
FEEDING ECOLOGY OF A GENERALIST PREDATOR, THE CALIFORNIA KINGSNAKE (*LAMPROPELTIS CALIFORNIAE*): WHY RARE PREY MATTER

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Abstract.—We studied the feeding ecology of California Kingsnakes (*Lampropeltis californiae*) based on stomach contents of 2,662 museum specimens, 90 published records, and 92 unpublished observations. These snakes typically are diurnal, wide-foraging generalists and ingest prey head-first. Twenty-nine percent of 447 diet items were mammals, 29% were snakes, 25% were lizards, 11% were birds, 4% were squamate eggs, 1% were unidentified squamates, and 1% were amphibians. We detected no differences in diet based on kingsnake sex or color pattern, nor evidence of individual specialization. Rodents, lizards, and birds were eaten more frequently by larger individuals; snakes were eaten with similar frequency independent of predator size. Predation on mammals, birds, and lizards, but not snakes, was seasonally restricted. Kingsnakes from arid bioregions consumed more snakes, fewer rodents, and fewer lizards than did those from non-arid bioregions. Overall frequencies were similar for rodents and snakes, yet snakes accounted for 45% of prey biomass; among snakes, rattlesnakes comprised 24% by frequency and 37% of snake prey biomass and energy. Prey-predator mass ratios averaged 0.24 ± 0.19 (range 0.01–0.73; $n = 43$); a positive relationship exists between prey mass and snake mass, but larger snakes also consumed small prey items. Rattlesnakes, amounting to only 7% of overall diet and 16% of total biomass and energy value, are available throughout the active season and provide higher payoff per item than other diet types. Our findings thus provide a resolution to the paradox that this generalist predator is specialized (i.e., venom immunity) to feed on rattlesnakes, a rare prey type.

Key Words.—feeding ecology; geographic variation in diet; lampropeltinines; Liem's Paradox; nest predation; ontogenetic variation in diet; ophiophagy; specialist versus generalist predators.

INTRODUCTION

Natural diets are a core aspect of animal biology, and ideally their study would encompass at least three topics: (1) sources of taxonomic variation, including individual, ontogenetic, sex, seasonal, and geographic (e.g., Fitch 1960; Godley 1980; Kephart and Arnold 1982; Greene 1984; Rodríguez and Drummond 2000); (2) aspects relevant to conceptual questions, such as predator-prey size and shape relationships for behavior and functional morphology (e.g., Arnold 1993; Cundall and Greene 2000; Jackson et al. 2004; Vincent et al. 2006), and species composition and diet breadth for community ecology (e.g., Arnold 1972; Shine 1977; Greene and Jaksic 1983; Luiselli 2006; Steen et al. 2014a,b); and (3) possible pitfalls and methodological biases (e.g., Greene 1989; Branch et al. 1995; Rodríguez-Robles 1998;

Glaudas et al. 2017), especially as relevant to the first two topics. Meeting these goals for snakes, however, is hampered by their secretive behavior and infrequent feeding, such that most of what we know comes from regurgitated prey items and stomach contents of museum specimens (e.g., Fitch 1941; Greene and Oliver 1965; Shine 1977; Kephart and Arnold 1982; Greene 1984), augmented by innovations such as stable isotope analyses (e.g., Willson et al. 2010), videography (e.g., Putman and Clark 2015; Glaudas et al. 2017) and attention to social media (e.g., Layloo et al. 2017). With these complexities as backdrop, this sixth paper in a series addressing the feeding biology of North American lampropeltinine colubrids (Rodríguez-Robles and Greene 1999; Rodríguez-Robles et al. 1999; Rodríguez-Robles 2002; Greene and Rodríguez-Robles 2003; Greene et al. 2010) provides a detailed dietary analysis



FIGURE 1. A California Kingsnake (*Lampropeltis californiae*) from Calaveras County, California. (Photographed by Marisa Ishimatsu).

for the California Kingsnake (*Lampropeltis californiae*; a member of the *L. getula* complex; Fig. 1).

Lampropeltinines (Rodríguez-Robles and de Jesus-Escobar 1999; Pyron and Burbrink 2009a) comprise about 40 species of New World bull, gopher, and pinesnakes (*Pituophis*); corn, fox, and rat snakes (*Bogertophis*, *Pantherophis*, *Pseudelaphe*); glossy (*Arizona*), long-nosed (*Rhinocheilus*), and scarletsnakes (*Cemophora*); and kingsnakes, milksnakes, and the Short-tailed Snake (*Lampropeltis*). Within Colubridae, lampropeltinines diverged from Old World relatives via trans-Beringian vicariance, during the late Oligocene to early Miocene, about 24 million y ago (mya), and initially radiated in western North America (Rodríguez-Robles and de Jesus-Escobar 1999; Burbrink and Lawson 2007; Pyron and Burbrink 2009a); extant lampropeltinine genera were present by the mid-Miocene to early Pliocene (about 13–18 mya), and most living species were present prior to the Pleistocene (about 2 mya; Pyron and Burbrink 2009a). Among these often moderately large serpents, kingsnakes are renowned as predators on pitvipers (*Crotalinae*) and are immune to their venom (e.g., Weinstein et al. 1992); indeed, an early synonym for *Lampropeltis* was *Ophibolus* (snake morsel in Latin and Greek, Baird and Girard 1853: 82). Despite that notoriety and recent attention to broader biological questions with studies of *Lampropeltis* (e.g., Rodríguez-Robles and de Jesus-Escobar 1999; Pyron and Burbrink 2009b; Ruane et al. 2014), few detailed surveys of kingsnake diets exist (e.g., Klimstra 1959; Fitch 1999; Godley et al. 2017).

The California Kingsnake was long considered one of six subspecies of a transcontinental *Lampropeltis getula* (Blaney 1977; Krysko 2001; Krysko and Judd 2006), but Pyron and Burbrink (2009b,c), based primarily on mtDNA sequence data, recognized it as a distinct species within that complex; we therefore incorporate dietary data for specimens previously referred to *L. g. californiae* and *L. g. nigrita* (Supplemental Information). As such, the California Kingsnake is found from Oregon, USA, south to Cabo San Lucas in Baja California Sur, Mexico, on numerous islands in the Sea of Cortez, in the mainland Mexican states of Sonora and northern Sinaloa, and in much of Arizona, southern Nevada and Utah, and the four-corners region, USA (Fig. 2; Stebbins 2003; Pyron and Burbrink 2009c). It occurs from sea level to about 2,164 m, although elevational upper limits are lower on western slopes of the Sierra Nevada (914 m), in the southern Sierra Nevada (1524 m), in Arizona (1707 m), and in the Sierra San Pedro de Mártir in Baja California Norte (Welsh 1988; Grismer 2002). These often-common serpents inhabit grassland, desert, chaparral, woodland, coniferous forest, and agricultural areas (Grismer 2002; Stebbins 2003; Brennan and Holycross 2006; Drost, in press).

California Kingsnakes are generally described as feeding on snakes, lizards, turtles, birds and their eggs, and mammals (e.g., Nussbaum et al. 1983; Stebbins 2003; Brennan and Holycross 2006), although previously there have been no species-wide analyses of diets and available details are sparse. During 6 y of field research, Fitch (1949) recorded prey from four of 43 kingsnakes in

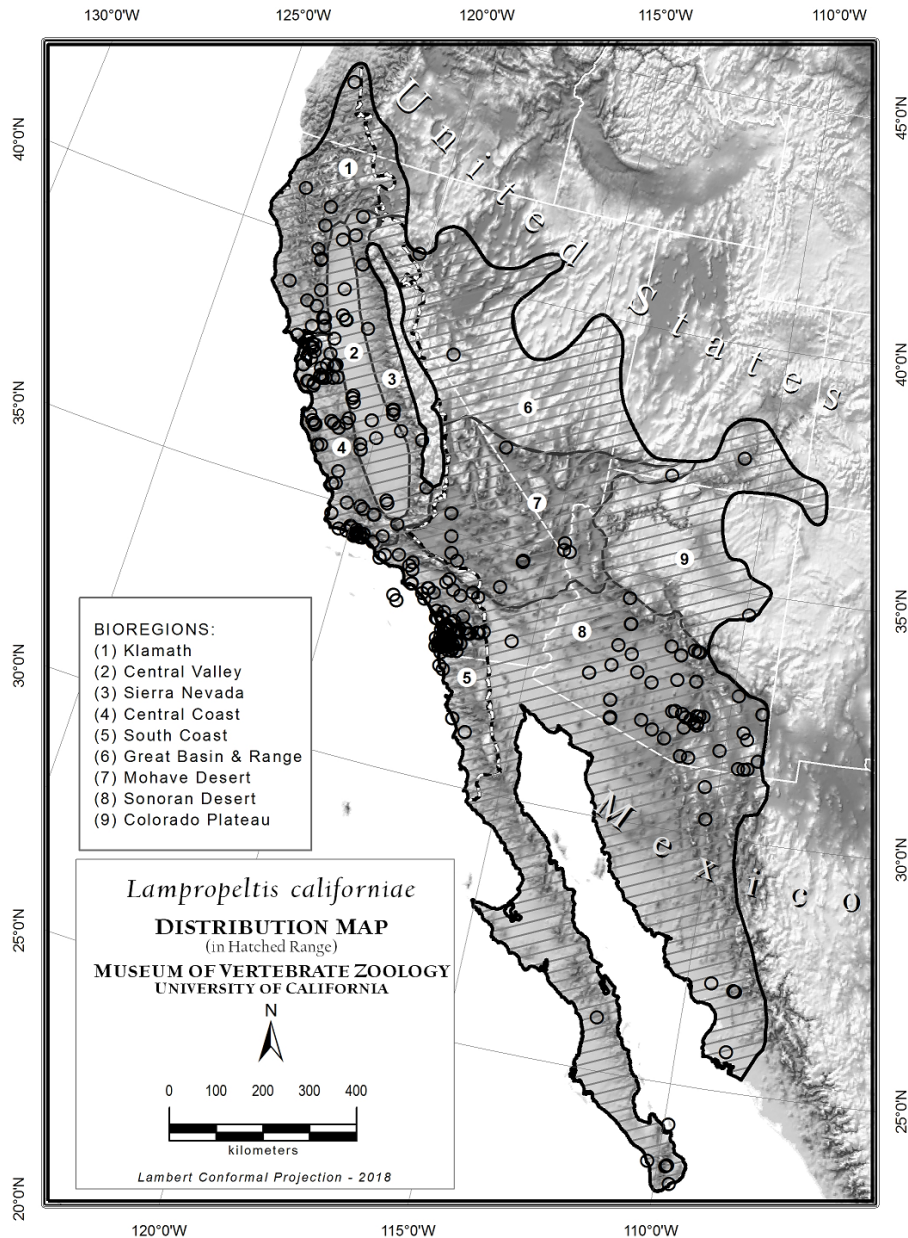


FIGURE 2. Distribution of *Lampropeltis californiae*, indicated by hatched area within solid line. Open circles represent localities of snakes with prey (n = 366); black-and-white dashed line represents division between the California Province and Arid Deserts regions.

