate two *Sceloporus occidentalis* (western fence lizard; Van Denburgh, 1897; MVZ 14386); one (MVZ 51706) ate two *Cnemidophorus tigris* (tiger whip-tailed lizard), and one (MVZ 71917) ate a *S. graciosus* (common sagebrush lizard) and an unidentified mammal. The first three specimens suggest that the behavior of *L. zonata* and/or of those particular prey species results in multiple captures of the same species within a relatively short time span, whereas the fourth demonstrates that an individual snake ate two
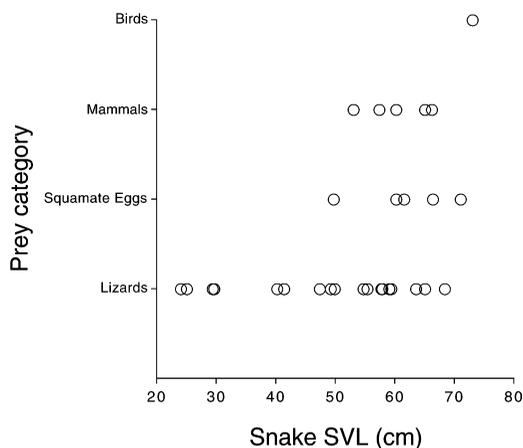

Fig. 1. Relationship between prey category and snake body size (SVL) in *Lampropeltis zonata* ($n = 30$).

prey types. Two *L. zonata* had taken three prey each, three *Peromyscus maniculatus* (deer mouse; MVZ 223159) and three *Empidonax oberholseri* (dusky flycatcher; Goodman and Goodman, 1976); one (MVZ 202496) had eaten five unidentified neonate mammals; and another one (MVZ 204991) preyed on an undetermined number of neonate mammals. Snakes that contained a single food item (SVL 24–71 cm, mean = 51.6 ± 13.7 cm, $n = 25$) and those that had eaten multiple prey (SVL 49.1–65 cm, mean = 57.8 ± 8.1 cm, $n = 3$) had similar body sizes, but our records of the latter were too few to detect any differences between these two groups. Differences in body size between *L. zonata* that preyed on lizards (SVL 24–68.3 cm, mean = 48.3 ± 13.8 cm, $n = 19$), squamate eggs (SVL 49.7–71 cm, mean = 61.8 ± 8 cm, $n = 5$), and mammals (SVL 53–66.1 cm, mean = 60.3 ± 5.4 cm, $n = 5$), were significant (ANOVA, $F = 3.23$, df = 2,26, $P = 0.04$), with the Games-Howell multiple comparison test indicating that pairwise differences between snakes that took lizards and those that ate squamate eggs and between serpents that consumed lizards and those that fed on mammals were significant (Fig. 1).

We estimated mass for 13 items eaten by *L. zonata*: one *Elgaria multicarinata* (southern alligator lizard), two *S. occidentalis* (from the same snake), one *Eumeces gilberti* (Gilbert's skink), three *P. maniculatus* (from the same snake), one *Sorex palustris* (water shrew), and five unidentified neonate mammals (from the same snake). Prey mass/predator mass ranged from 0.11 to 0.62 (mean = 0.33 ± 0.23); the relatively largest item was a 7.1 g *E. multicarinata* in an 11.5 g snake. A litter of five neonate rodents, each

TABLE 1.   MONTHLY FREQUENCY OF PREDATION ON DIFFERENT FOOD TYPES BY *Lampropeltis zonata*.

Prey type	Month								Total
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	
Lizards	1	—	6	8	5	—	—	1	21
Squamate eggs	—	—	1	1	3	—	—	—	5
Mammals	—	—	—	2	1	—	1	—	4
Birds	—	—	—	—	1	—	—	—	1
Total	1	—	7	11	10	—	1	1	31

weighing 1 g, would collectively amount to 10% of a 50 g California mountain kingsnake's mass (based on MVZ 202496), and a clutch of 10 squamate eggs each weighing 1 g (cf. Fitch, 1954) would collectively amount to 22% of a 45 g snake's mass (based on MVZ 93912).