the Sierra Nevada foothills of California, including two lizards, a snake, bird eggs, and an adult mouse. In two unpublished studies, Clark (1968) found seven snakes, bird eggs, a lizard, and young rodents in the stomachs of nine Mohave Desert California Kingsnakes, and Hansen (1982) recorded 18 lizards, 24 rodents, and one conspecific as prey in the Central Valley. Accordingly, we herein describe foraging behavior and analyze diet variation in California Kingsnakes, based upon stomach contents of museum specimens, published literature, and unpublished observations. Our goals are as follows: (1) analyze taxonomic, ontogenetic, individual,

sexual, morphological, seasonal, and geographic variation in diet; (2) summarize foraging behavior; (3) examine predator/prey size relationships; (4) explore evolutionary, ecological, functional morphological, and conservation implications of our findings; and (5) exemplify a comprehensive, species-centered study of snake feeding biology.

MATERIALS AND METHODS

We retrieved unpublished observations of California Kingsnakes with prey and foraging behavior from

archived field notes in the Grinnell-Miller Library at the University of California, Berkeley's Museum of Vertebrate Zoology (MVZ, abbreviations for museum collections from Leviton et al. 1980), the University of California's Hastings Natural History Reserve (HNHR, for 1938–1974), and the Laurence M. Klauber Library at the San Diego Museum of Natural History (SDSNH, for 1923–1959). To obtain additional data, we also examined the stomachs of 2,662 preserved California Kingsnake specimens in the California Academy of Sciences (CAS, 431 specimens), MVZ (432), Los Angeles County Museum of Natural History (LACM, 321), Arizona State University at Tempe (ASU, 146), University of Nevada at Las Vegas Barrick Museum of Natural History (UNLV, nine), University of California at Santa Barbara (UCSB, 266), SDSNH (751), Santa Barbara Museum of Natural History (SBMNH, 45), and University of Arizona at Tucson (UAZ, 261; Table 1; Supplemental Information).

Prey items in museum specimens were exposed by midventral incisions through the skin and stomach; we did not open types and fragile specimens. For snakes with prey, we recorded locality data, sex, snout-vent length (SVL \pm 1 mm), body mass (\pm 0.1 g), head length (\pm 1 mm, measured from the tip of the rostral scale to the retroarticular process of the right mandible), head width (\pm 1 mm, measured at the widest point on the head), and minimum number of items in the stomach. We identified prey items as precisely as possible based upon standard diagnostic characters (e.g., dentition, scalation, pelage), geographic range, and comparison with museum specimens. When possible, direction of ingestion was inferred from orientation in the stomach. We weighed snakes and intact prey after blotting and draining them briefly on paper towels to remove excess fluids. For 20 partially digested prey, we estimated their linear measurements and/or masses by comparison with conspecific specimens at CAS of similar size, from the nearest locality available. We derived estimates for prey taxon mass (see footnotes, Supplemental Information) from literature sources or specimens at CAS, and care was taken into account for predator SVL, ages of nestling birds, and average clutch sizes of birds.

We assumed that captured prey items that were abandoned as a result of disturbance by the observer (e.g., Banks and Farmer 1962) would otherwise have been consumed, and thus included them in our data set. We treated bird eggs and nestlings, rodent nestlings, and clutches of squamate eggs as single feeding events of clustered prey, rather than as multiple feeding events of the same prey type. We excluded as records general statements (e.g., Nussbaum et al. 1983), prey taken in captivity (e.g., Hoyer and Stewart 2000), and snakes we suspected were fed domestic mice prior to preparation as museum specimens (e.g., UAZ 49158; see Rodriguez-

Cabrera et al. 2017). We watched for redundancy among literature records (e.g., Fitch 1949 with Jaksic and Greene 1984), between museum specimens and literature records (e.g., MVZ 15964 and Compton 1933), between literature records and unpublished observations (e.g., Klauber 1997 and his field notes for 25 September 1938), and between unpublished observations and museum specimens (e.g., Robert C. Stebbins, field notes for 22 June 1990 and MVZ 215931). We were alert for biases arising from different data sources (Rodriguez-Robles 1998).

We georeferenced localities of California Kingsnakes with prey following Chapman and Wieczorek (2006), mapped them with ArcGIS 9.2 (Esri, Redlands, California, USA), and assigned each locality to one of nine bioregions: (1) Klamath; (2) Central Valley; (3) Sierra Nevada; (4) Central Coast; (5) South Coast; (6) Great Basin; (7) Mohave Desert; (8) Sonoran Desert; and (9) the Colorado Plateau (Welsh 1994; California Biodiversity Council. 2008. Bioregions of California. Available from <http://biodiversity.ca.gov>. [Accessed 15 October 2011]). For additional analyses, we combined these bioregions to form two broader categories, the California Province (Klamath + Central Valley + Sierra Nevada + Central Coast + South Coast) and Arid Deserts (Mohave Desert + Sonoran Desert + Great Basin +

TABLE 1. Sources of feeding records for the California Kingsnake (*Lampropeltis californiae*). Museum abbreviations are as follows (Leviton et al. 1980): CAS (California Academy of Sciences), MVZ (Museum of Vertebrate Zoology at the University of California, Berkeley), LACM (Los Angeles County Museum of Natural History), UCSB (University of California at Santa Barbara), SBMNH (Santa Barbara Museum of Natural History), SDSNH (San Diego Museum of Natural History), UNLV (University of Nevada at Las Vegas Barrick Museum of Natural History), ASU (Arizona State University at Tempe), UAZ (University of Arizona at Tucson).

Museum collections	# Specimens examined	# Snakes with prey (% with prey)	# Prey items
CAS	431	41 (10%)	45
MVZ	432	46 (11%)	55
LACM	321	24 (7%)	26
UCSB	266	21 (8%)	26
SBMNH	45	8 (18%)	9
SDSNH	751	44 (6%)	48
UNLV	9	2 (22%)	2
ASU	146	7 (5%)	7
UAZ	261	21 (8%)	26
Subtotal	2662	214 (8%)	244
Literature records		90	94
Unpublished field notes		33	44
Personal communications		59	65
Total		396	447

TABLE 2. Relative frequencies, estimated mass, and energy content from prey types consumed by the California Kingsnake (*Lampropeltis californiae*).

Prey Type	Frequency	Relative Frequency	Estimated Taxon Mass (g)	Relative Mass	Energy (cal)	Relative Energy
Snakes	129	0.29	5099	0.45	19937	0.49
Mammals	130	0.29	2912	0.26	11616	0.29
Lizards	111	0.25	1608	0.14	6287	0.15
Birds	50	0.11	1345	0.12	1927	0.05
Squamate eggs	16	0.04	139	0.01	222	< 0.01
Unid. Squamates	6	0.01	112	0.01	438	0.01
Amphibians	5	0.01	49	< 0.01	31	< 0.01
Total	447	1.00	11264	1.00	40459	1.00

Colorado Plateau). The Sonoran Desert bioregion was slightly extended to encompass southeast Arizona and all of Baja California Sur. We eliminated the Bay Delta, Modoc, Sacramento Valley, and San Joaquin Valley bioregions due to small sample size, and we replaced them with extensions of the Klamath, Central Coast, and Sierra Nevada bioregions; the Sacramento Valley, San Joaquin Valley, and inland portions of the Bay Delta bioregions were combined to form the Central Valley bioregion. For statistical analyses, we used single-factor ANOVA with Tukey's pairwise comparisons, regression analyses, and Chi-square tests. We rounded prey frequency values to the nearest whole percentage; other values given are means \pm one standard deviation (SD), and P-values are two-tailed ($\alpha = 0.05$).

RESULTS

Taxonomic variation in prey.—We recovered information on 447 prey items from 396 California Kingsnakes from museum specimens, published literature, unpublished field notes, and personal communications (Table 1). Of the 2,662 museum specimens we examined, 214 (8%; mean SVL = 65.5 ± 23.6 cm; range, 23.4–115.4 cm, $n = 202$; mean mass = 131.5 ± 110.2 g, range, 7.5–548 g, $n = 200$) contained 244 prey. We included 94 prey (from 90 snakes) from published literature, 44 prey (from 33 snakes) from unpublished field notes, and 65 prey (from 59 snakes) from personal communications.

One hundred-thirty (29%) of 447 prey eaten by California Kingsnakes were mammals (all but one rodents), 129 (29%) were snakes, 111 (25%) were lizards, 50 (11%) were birds, 16 (4%) were squamate eggs, six (1%) were unidentified squamates (lizards or snakes), and five (< 1%) were amphibians (Table 2; Fig. 3). Estimated prey biomass totaled 11,264 g (mean = 25.5 g/meal) and was comprised predominantly of snakes (45%), followed by mammals (26%), lizards (14%), birds (12%), unidentified squamates and their eggs (each 1%) and amphibians (< 1%). Estimated energy derived from prey biomass totaled 40,459

calories, comprised predominantly of snakes (49%), followed by mammals (29%), lizards (15%), birds (5%), unidentified squamates (1%), and squamate eggs and amphibians (each < 1%; Fig. 3). Ectothermic prey comprised 60%, 62%, and 67% in relative frequency, relative mass, and relative energy, respectively.

Of the 129 snakes consumed by California Kingsnakes, 83 (65%) were colubrids, 30 (24%) were rattlesnakes, nine (7%) were unidentified snakes, and five (4%) were Western Blind Snakes (*Rena humilis*; Supplemental Information). We found 83 individual colubrid snakes from at least 23 species in 14 genera including *Arizona*, *Chilomeniscus*, *Chionactis*, *Coluber*, *Diadophis*, *Hypsiglena*, *Lampropeltis*, *Masticophis*, *Phyllorhynchus*, *Pituophis*, *Rhinocheilus*, *Sonora*, *Thamnophis*, and *Trimorphodon*, which in total accounted for 56% of relative biomass and of energy among snake prey. The most frequently consumed species was the Gopher Snake (*Pituophis catenifer*; $n = 24$), accounting for 19% of all snake prey and 5% of all prey. Also, relatively common snake prey were Western Yellow-bellied Racers (*Coluber constrictor*), California Striped Whipsnakes (*Coluber lateralis*), and Coachwhips (*Coluber flagellum*), each accounting for

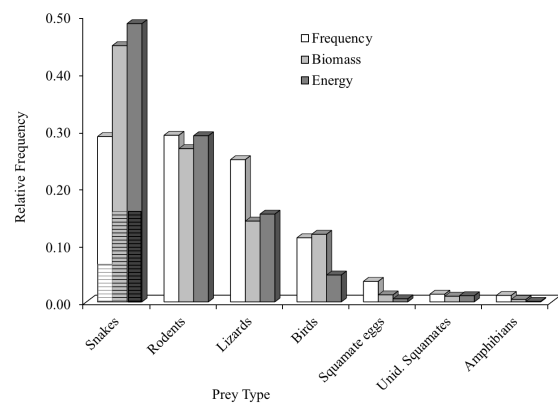


FIGURE 3. Relative frequencies of prey, biomass, and energy in California Kingsnakes (*Lampropeltis californiae*) from throughout their geographic range. Horizontal bars represent proportions of categories from rattlesnake prey.

5% of snake prey consumed. Rattlesnakes comprised 24% of the snake diversity consumed by California Kingsnakes and 37% of the relative biomass and energy among snake prey. For all prey combined, rattlesnakes comprised 7% of the diet, yet accounted for 16% total relative biomass and energy (Fig. 3). Thirty rattlesnakes of at least seven species were consumed, including the Pacific Rattlesnake (*Crotalus oreganus*; $n = 17$), Sidewinder (*C. cerastes*; $n = 3$), Great Basin Rattlesnake (*C. lutosus*; $n = 2$), Red Diamond Rattlesnake (*C. ruber*; $n = 2$), Mohave Rattlesnake ($n = 2$), Western Diamond-backed Rattlesnake (*C. atrox*; $n = 1$), Tiger Rattlesnake (*C. tigris*; $n = 1$), and one unidentified rattlesnake.

Of the 130 mammalian prey consumed by California Kingsnakes, 111 (85%) were rodents, 18 (14%) were unidentified mammals (hair in stomachs of museum specimens), and one (1%) was a lagomorph (Supplemental Information). Of the 111 rodent prey, 66 (59%) were murids (*Microtus*, *Mus*, *Peromyscus*, *Reithrodontomys*), 24 (22%) were unidentified, 11 (10%) were heteromyids (*Chaetodipus*, *Dipodomys*, *Perognathus*), eight were geomyids (7%; *Thomomys* sp.), one was a cricetid (1%; *Neotoma* sp.), and one (1%) was a sciurid (*Tamias* sp.). For rodent prey, murids had the largest estimated biomass (49%), followed by unidentified rodents (24%), geomyids (16%), heteromyids (9%), and sciurids (2%). We recorded 27 instances of kingsnakes raiding rodent nests, including those of eight voles (*Microtus* sp.), four deer mice (*Peromyscus* sp.), three pocket gophers (*Thomomys* sp.), four pocket mice (*Chaetodipus* sp., *Perognathus* sp.), four unidentified rodents, two kangaroo rats (*Dipodomys* sp.), one unidentified murid, and one chipmunk (*Tamias* sp.). Of these 27 rodent nest raids, two kingsnakes (CAS 182212 and LACM 102555) had each raided the nests of two rodent species. Overall, nest raids accounted for 24% of all rodent prey where age class could be determined (either as neonates or adults), while predation on adults accounted for the remainder.

Lizards ($n = 111$) consumed by California Kingsnakes encompassed 14 species in nine genera (Supplemental Information): 46 (41%) were phrynosomatids (mainly fence and spiny lizards, *Sceloporus* sp.), 29 (26%) were alligator lizards (*Elgaria* sp.), 18 (16%) were skinks (*Plestiodon* sp.), seven (6%) were unidentified, six (6%) were whiptails (*Aspidoscelis* sp.), two (2%) were Silvery Legless Lizards (*Anniella pulchra*), and one each (1%) of a Desert Night Lizard (*Xantusia vigilis*), a Desert Iguana (*Dipsosaurus dorsalis*), and a Gila Monster (*Heloderma suspectum*). Estimated relative biomass and energy for each taxonomic group are 38% phrynosomatids, 29% *Elgaria*, 19% *Plestiodon*, 7% unidentified lizards 7% other taxa. We recorded 23 lizard tails in stomachs of 22 museum specimens, of which nine, judging from appearance, were certainly autotomized; these included

four Southern Alligator Lizards (*Elgaria multicarinata*; SDSNH 32667 [two tails], UCSB 16062, UCSB 28212), one Western Skink (SDSNH 34785), two skinks (*P. skiltonianus* or Gilbert's Skink, *P. gilberti*; SDSNH 28314, MVZ 97114), one Yellow-backed Spiny Lizard (*Sceloporus uniformis*; LACM 2514), and one Side-blotched Lizard (*Uta stansburiana*; SDSNH 25700). We were less confident that 14 additional tails were autotomized, although they occurred in stomachs without more anterior scales or bones suggestive of a largely digested but consumed intact lizard; these included a Western Whiptail (*Aspidoscelis tigris*; LACM 64029), six Southern Alligator Lizards (CAS 190517; CAS 190534; CAS 192103; CAS-SU 11899; SBNHM 1081; KDW 187 [CAS]), three Western Skinks (CAS 190513; CAS 27282; CAS 64594), two skinks (*P. skiltonianus* or *P. gilberti*; LACM 2490; MVZ 21891), one Sagebrush Lizard (*Sceloporus graciosus*; CAS 203132), one Western Fence Lizard (*S. occidentalis*; UCSB Field No. SSS 23827), and one unidentified *Sceloporus* sp. (MVZ 204223). *Elgaria* and *Plestiodon*, for which 36% of our records are for tails only, have more massive tails relative to their bodies (after Vitt et al. 1977) than do sceloporine phrynosomatids, for which only 12% of our diet records are of autotomizable tails; nonetheless, autotomized tails of even those two genera provide low payoff/item compared to consumption of intact lizards ($F_{1,15} = 22.77$, $P < 0.001$).

Forty avian prey (80%) resulted from raids to active nests (eggs or nestlings), seven (14%) prey were nestlings or fledglings, and three (6%) were fledgling birds; no adult birds were recorded as prey. Of raids to active bird nests, 24 (60%) resulted in consumption of 1–4 nestlings, while 16 (40%) were depredations on 1–7 eggs. Estimated biomass for bird prey totaled 1344.8 g, with 61% from nestlings, 24% from eggs, and 14% from fledglings. Of the 50 birds consumed by California Kingsnakes, 29 (57%) were passeriforms, 11 (23%) were unidentified, seven (14%) were galliforms, and three (6%) were columbiforms (Supplemental Information). Galliforms included California Quail (*Callipepla californica*) and Domestic Chicken (*Gallus domestica*); one columbiform was a Mourning Dove (*Zenaidura macroura*). Eighteen (62%) of 29 passeriforms were emberizids, including Rufous-crowned Sparrow (*Aimophila ruficeps*), California Towhee (*Melospiza crissalis*), Spotted Towhee (*Pipilo maculatus*), Dark-eyed Junco (*Junco hyemalis*), Brown-headed Cowbird (*Molothrus ater*), and Lark Sparrow (*Chondestes grammacus*). The nests of seven additional passeriform species in seven families were raided at least once: Willow Flycatcher (*Empidonax traillii*), Western Bluebird (*Sialia mexicana*), thrasher (*Toxostoma* sp.), Least Bell's Vireo (*Vireo bellii pusillus*), Tricolored Blackbird (*Agelaius tricolor*), Orange-crowned Warbler

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TABLE 3. Multiple prey types consumed by 23 California Kingsnakes (*Lampropeltis californiae*). The abbreviation SVL = snout-vent length. See Table 1 for museum abbreviations.