Our ability to investigate geographic variation in food preferences across the range of *L. zonata* is hampered because this species has a limited distribution in Baja California, Oregon, and Washington (Storm and Leonard, 1995; Grismer, 2002). Our dietary records reflected this sampling bias, as 41 (93%) of the snakes with food were from California, compared with only two from Oregon and one from Baja California. However, we can investigate geographic variation in the diet of *L. zonata* in the context of three distinct, seemingly allopatric units within this species that have been identified by molecular genetic studies: a ''northeastern'' clade (composed of populations from the central and northern Sierra Nevada of California and Mount Hamilton, Santa Clara County, north to Washington), a ''coastal'' clade (occurring in the central California coast and the southern Sierra Nevada), and a ''southern'' clade (distributed from south of the Tehachapi Mountains in southern California to northern Baja California; Rodríguez-Robles et al., 1999c). Among the 44 snakes with food, 23 could be assigned to the northeastern clade, six to the coastal clade, and 14 to the southern clade. The frequencies of lizards, mammals, and squamate eggs consumed by snakes from the northeastern, coastal, and southern clades were statistically indistinguishable (16:3:4, 3:2:1, 13:0:0, respectively; $\chi^2 = 7.77$, df $= 4$, $P = 0.10$). Ten of 13 of the snakes from the northeastern clade that consumed lizards were adults, whereas 13 of 14 items in snakes from the southern clade were lizards, but we lack SVL for most of them and, thus, cannot assess whether they were mainly small individuals or adults that specialized on that prey type. Because the prey types commonly eaten by *L. zonata* in California (e.g., *Eumeces*, *Sceloporus*) also coexist with these snakes in Oregon, Washington, and/or Baja California (Storm and Leonard, 1995; Grismer, 2002), our conclusions about diet based primarily on stomach contents from California probably also apply to those peripheral regions from which we have little data.

There is evidently seasonal variation in the food habits of *L. zonata*. Monthly frequency of predation on different food types by California mountain kingsnakes indicates that lizards and squamate eggs are mainly eaten in spring and early summer (Table 1), a pattern consistent with a general decline in lizard activity in late summer (pers. obs.) and availability of squamate eggs only subsequent to the onset of adult activity.

DISCUSSION

Our findings indicate that *L. zonata* feeds mainly on lizards, occasionally on mammals, and only rarely on birds. Three factors suggest caution in interpreting these results. (1) Our sample is relatively small, perhaps reflecting infrequent collection of *L. zonata* (cf. Goldberg, 1995), as well as failure by some collectors to immediately preserve these attractive snakes, such that prey in their stomachs do not remain available for study. (2) Predation on endotherms by larger snakes (five of 22 items, 22.7%, from 21 snakes $\geq$ 45 cm SVL) may be more prevalent than our records indicate, because our largest specimen containing food (CAS-SU 1812, SVL 71 cm) was approximately 35 cm shorter than the maximum SVL known for *L. zonata* (105.6 cm; McKeown and Morgan, 1996) and/or because we have few records from summer and fall ($n = 10$), when endotherms are perhaps more frequently eaten than in spring. (3) Birds may be eaten under circumstances (e.g., high in trees) such that snakes are less likely to be collected, and avian prey is, therefore, poorly represented in stomachs of museum specimens (cf. Rodríguez-Robles, 1998). In the San Bernardino Mountains of southern California, Goodman and Goodman (1976) found

several dozen *L. zonata* climbing toward, or in the nests of birds, usually *E. oberholseri* or *Pipilo chlorurus* (green-tailed towhee); hence, birds perhaps are important prey in this region despite their low incidence (one of 14 items) in our southern clade sample. Alternatively, *L. zonata* may be seldom successful in its predatory attempts on birds, or else satiated snakes promptly retire to hidden refuges to reduce the likelihood of encountering a predator, which would also make them less likely to be collected. Additional data are obviously desirable to better elucidate ontogenetic, seasonal, and geographic variation in diet, but our findings nonetheless document several interesting aspects of the feeding biology of *L. zonata*.