Source	SVL (cm)	Sex	Stomach contents
UAZ 25104	113.7	—	1 <i>Crotalus</i> sp., 2 snake eggs
SDSNH 49966	106.1	♀	1 <i>Crotalus oreganus helleri</i> , 1 unidentified mammal
MVZ 204223	97.2	♂	1 <i>Sceloporus</i> sp., 1 <i>Coluber flagellum piceus</i>
MVZ 33771	96.2	♂	1 nestling <i>Melozone crissalis</i> , 1 adult <i>Peromyscus</i> sp., 1 squamate egg
MVZ 13847	89.3	♀	1 unidentified rodent, 1 passerine nestling bird, 1 squamate egg
Anguiano, M.P., pers. comm.	86.5	♀	1 <i>Coluber lateralis lateralis</i> , 2 unidentified neonate rodents
Fitch 1949	“adult”	—	7 <i>Callipepla californica</i> eggs, 1 <i>Reithrodontomys megalotis</i>
SDSNH 49472	82.3	♀	1 <i>Hypsiglena ochrorhyncha klauberi</i> , 2 <i>Chaetodipus</i> sp. neonates
CAS (Field no. KDW-187)	74.0	♂	1 <i>Pituophis catenifer catenifer</i> , 1 <i>Elgaria coerulea principis</i> or <i>E. multicarinata scincicauda</i>
LACM 132468	72.5	♀	1 <i>Sceloporus occidentalis longipes</i> , 10 squamate eggs
MVZ 74689	68.1	—	1 <i>Elgaria multicarinata webbiai</i> , 8 squamate eggs
UAZ 31294	67.3	♀	1 unidentified squamate, 1 squamate egg
UAZ 25068	64.6	♂	1 unidentified mammal, 1 <i>Chionactis occipitalis klauberi</i>
Anguiano, M.P., pers. comm.	63.5	♂	2 <i>Sceloporus occidentalis longipes</i> , 1 <i>Reithrodontomys megalotis</i>
UCSB 13207	56.7	—	1 unidentified lizard, 1 unidentified mammal
SBNHM 2324	55.8	♀	1 <i>Sceloporus occidentalis bocourti</i> , 6 squamate eggs
UCSB 9273	51.6	♂	1 <i>Elgaria multicarinata multicarinata</i> , 1 squamate egg
UAZ 56248	47.6	♀	1 <i>Elgaria kingii nobilis</i> , 5 squamate eggs
UAZ 46380	31.6	—	1 unidentified lizard, 1 unidentified mammal
Hansen 1982	—	—	1 <i>Sceloporus occidentalis</i> , 1 <i>Peromyscus californicus</i> , <i>Mus musculus</i> , or <i>Microtus californicus</i>
Lawrence M. Klauber, unpubl. field notes, 1926	—	—	1 unidentified rodent, 1 <i>Pituophis catenifer annectans</i>
Lawrence M. Klauber, unpubl. field notes, 26 June 1931	—	—	1 <i>Pituophis catenifer annectans</i> , 1 <i>Plestiodon skiltonianus</i> or <i>Plestiodon gilberti</i>
Lawrence M. Klauber, unpubl. field notes, 19 April 1938	—	—	1 unidentified lizard, 1 unidentified mammal

(*Oreothlypis celata*), and Domestic Canary (*Serinus canaria*).

Sixteen California Kingsnakes consumed sets of squamate eggs (range, 1–10; mean = 3.8, mode = 1; Supplemental Information). One kingsnake (MVZ 57603) consumed seven snake eggs, and two (CAS 170538 and UAZ 25104) consumed clutches of two snake eggs each. Two kingsnakes (MVZ 39158 and CAS 190526) consumed sets of four and eight lizard eggs, respectively, and 11 others consumed the clutches of either snakes or lizards. Five kingsnakes consumed adult lizards, including the Western Fence Lizard, Southern Alligator Lizard, and Madrean Alligator Lizard (*E. kingii*), in addition to sets of 1–10 squamate eggs, accounting for more than a third of all snakes that included squamate eggs as prey (Table 3). Four California Kingsnakes consumed five amphibians, including Clouded Tiger Salamanders (*Ambystoma mavortium nebulosum*; n = 2), a Red-spotted Toad

(*Anaxyrus punctatus*), and Pacific Chorus Frogs (*Pseudacris regilla*, n = 2; Supplemental Information).

Foraging behavior.—Field observations and stomach contents of museum specimens confirm that California Kingsnakes typically are diurnal and crepuscular, wide-searching foragers. We determined precise time of day for 26 predation events and categorized 25 others as having occurred in the daytime or nighttime. Forty-three (84%) of those 51 predation events took place during daytime, including 22 on snakes, 15 on bird nestlings or fledglings, three on lizards, and three on mammals. Eight events occurred at night, involving three amphibians and six snakes (including two rattlesnakes).

Scavenging and cannibalism are evidently rare among California Kingsnakes. We recorded three occurrences of feeding on road-kills (Gopher Snake, Shawn Silva, pers. comm.; Desert Night Snake,



FIGURE 4. A 7.5 g California Kingsnakes (*Lampropeltis californiae*; UAZ 48859) that consumed a 5.5 g Desert Nightsnake (*Hypsiglena chlorophaea chlorophaea*) as carrion, resulting in the greatest RPM value (0.733) from this study. (Photographed by Kevin Wiseman).

Hypsiglena chlorophaea; UAZ 48859, Fig. 4; Mohave Rattlesnake, Trevor Hare, pers. comm.). Lawrence Klauber (unpubl. field notes, 30 June 1934) recorded a banded California Kingsnake swallowing a striped conspecific, and Hansen (1982) found a juvenile female (36.5 cm SVL) that regurgitated a juvenile male of similar size. Two California Kingsnakes were found in a tightly coiled ball at Fort Ord, California, USA, but the cause and outcome of this event are unknown (Brian Delgado, pers. comm.).

Of 187 prey items for which we could determine direction of ingestion, 177 (95%) were swallowed head-first. Ten items, usually relatively small or attenuate, were swallowed tail or rump-first, including three neonate pocket mice (CAS 190516), neonate voles (MVZ 11434, MVZ 191325), a neonate pocket mouse (*Perognathus* sp.; LACM 102555), a neonate Pocket Gopher (LACM 102555), an adult kangaroo rat (*Dipodomys* sp.; MVZ 34635), one fledgling Least Bell's Vireo (Clark 2009), a Western Blindsnake (CAS 80759), a Silvery Legless Lizard (SDSNH 4819), and a Western Skink (*Plestiodon skiltonianus*; MVZ 229869).

Ontogenetic and individual variation in diet.—

Differences in body size (SVL) between California Kingsnakes that consumed different prey types were significant ($F_{5,256} = 4.03, P < 0.001$; Fig. 5). California Kingsnakes that consumed birds (SVL mean = 86.8 ± 13.2 cm; range, 58.7–107.7 cm, $n = 18$) were significantly longer than those that ate snakes (SVL mean = 66.7 ± 24.5 cm; range, 27.2–113.7 cm, $n = 61$), lizards (SVL mean = 56.4 ± 21.1 cm; range, 25.7–112.4 cm, $n = 81$), and amphibians (SVL mean = 33 ± 6.9 cm; range, 28.1–37.9 cm, $n = 2$); for all comparisons, Tukey HSD, $P \leq 0.05$); those that consumed squamate eggs (SVL mean = 73.8 ± 17.5 cm; range, 47.6–113.7 cm, $n = 15$) were significantly longer than those that ate lizards

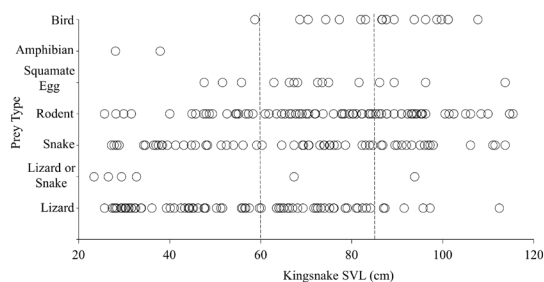


FIGURE 5. Relationship between prey category and snake body size (SVL) for 234 California Kingsnakes (*Lampropeltis californiae*) containing 268 prey items. Vertical dashed lines indicate age class subdivisions following Hansen (1982): juveniles = 20–60 cm snout-vent length (SVL); subadults = 60–85 cm SVL; and, adults ≥ 85 cm SVL.

(Tukey HSD, $P \leq 0.05$); those that consumed mammals (SVL mean = 76.1 ± 20.9 cm; range, 25.7–115.4 cm, $n = 85$) were significantly longer than those that ate lizards (Tukey HSD, $P \leq 0.05$), but similar in size compared to those that ate snakes, squamate eggs, and birds (Tukey HSD, $P > 0.05$). We also divided California Kingsnakes with body size data (234 snakes containing 268 prey) into three age class categories, following Hansen (1982): juveniles (20–60 cm SVL; $n = 98$ prey from 91 snakes), subadults (60–85 cm SVL; $n = 100$ prey from 89 snakes), and adults (≥ 85 cm SVL; $n = 70$ prey from 54 snakes). Relative frequencies of lizards decreased with greater SVL, mammals and birds increased with greater SVL, and snakes were consumed with similar frequency independent of California Kingsnake SVL (Fig. 6).

To evaluate short-term individual (as opposed to ontogenetic) dietary variation, we evaluated 23 California Kingsnakes with multiple prey types (e.g., lizards and snakes or birds and rodents) in their stomach content (Table 3). Of 378 California Kingsnakes for which we determined number of prey in the stomach, 310 (82%) contained single items, 34 (9%) two items, 14 (4%) three

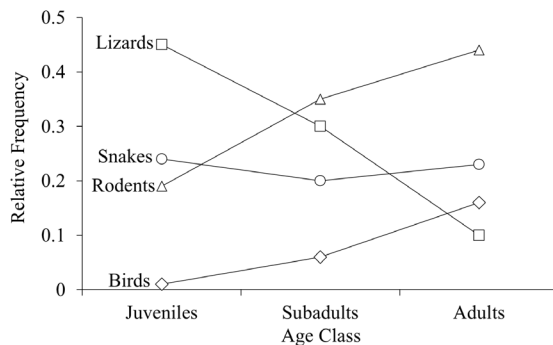


FIGURE 6. Ontogenetic change in relative frequencies of four major prey types for juvenile, subadult, and adult California Kingsnakes (*Lampropeltis californiae*) following Hansen (1982): juveniles = 20–60 cm snout-vent length (SVL); subadults = 60–85 cm SVL; and, adults ≥ 85 cm SVL.