Small California mountain kingsnakes eat mainly lizards, usually *Sceloporus* and *Eumeces*, whereas adults add squamate eggs, mammals, and birds to their diet. *Lampropeltis zonata* resembles many other colubrids by (1) switching from a juvenile diet of ectotherms to one that for larger individuals includes endotherms (e.g., Rodríguez-Robles et al., 1999a, and references therein), (2) consuming items that average 11–40% of predator mass (Rodríguez-Robles, 2002), and (3) typically eating prey head-first. Eggs are a potentially rich food source (Orians and Janzen, 1974), yet among western North American snakes predation on them is relatively uncommon and varies inconsistently with body size: squamate eggs are eaten only by adult *L. zonata* (SVL approximately 50–71 cm), by both juvenile and adult *Hypsiglena torquata* (desert nightsnake, SVL approximately 16–35 cm; Rodríguez-Robles et al., 1999d) and *Rhinocheilus lecontei* (long-nosed snake, SVL approximately 22–67 cm; Rodríguez-Robles and Greene 1999), and only by juvenile *Charina bottae* (rubber boa, SVL approximately 13–24 cm; Rodríguez-Robles et al., 1999b). The incidence of predation on nestlings by *L. zonata* (three of eight snakes containing endothermic prey, 37.5%) was higher than in some other colubrids that also eat mammals and birds (10 of 35, 28.6%, for the sympatric *C. bottae* [Rodríguez-Robles et al., 1999b], one of 50, 2%, for *Arizona elegans* [glossy snake; Rodríguez-Robles et al., 1999a] and zero of 35, for *R. lecontei* [Rodríguez-Robles and Greene, 1999]).

Direct observations confirm that California mountain kingsnakes hunt by actively foraging rather than by ambushing immobile prey. Wentz (1953) saw a *L. zonata* invade the nest of an *Oreortyx pictus* (mountain quail) in which there were three eggs, and when the snake was displaced several dozen meters it rapidly returned and began devouring one of the eggs.

Goodman and Goodman (1976) observed several *L. zonata* climbing trees and apparently using the mobbing behavior of adult birds to locate nests. *Lampropeltis zonata* frequents riparian habitats (McGurty, 1988), as do some of its prey species (e.g., *Sceloporus occidentalis*; Sabo and Power, 2002; *Sorex palustris*; Beneski and Stinson, 1987). A "young [*L. zonata*] male . . . on a sandy beach several meters from the river . . . appeared to be trailing a potential prey item and occasionally would probe its head and the first few centimeters of its body into the sand . . . " (Cranston, 1994:42). Some *S. occidentalis* females oviposit in sand under riverbank cobbles (J. L. Sabo, unpubl. data); thus, perhaps the snake Cranston watched was searching for lizard eggs. California mountain kingsnakes may also forage for squamate eggs in rock slides and rodent burrows, since several species of western North American reptiles oviposit in those microhabitats (e.g., Fitch, 1935; Brodie et al., 1969).