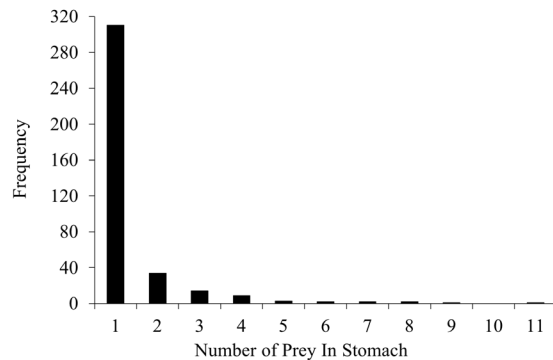


FIGURE 7. Figure 7. Frequency distribution of number of prey items taken by California Kingsnakes (*Lampropeltis californiae*; $n = 378$).

items, and nine (2%) four items. Eleven kingsnakes had consumed 5–11 items each, most of which resulted from nest raids to rodents, birds, or clutches of squamate eggs (Fig. 7). Twenty-one kingsnakes consumed two different prey types including lizards and rodents (6 kingsnakes), lizards and squamate eggs (5), rodents and snakes (5), lizards and snakes (2), snakes and squamate eggs (1), an unidentified squamate and a squamate egg (1), and bird eggs and a rodent (1). Two kingsnakes consumed three prey types each, including an unidentified rodent, one nestling passerine bird, and squamate egg in MVZ 13847, and an adult deer mouse, a nestling California Towhee, and a squamate egg in MVZ 33771 (Table 3). Nine kingsnakes consumed the same prey type twice (excluding clustered prey from nests, e.g., MVZ 39346 contained two Sagebrush Lizards and CAS 80761 two Western Blindsnakes). California Kingsnakes that had eaten multiple prey types (SVL mean = 74.9 ± 21.7 cm; range, 31.6–113.7 cm, $n = 18$) were similar in size than those that contained a single prey type (SVL mean = 64.8 ± 23.3 cm; range, 23.4–115.4 cm, $n = 215$; $F_{1,231} = 3.88$, $P = 0.077$).

Sexual and morphological variation in diet.—We determined the sex of 202 (64 females, 138 males) California Kingsnakes with prey. Females and males of all size classes did not differ significantly in SVL (females, mean = 63.8 ± 23.9 cm; range, 27.4–115.4 cm; $n = 64$; males, mean = 70 ± 20.7 cm; range, 26.5–114.7 cm; $n = 135$; $F_{1,197} = 3.89$, $P = 0.060$), mass (females, mean = 142.3 ± 120.1 g; range, 11–548 g, $n = 61$; males, mean = 148.6 ± 119.9 g; range, 7.5–831.1 g, $n = 131$; $F_{1,190} = 3.89$, $P = 0.737$), or head length (females, mean = 24.2 ± 6.4 mm, range, 14–36 mm, $n = 48$; males, mean = 25.1 ± 5.5 mm; range, 13–38 mm, $n = 120$; $F_{1,166} = 3.90$, $P = 0.383$). We also did not detect significant variation in proportions of lizards, snakes, or rodents consumed by females versus males of all three size classes combined (lizards: $\chi^2 = 0.463$, $df = 1$, $P = 0.496$; snakes: $\chi^2 = 1.112$, $df = 1$, $P = 0.291$; rodents: $\chi^2 = 0.832$,

$df = 1$, $P = 0.362$). Adult females and males also did not differ significantly in SVL (females, mean = 93.1 ± 8.4 cm; range, 85.3–115.4 cm, $n = 17$; males, mean = 98.1 ± 8.1 cm; range, 86.1–114.7 cm, $n = 29$; $F_{1,44} = 3.98$, $P = 0.052$), and we did not detect significant variation in proportions of lizards, snakes, or rodents consumed by adults of the two sexes (lizards: $\chi^2 = 0.04$, $df = 1$, $P = 0.856$; snakes: $\chi^2 = 0.53$, $df = 1$, $P = 0.467$; rodents: $\chi^2 = 0.74$, $df = 1$, $P = 0.393$).

To evaluate dietary variation among the two prevalent color pattern morphs (banded and striped) of the California Kingsnake, we analyzed prey composition within the geographic area where they co-occur, in upper coastal Baja California Norte, Mexico, and San Diego and Riverside counties, California (Klauber 1936; Zweifel 1982; Hubbs 2009). We were able to categorize by morphology 38 banded kingsnakes with 44 prey and 36 striped kingsnakes with 42 prey (three with intergrade patterns were coded as striped). There were no significant differences in proportions of rodents, snakes, or lizards taken between the two different pattern types within areas of sympatry (Table 4); there was no significant difference in size between groups (striped, mean = 65.7 ± 28.1 cm; range, 27.8–112.4 cm, $n = 24$; banded, mean = 58.7 ± 22.4 cm; range, 25.7–101.2 cm, $n = 22$; $F_{1,44} = 0.855$, $P = 0.360$).

Seasonal variation in diet.—We determined date of collection or observation, categorized as by month, for 346 food items from 300 kingsnakes; prey taken from throughout the species range were consumed during every month of the year, but 316 (91%) prey items were consumed between April and September (Fig. 8). The greatest proportion of prey were taken in May (27%), followed by June (19%), April (17%), July (15%), August (8%), and September (6%; Fig. 8). Snakes ($n = 99$) were consumed during every month of the year and 87% were consumed between April and September (Fig. 8). The greatest proportion of snakes consumed throughout the species range occurred in June (24%), a pattern also observed for South Coast Kingsnakes; in the Mohave Desert and Great Basin, snakes were consumed from May–June. Sonoran Desert Kingsnakes consumed most snakes in April and May followed by a relative reduction in snake consumption from June–July with a secondary peak of snake feeding in August and September (Fig. 9). Rodents ($n = 99$) were consumed throughout the year except for December and January, with the highest proportion (43%) taken in May (Fig. 8), a pattern also observed within the Central Coast, South Coast, and the Sonoran Desert bioregions (Fig. 9). Rodent nest raids ($n = 24$) occurred in every month except for March, August, and October. Twenty (83%) nest raids occurred from April–July, with 46% of these raids occurring in May. Lizards ($n = 84$) were consumed

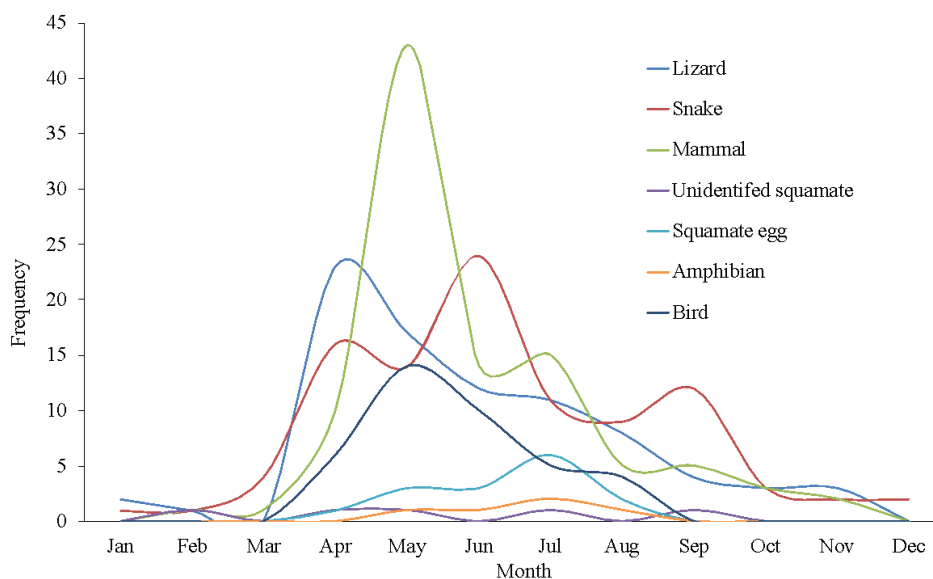


FIGURE 8. Seasonal variation in the diet of California Kingsnakes (*Lampropeltis californiae*; n = 346 prey items) from throughout the species range.

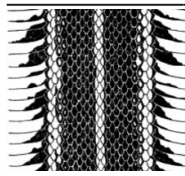
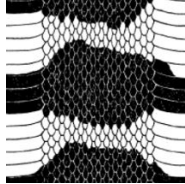
throughout the year except for March and December by kingsnakes range-wide with the highest proportion taken in April (26%) and May (20%). This general pattern of higher proportions of lizards taken in April was observed in the South Coast and Central Coast bioregions, but not in the Sonoran or Mohave Desert (Fig. 9). Seasonally restricted prey, including eggs and nestlings of birds (n = 39) and squamate eggs (n = 15), were consumed from April to August. Bird eggs and nestlings were taken most often in May (36%), while squamate eggs were most often consumed in July (40%; Fig. 9).

Geographic variation in diet.—We georeferenced 366 California Kingsnakes containing 415 prey and

assigned them to one of nine bioregions. We assigned an additional 19 snakes with 21 prey to bioregions but lacked sufficient locality data for georeferencing (Fig. 2). We could not assign seven snakes containing eight prey items to a specific bioregion.

California Kingsnakes from the Arid Deserts consumed a greater proportion of ectotherms (71%; 79/112) than those from the California Province (56%, 182/324; $\chi^2 = 7.11$, $df = 1$, $P = 0.008$). Kingsnakes from the Arid Deserts consumed a greater proportion of snakes (47%, 53/112) than those from the California Province (22%, 71/324; $\chi^2 = 26.33$, $df = 1$, $P = < 0.001$). Kingsnakes from the Sonoran Desert, Mohave

TABLE 4. Number of prey taken by sympatric striped (n = 36) and banded (n = 38) California Kingsnakes, *Lampropeltis californiae* (illustrations from Klauber 1936).