The diet of California mountain kingsnakes overlaps substantially with several other species of sympatric, medium- to large-sized snakes in mesic western North American woodlands. *Lampropeltis zonata* is parapatric or narrowly sympatric with the larger and more widely distributed *Lampropeltis getula californiae* (California kingsnake), adult SVL approximately 50–100 cm, Wright and Wright, 1957), but the latter generally occurs in more xeric habitats and at lower elevations than the former (Fitch, 1936; Stebbins, 1954; H. W. Greene, J. V. Vindum, and S.-M. Koo, unpubl. data). The two species overlap in diet to the extent that California kingsnakes occasionally eat *Sceloporus*, *Eumeces*, nestling mammals, and the eggs of ground-nesting birds (H. W. Greene, K. Wiseman, and D. Long, unpubl. data); unlike *L. zonata*, *L. getula* frequently eats other snakes, and one *L. getula* ate a *L. zonata* in nature (R. Staub, unpubl.). Other sympatric snake species with which *L. zonata* shares predation on *Sceloporus* include *Charina bottae* (Rodríguez-Robles et al., 1999b), *Masticophis lateralis* (striped whipsnake; Jennings, 1983), and juvenile *Crotalus oreganus* ([fide Ashton and de Queiroz, 2001] western rattlesnake; Fitch, 1949). Those same species at least occasionally eat rodents and birds, and there is one report of a *Thamnophis* sp. (gartersnake) attacking a *Sorex palustris* (Jackson, 1961), a prey species of *L. zonata* (Appendix 1).

Lampropeltis zonata is similar to the closely related *L. alterna* (gray-banded kingsnake) and *L. pyromelana* (Arizona mountain kingsnake) in frequently eating lizards, especially *Sceloporus* and also resembles the latter species by adding

mammals and occasionally birds to the adult diet. California mountain kingsnakes differ from other species of *Lampropeltis* and resemble a more distantly related lampropeltine, *Rhinocheilus lecontei*, in occasionally eating squamate eggs (see Rodríguez-Robles and de Jesús-Escobar, 1999 for phylogenetic analysis and dietary references). Perhaps information on oviposition sites for western North American squamates will eventually shed light on why various colubrids differ in the extent to which they eat squamate eggs and why *L. zonata* has diverged from its closest relatives in that respect.

Acknowledgments

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APPENDIX 1. PREY EATEN BY *Lampropeltis zonata.* ''Frequency'' refers to the frequency with which each prey item was consumed; groups of nestling birds or mammals in a stomach (*) were counted as one item for total count. Numbers in parentheses indicate the number of snakes that had ingested that particular prey type. Relatively high numbers of unidentified lizards and mammals reflect stomachs that contained only a few isolated scales or hair clumps with no cranial material, respectively.

Prey taxon	Frequency	% of total number of prey	Source
REPTILIA, Squamata			
Anguidae			
Elgaria multicarinata	1 (1)	2.0	Parham and Feldman, 2003
cf. *Elgaria* sp.	1 (1)	2.0	this study
Phrynosomatidae			
Sceloporus graciosus	8 (8)	15.7	this study; McGurty, 1988
Sceloporus occidentalis	6 (4)	11.8	this study; Fitch, 1936; Van Denburgh, 1897
Sceloporus sp.	5 (5)	9.8	this study; Cranston, 1994
Scincidae			
Eumeces gilberti	2 (2)	3.9	this study
Eumeces skiltonianus	6 (6)	11.8	this study, McGurty 1988
Eumeces sp.	3 (3)	5.9	this study
Teiidae			
Cnemidophorus tigris	3 (2)	5.9	this study
Unidentified lizard	2 (2)	3.9	this study
Squamate eggs	6 (6)	11.8	this study; Fitch, 1936
MAMMALIA			
Muridae			
Peromyscus maniculatus	3*(1)	2.0	this study
cf. *Peromyscus* sp.	1 (1)	2.0	Cranston, 1994
Soricidae			
Sorex palustris	1 (1)	2.0	this study
Unidentified mammal	1 (1)	2.0	this study
Unidentified neonate mammals	5*(1)	2.0	this study
Unknown number of unidentified neonate mammals	1 (1)	2.0	this study
AVES			
Tyrannidae			
Empidonax oberholseri	3*(1)	2.0	Goodman and Goodman, 1976
Turdidae			
Catharus ustulatus	1 (1)	2.0	Petrides, 1941
Total	51 (48)		