Pattern Type		Number of Prey					Total	
		Lizards	Rodents	Snakes	Squamate eggs	Unidentified squamate		Bird eggs or nestlings
	Striped	13	13	9	1	1	5	42
	Banded	12	9	13	1	0	9	44

$\chi^2 = 3.42$, $df = 6$, $P = 0.6207$

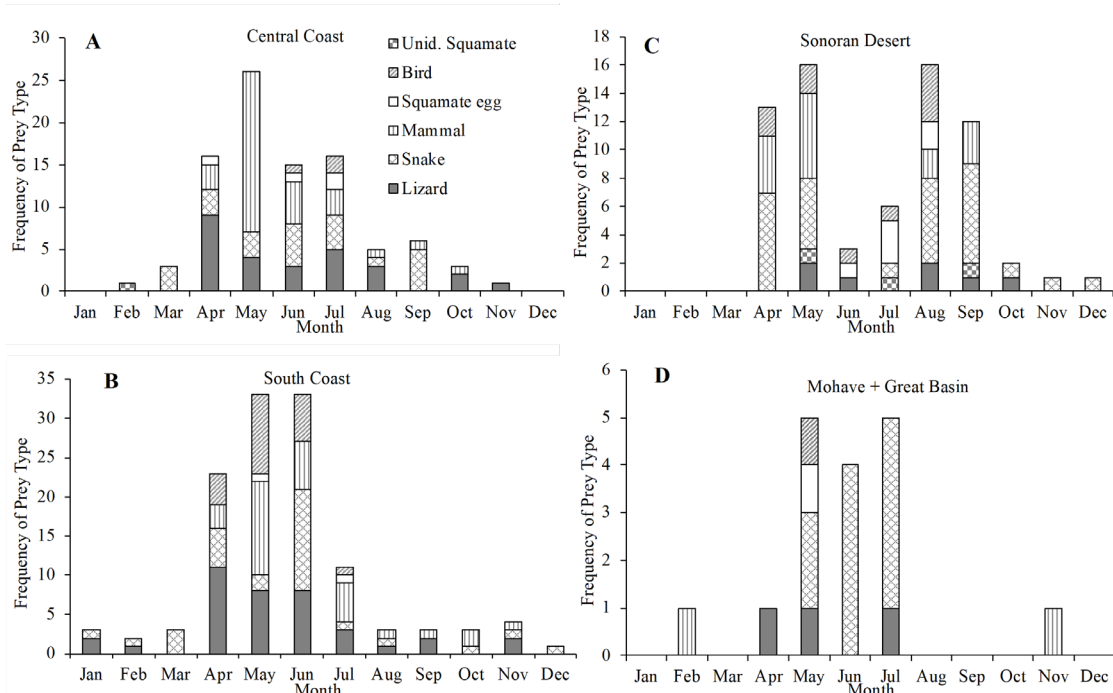


FIGURE 9. Geographic and seasonal variation in the diet of California Kingsnakes (*Lampropeltis californiae*): (A) Central Coast bioregion (n = 93); (B) South Coast bioregion (n = 123); (C) Sonoran Desert bioregion (n = 73); and (D) Mohave + Great Basin bioregions (n = 17).

Desert, and Great Basin bioregions consumed a greater proportion of snakes (33/80, 14/25, and 5/5, respectively) in comparison to kingsnakes from other bioregions ($\chi^2 = 49.11$, $df = 7$, $P < 0.001$). Kingsnakes from the Sonoran Desert consumed significantly more snakes proportionately than those from the Mohave Desert ($\chi^2 = 15.75$, $df = 1$, $P < 0.001$), and all of our prey (n = 5) recorded from the Great Basin Desert were snakes (Table 6).

California Kingsnakes from the California Province consumed a greater proportion of rodents (33%, 108/324) than those from the Arid Deserts (18%, 20/112; $\chi^2 = 9.64$, $df = 1$, $P = 0.002$). California Kingsnakes from both provinces did not differ significantly in body size (Arid Deserts, mean SVL = 64.4 ± 22.9 cm; range, 27.8–113.7 cm; n = 66; California Province, mean SVL = 66.9 ± 23.6 cm; range, 23.4–115.4 cm, n = 168; $F_{1,232} = 3.88$, $P = 0.474$). Kingsnakes from the Central Valley consumed a higher proportion of rodents (53%, 32/60) compared to those from all other bioregions ($\chi^2 = 29.57$, $df = 21$, $P < 0.001$), especially the Sonoran Desert (20%, 16/80), Mohave Desert (12%, 3/25), and Great Basin Desert (0%, 0/5). California Kingsnakes from the Arid Deserts consumed significantly fewer lizards (12%, 13/112) than those from the California Province (30%, 97/324; $\chi^2 = 14.91$, $df = 1$, $P < 0.001$), and kingsnakes from the Sonoran Desert consumed a smaller proportion of lizards compared to those from all other bioregions. Kingsnakes from the Central Valley consumed a slightly higher proportion of lizards (35%; 21/60) compared to

those from the South Coast (30%, 41/135; $\chi^2 = 4.77$, $df = 1$, $P = 0.029$), Mohave Desert (16%; 4/25; $\chi^2 = 4.08$, $df = 1$, $P = 0.043$), and Great Basin (0%; 0/5; $\chi^2 = 4.96$, $df = 1$, $P = 0.026$).

Predator-prey size relationships.—We detected a positive relationship between California Kingsnake mass and prey mass (adjusted $r^2 = 0.414$, $F_{1,41} = 30.7$, $P < 0.001$; Fig. 10). Relative prey mass (prey mass/predator mass; RPM) values averaged 0.24 ± 0.19 (range, 0.01–0.73; n = 43), which included the mass of 20 prey items estimated by comparison with conspecifics at CAS. Eighteen of 20 kingsnakes with RPM values > 0.2 contained snakes (Fig. 11). The highest RPM value was 0.733, from a 7.5 g juvenile (UAZ 48859) that contained a road-killed Desert Nightsnake (*Hypsiglena*

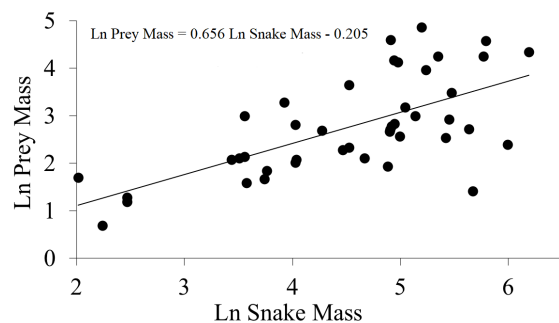


FIGURE 10. Log_n-transformed prey mass (g) as a function of snake mass (g) in 42 California Kingsnakes, *Lampropeltis californiae* (adjusted $r^2 = 0.414$, $F_{1,41} = 30.72$, $P < 0.001$).

chlorophaea chlorophaea; Fig. 4; Table 5). Larger California Kingsnakes sometimes ate absolutely, but not relatively, heavier prey (Fig. 10); the lower limit of prey mass did not increase with snake mass (adjusted $r^2 = 0.15$, $F_{1,41} = 8.40$, $P = 0.006$), demonstrating that larger individuals continued to sometimes eat relatively small prey: one adult (MVZ 42404; 289.1 g) contained a juvenile Gopher Snake (about 4.1 g, RPM = 0.014), another (CAS 161393; 399.2 g) a juvenile Pacific Rattlesnake (about 11 g, RPM = 0.028), and several kingsnakes weighing > 300 g had eaten relatively tiny squamate eggs. Relative prey length ratios (prey total length/kingsnake SVL) values averaged 0.53 ± 0.37 (range, 0.05–1.37, $n = 38$), including 17 prey lengths that were estimated by comparison with conspecific specimens at CAS (Table 5). Five specimens contained prey that ranged from 100–137% of kingsnake SVL, all of which were snake prey, including three California

Striped Whipsnakes (Fig. 12), one Yellow-bellied Racer, and a Desert Nightsnake (Fig. 4; Table 5).

DISCUSSION

Taxonomic variation in prey.—Kingsnakes are renowned for eating other serpents, especially rattlesnakes. Native Americans in the Okefenokee Swamp of Georgia, USA, believed that the Eastern Kingsnake did not “deliberately search out poisonous snakes in particular, but rather was the enemy of every species of snake” (Wright and Bishop 1915: 169), and likewise, we documented California Kingsnakes consuming at least 23 species of colubrids (in 14 genera) and seven species of rattlesnakes; however, we have no records of predation on species in several sympatric genera, including (rubber boas, *Charina* sp.; rosy boas, *Lichanura* sp.; patch-nosed snakes,

TABLE 5. Highest relative prey mass (RPM; prey mass/kingsnake mass) values and corresponding length ratios (LR; total prey length/kingsnake SVL) from 23 California Kingsnakes (*Lampropeltis californiae*). Prey types are: S = snake; L = lizard; M = mammal; A = amphibian; * = multiple prey item. See Table 1 for museum abbreviations.

Source	Prey Type	Prey	RPM	LR
UAZ 48859	S	<i>Hypsiglena chlorophaea chlorophaea</i>	0.733	1.137
MVZ 215931	S	<i>Coluber lateralis eurynanthus</i>	0.718	1.371
M.P. Anguiano, pers. comm.	S	<i>Coluber lateralis lateralis</i>	0.571	1.354
CAS (Field no. KDW-187)	S*	<i>Pituophis catenifer catenifer</i>	0.547	0.993
	L*	<i>Elgaria multicarinata</i> or <i>E. coerulea</i>	0.185	—
MVZ 193343	S	<i>Coluber constrictor mormon</i>	0.529	1.004
CAS 44166	S	<i>Coluber constrictor mormon</i>	0.431	0.894
CAS 207161	S	<i>Pituophis catenifer catenifer</i>	0.415	0.829
MVZ 4908	S	<i>Crotalus oreganus oreganus</i>	0.362	0.697
	S	<i>Pituophis catenifer catenifer</i>	0.104	0.513
M.P. Anguiano, pers. comm.	S	<i>Coluber lateralis lateralis</i>	0.333	1.277
CAS 190525	S	<i>Thamnophis</i> sp.	0.305	0.794
UAZ 32923	S	<i>Pituophis catenifer deserticola</i>	0.298	0.448
Staub et al. 2006	S	<i>Lampropeltis zonata</i>	0.282	—
CAS 27281	L	<i>Uta stansburiana elegans</i>	0.280	0.382
LACM 138155	S	<i>Hypsiglena ochrorhyncha ochrorhyncha</i>	0.258	0.686
MVZ 204223	S*	<i>Coluber flagellum piceus</i>	0.252	0.807
	L*	<i>Sceloporus</i> sp.	0.046	—
MVZ 229464	S	<i>Arizona elegans eburnata</i>	0.246	0.824
ASU 13891	S	<i>Sonora semiannulata semiannulata</i>	0.242	0.159
M.P. Anguiano, pers. comm.	S	<i>Coluber lateralis lateralis</i>	0.219	1.225
	M	2 neonate rodents	0.045	—
LACM 122103	A	<i>Pseudacris regilla</i>	0.213	0.050
SDSNH 11702	S	<i>Pituophis catenifer annectans</i>	0.206	0.487
UCSB 25306	M	<i>Thomomys bottae</i> , adult	0.137	—
	M	<i>Thomomys bottae</i> , young $n = 4$	0.033	—
M.P. Anguiano, pers. comm.	M	<i>Chaetodipus fallax</i>	0.155	—
CAS 203132	L	<i>Sceloporus graciosus</i>	0.147	0.225

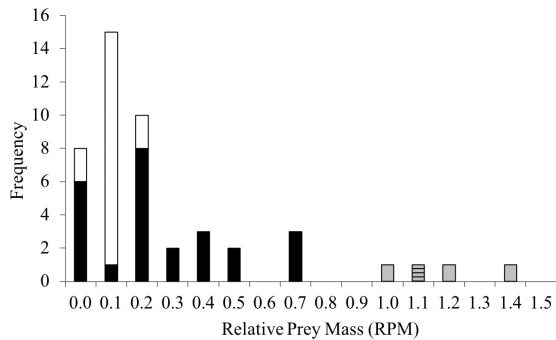


FIGURE 11. Frequency distribution of relative prey mass values from California Kingsnakes, *Lampropeltis californiae* (n = 43; black bars = snake prey; white bars = non-snake prey). Banded gray bar = completely digested snake prey; solid gray bars = regurgitated snake prey from captive trials from Jackson et al. (2004).

Salvadora sp.; hook-nosed snakes, *Gyalopion* sp.; vinesnakes, *Oxybelis* sp.; and sharp-tailed snakes, *Contia* sp.), nor on black-headed snakes (*Tantilla* sp.) or hog-nosed snakes (*Heterodon* sp.), which are known prey for other kingsnake species (Clark 1949; Palmer and Braswell 1995; LaDuc et al. 1996). Some of these taxa might be missing because of non-overlapping habitat preferences, rarity, and/or small diet samples from areas of sympatry; other species perhaps avoid predation by chemosensory recognition of California Kingsnakes, defensive behavior, or differential use of habitat, all of which deserve further scrutiny. Common Garter Snakes (*Thamnophis sirtalis*) chemosensorily distinguish snake-eating *Pituophis* and *Coluber* from non-ophiophagous *Pituophis* and *Heterodon* (Weldon 1982); most naïve hatchling Pinesnakes (*P. melanoleucus*) avoid chemical trails of kingsnakes in Y-maze experiments, and those that followed trails reduced crawling speed and increased tongue-flick



FIGURE 12. In 1990, Gary Beeman was radiotracking this Alameda Whipsnake (*Coluber lateralis euryxanthus*; MVZ 215930) and found that this 180 g California Kingsnake, *Lampropeltis californiae* (MVZ 215931), had consumed it, resulting in a RPM value of 0.71. The total length of the whipsnake (115 cm) is 137% greater than the snout-vent length of the kingsnake, made possible by the Accordion-folding of the whipsnake; note the hairpin loop near the tail of the whipsnake (see Jackson et al. 2004). (Photographed by Kevin Wiseman).

rates (Burger 1989). A Coastal Rosy Boa (*Lichanura trivirgata roseofusca*) from Cabrillo National Monument was found in a tightly coiled ball with its head tucked inside, while a California Kingsnake repeatedly attacked it without success (Carlton Rochester, pers. comm.), a behavior that might explain why rosy boas have not been recorded as prey for California Kingsnakes. Captive California Kingsnakes will consume Northern Rubber Boas (*Charina bottae*) and were suspected as important predators of this species where they co-occur (Hoyer and Stewart 2000), but we found no evidence of this. We did not record Southwestern Speckled Rattlesnakes (*C. pyrrhus*), Black-tailed Rattlesnakes (*C. molossus*), or Baja California Rattlesnakes (*C. enyo*) as prey, likely due to small sample sizes from within areas of sympatry (in captivity Speckled Rattlesnakes were killed and eaten; Klauber 1972, pp. 1099). We also did not record the Sonoran Coralsnake (*Micruroides euryxanthus*) as prey, although Eastern Kingsnakes (*L. getula*) and

TABLE 6. Number of prey taken by California Kingsnakes (*Lampropeltis californiae*) from nine bioregions.

Bioregion	Ectotherms					Endotherms		Total
	Snakes	Lizards	Unid. squamates	Sq. eggs	Amphibian	Mammals	Birds	
California								
Klamath	6	4	1	1	—	5	—	17
Central Valley	3	21	—	1	—	32	3	60
Central Coast	25	27	1	4	1	34	5	97
South Coast	33	41	1	3	1	33	23	135
Sierra Nevada	4	4	—	—	—	4	3	15
Arid Deserts								
Mohave Desert	14	4	—	1	—	3	3	25
Sonoran Desert	33	9	3	6	3	16	10	80
Great Basin	5	—	—	—	—	—	—	5
Colorado Plateau	1	—	—	—	—	1	—	2
Total	124	110	6	16	5	128	47	436



FIGURE 13. A fatal encounter between a California Kingsnake, *Lampropeltis californiae* (SDSNH 39987) collected in 1949 by E.D. Price in Ramona, California, and a gravid Blainville's Horned Lizard (*Phrynosoma blainvilli*), whose head spines had completely pierced through the skin of the kingsnake, killing both animals. (Photographed by Kevin Wiseman).

Speckled Kingsnakes (*L. holbrooki*) consume Harlequin Coralsnakes (*Micrurus fulvius*; Carr 1940; Clark 1949).

Rodents were the primary mammalian prey taken by California Kingsnakes, and with the exception of *Mus* and *Reithrodontomys*, these snakes raided nests of all rodent genera recorded in their diet. An even larger diversity of rodent species and their young likely are consumed, given the frequent use of burrows, cracks, and other underground refugia by this serpent (Hansen 1982; Anguiano and Diffendorfer 2015). Linsdale and Tevis (1951) observed California Kingsnakes sheltering in nests of Dusky-footed Woodrats (*Neotoma fuscipes*), and suspected that they regularly consumed the young; however, we found only a single record of a California Kingsnake that had consumed a woodrat neonate. Squirrels and chipmunks (Sciuridae) are often abundant within the range of California Kingsnakes but evidently rarely eaten. A California Kingsnake from southern Nevada had consumed two young chipmunks (Clark 1968), and Walker (1946) claimed that California Ground Squirrels (*Otospermophilus beechyii*) are eaten. Most adult sciurids likely are too bulky for California Kingsnakes to ingest, and depredation of young might be precluded by protective parents, who aggressively mob and even kill prowling Gopher Snakes (Fitch 1949; Owings and Coss 1977). Hansen (1982) noted that California Ground Squirrels were common within the 56-ha study area where he tracked 354 individual California Kingsnakes, but densities were lower near the colonies of squirrels. Moreover, Pacific Rattlesnakes and Gopher Snakes only consume young squirrels once they have ventured out of the burrow, at which point those rodents are too large for most California Kingsnakes to consume (Fitch 1949; Donald Owings, pers. comm.). One adult (105 cm SVL) ingested a baby Desert Cottontail (*Sylvilagus audubonii*), a non-rodent

mammalian prey available only to larger California Kingsnakes, whereas sympatric, wider-gaped species such as Gopher Snakes and rattlesnakes more readily engulf bulky rabbits (Rodriguez-Robles 2002; Phil Rosen, pers. comm.). Insectivores (shrews and moles) were not recorded as prey in California Kingsnakes, but perhaps they are eaten occasionally because Black Kingsnakes (*L. nigra*) and Speckled Kingsnakes consume them (Byrd and Jenkins 1996; unpubl. data).

Although diverse lizards are sympatric with California Kingsnakes across its range, relatively few species are eaten; California Kingsnakes prey mostly upon species of *Sceloporus*, *Elgaria*, and *Plestiodon*, only occasionally on others. Sympatric lizard genera not recorded in their diet include *Coleonyx*, *Phyllodactylus*, *Sauromalus*, *Gambelia*, *Crotaphytus*, *Callisaurus*, *Cophosaurus*, *Holbrookia*, *Uma*, *Urosaurus*, *Petrosaurus*, and *Phrynosoma* (but see Fig. 13). Most of these genera are xeric-adapted and might avoid significant predation by California Kingsnakes by divergent diel activity patterns or because they use different, often rocky microhabitats. Likewise, Zweifel and Lowe (1966) suspected that California Kingsnakes only occasionally take Desert Night Lizards because they are rarely found underneath the fallen limbs and trunks of Joshua Trees (*Yucca brevifolia*) preferred by these lizards, and that species was only recorded once as prey in Nevada (Clark 1968). Tree lizards (*Urosaurus* sp.) similarly might avoid predation by California Kingsnakes due to their arboreal habits (Vitt and Ohmart 1975). Other lizards employ antipredator behaviors that might deter snakes, including chemosensory recognition (Banded Geckos, *Coleonyx variegatus*, Dial et al. 1989; Desert Iguana, Bealor and Krekorian 2002, 2006; Gray-checked Whiptail, *Aspidoscelis dixonii*, Punzo 2007; Mexican Beaded Lizard, *Heloderma horridum*, Balderas-Valdivia and Ramirez-Bautista 2005), defensive inflation (Common Chuckwalla, *Sauromalus ater*; Prieto and Sorenson 1975; Deban et al. 1994), reduction of activity and body movement rates (Desert Grassland Whiptail, *A. uniparens*, Eifler et al. 2008), flight behavior (Zebra-tailed Lizard, *Callisaurus draconoides* and the Greater Earless Lizard, *Cophosaurus texanus*, Bulova 1994; Eastern Collared Lizard, *Crotaphytus collaris*, Husak 2006), keratophagy, and the use of communal latrines (Banded Geckos; Mitchell et al. 2006). The formidable head spines of Horned Lizards (*Phrynosoma*) might preclude predation by California Kingsnakes (Fig. 13). At the San Joaquin Experimental Range in California, Blainville's Horned Lizards (*P. blainvilli*) were determined to be moderately common in grassy areas, but not eaten by any snakes, including California Kingsnakes (Fitch 1949). Southern Alligator Lizards, however, are frequently attacked by California Kingsnakes despite antipredator behaviors that include tail-biting, mouth gaping, and biting. In response to

an attack by a snake, alligator lizards sometimes bite their own tails or hindlimbs, becoming a more awkward potential meal (Compton 1933; Rodgers and Fitch 1947; Bowker 1987; Arnold 1993); these lizards were captured and eaten in about 20 min by captive Alameda Whipsnakes (*Coluber lateralis euryxanthus*), but took up to 115 min when they employed the tail-biting behavior (Swaim 1994). A captive California Kingsnake did not attempt subsequent attacks on an adult alligator lizard living in the same cage after being bit during an initial predation attempt (Vitt et al. 1977).

Another effective anti-predator behavior employed by many lizards is autotomizing the tail, and all species preyed upon by California Kingsnakes, other than the Gila Monster, can do so (Etheridge 1967). Vitt et al. (1977) and Jaksic and Greene (1984) reported high tail-break frequencies for Western Fence Lizards (45.5%), Southern Alligator Lizards (69.2–74%), and Western Skinks (62%), but those lost tails resulted from failed attempts by a suite of predator species rather than only California Kingsnakes (Schoener 1979; Jaksic and Greene 1984), as well as perhaps breakage due to intraspecific aggression (Tinkle and Ballinger 1972; Parker and Pianka 1973; Jaksic and Fuentes 1980; Schoener and Schoener 1980). Granting that tail-break frequencies might also be affected by species, sex, age, season, elevation, and latitude (e.g., Turner et al. 1982), we found a non-significant relationship with predation frequencies on lizard species consumed by California Kingsnakes (adjusted $r^2 = 0.3809$, $F_{1,4} = 1.845$, $P = 0.162$; Fig. 14). Our observations from museum specimens containing tails thus confirm that for several prey species, autotomy facilitates their escape from California Kingsnakes as well as reduces the payoff/encounter for those predators. Although bite force increases with lizard body size (Anderson et al. 2008), the fact that autotomized tails provide uniformly small meals suggests that for the snakes they amount to consolation prizes rather than deliberately less risky alternatives to subduing intact lizards.

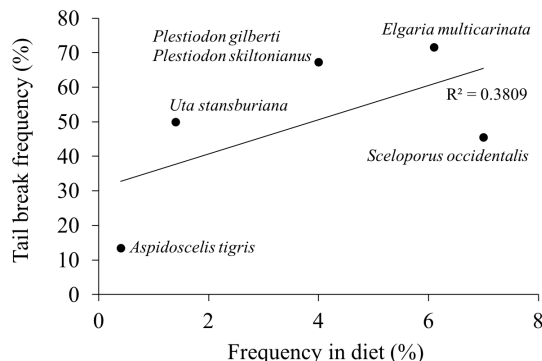


FIGURE 14. Frequency of lizard species preyed upon by California Kingsnakes (*Lampropeltis californiae*) in relation to tail-break frequencies reported in the literature.

California Kingsnakes raid bird nests during the breeding season, often taking eggs and nestlings (24% and 61% of bird biomass, respectively) but rarely fledglings. Given the wide habitat preferences of California Kingsnakes and their ability to climb up to at least 6 m, a much larger diversity of bird species likely are eaten than we report here. More than half of bird species consumed nest on or near the ground, ground nesters account for > 75% of bird prey identified to species level, and 61% of all passeriform prey were emberizid sparrows. Beyond prey in our sample, Braden et al. (1997) suspected that California Kingsnakes were important nest predators of California Gnatcatchers (*Polioptila c. californica*), Lawrence Klauber (unpubl. field notes, 14 June 1943) noted that a striped California Kingsnake was killed in a pigeon (*Columba livia*) nest, and Bowles (1910) observed a female Anna's Hummingbird (*Anna calypte*) mobbing a California Kingsnake that was in the center of a large wild rose bush. At Hastings Reservation, a California Kingsnake with a conspicuous lump in its belly was in a chicken coop (Jean M. Linsdale, unpubl. field notes, 16 June 1945), and another climbed up a bush into the nest of a Lazuli Bunting (*Passerina amoena*) that had been raided a month earlier (Jean M. Linsdale, unpubl. field notes, 3 July 1948). The diversity of birds consumed by California Kingsnakes might be limited by gape, because their eggs and nestlings are bulky prey for many snakes (Cundall and Greene 2000; Gartner and Greene 2008; see below), and larger birds might prevent successful nest raids by mobbing or attacking the predator.

Squamate eggs were found in 16 California Kingsnakes and accounted for 4% of prey. Five California Kingsnakes contained adult lizards (Western Fence Lizards, Southern Alligator Lizards, and a Madrean Alligator Lizard) in addition to sets of squamate eggs (range, 1–10), perhaps reflecting (1) depredation of a set of eggs with their nest-guarding adult; (2) depredation of eggs with a female during oviposition; and/or (3) depredation of a gravid female lizard and subsequent digestion, such that eggs separated from her body. Southern Alligator Lizards and Madrean Alligator Lizards guard their eggs throughout incubation (Greene et al. 2006; Mulroy and Wiseman 2012), making the first scenario especially plausible. Similar chemical cues might be used by snakes to locate both squamates and their eggs (de Queiroz and Rodriguez-Robles 2006), so perhaps California Kingsnakes detect and depredate ovipositing lizards. A similar behavior has been observed in Eastern Kingsnakes and Speckled Kingsnakes, which evidently seek out ovipositing turtles and eat their freshly laid eggs (Knight and Lorraine 1986; Brauman and Fiorillo 1995; Winne et al. 2007). Alternative 3 is also possible, as we have observed that shells of squamate eggs in snake gut contents often

appear to be undigested, and indeed some snakes that mainly eat squamate eggs have specialized dentition for slicing the shells and releasing their contents (e.g., Gardner and Mendelson 2003; Huang et al. 2011).

With regard to more rarely taken prey types, amphibians comprised < 1% of the total diet of California Kingsnakes, although perhaps juveniles consume them more often, especially at night. A captive California Kingsnake ate the tail of a California Slender Salamander (*Batrachoseps attenuatus*) and died an hour later (Cunningham 1959). Turtle eggs have not been recorded in the diet of California Kingsnakes, although Stebbins (2003) stated that small turtles are eaten, perhaps because closely related kingsnake species consume eggs of box turtles (*Terrapene* sp.; Jenkins et al. 2001), mud turtles (*Kinosternon* sp.; Wright and Bishop 1915; Tennant 1984; Knight and Lorraine 1986), Painted Turtles (*Chrysemys picta*, Wright and Bishop 1915), and sliders (*Trachemys* sp.; Tamarack and Doherty 1993; Winne et al. 2007; Godley et al. 2017). Apparent lack of predation upon turtle eggs in California Kingsnakes might reflect lower turtle abundance and diversity in western North America (Ernst et al. 1994; Stephens and Wiens 2003), and indeed Holland (1994) and Ashton et al. (1997) suspected California Kingsnakes as a nest predator of Western Pond Turtles (*Actinemys [Emys] marmorata*); however, this has yet to be observed.

Foraging behavior.—California Kingsnakes are often underground, in mammal burrows and nests (Linsdale and Tevis 1951; Wong 1982; Anguiano and Diffendorfer 2015), but also are skilled climbers and have been observed as high as 6 m above ground in willow trees (Dennis Strong, pers. comm.). When active terrestrially, they crawl at average speeds of 1.3 m/min (range, 3.3–11.2 m/min) for males and 1.1 m/min (range, 0.3–2.6 m/min) for females (Hansen 1982), that is, approximately one total length per minute. During above-ground forays, California Kingsnakes at HNHR tongue-flicked while investigating burrows, soil cracks, man-made structures, rock piles and woodpiles, as well as when entering nests of woodrats (*Neotoma* sp.). These movement bouts often were punctuated with long periods of immobility, usually in vegetation, with the head tilted upwards and occasional tongue-flicking. California Kingsnakes rely upon chemical and visual stimuli to locate prey with the former evidently more important based upon an adult male that had gone completely blind yet continued to successfully forage with above average mass for his size (Hansen 1982). Prior to ingestion, most prey are subject to powerful constriction, using lateral coils of the anterior trunk. Death results from cardiac arrest, circulatory arrest, and suffocation (Moon 2000; Penning and Moon 2017).

Although additional quantitative data would be desirable, observations of hunting behavior and dietary variation confirm with a level of evidence available for few other serpents that California Kingsnakes are wide-foraging, often diurnal, generalist predators on terrestrial vertebrates, mainly snakes, lizards, mammals, and birds. Like many other snakes, they typically swallow all but unusually small and/or elongate prey head-first, presumably for reasons of safety and efficiency (e.g., Greene 1976; Rodríguez-Robles et al. 1999; Rodríguez-Robles 2002). Hungry California Kingsnakes probably rarely ignore size-appropriate items, as predicted by foraging theory (e.g., Arnold 1993; Huey and Pianka 2007) and implied by our findings on diet variation: within each of four main taxonomic prey types, diverse species are eaten and at least occasionally taken throughout the active season. Multiple prey types are found in individual stomachs, and adult California Kingsnakes continue to prey upon small items (also see below). Prey species are likely taken roughly in proportion to seasonally variable encounter rates, although these snakes do adopt particular hunting tactics (e.g., for arboreal bird nests), suggesting that they also seek out specific prey types. Scavenging by California Kingsnakes is evidently rare but has been documented in at least 35 species of snakes (DeVault and Krochmal 2002), including Eastern Kingsnakes, which occasionally consume dead snakes and fledgling birds (Brown 1979; Durso et al. 2010). Similarly, cannibalism in wild California Kingsnakes is rare: Hansen (1982) and Anguiano (2008) observed temporal staggering of surface activities by individual California Kingsnakes and suspected this reduced the risk of cannibalism, and Burger et al. (1991) reported that hatchling Eastern Kingsnakes can distinguish conspecific chemical trails, avoiding them in y-maze experiments. Cannibalism is also rarely observed in related kingsnakes such as Black Kingsnakes (Jenkins et al. 2001) and Eastern Kingsnakes (Winne et al. 2007).

California Kingsnakes facilitate consumption of bird eggs and nestlings by defensive body bridging, nestling pinning, and egg or nestling displacement (Fig. 15). Defensive body bridging behavior against adult birds was observed twice during nest raids, in response to mobbing by Orange-crowned Warblers (Katie Langin, pers. comm.) and California Quail (Jean M. Linsdale, unpublished field notes, 29 May 1945); Hansen (1982) saw similar defensive body bridging behavior by a copulating male California Kingsnake in response to an intruding male. These snakes also pin nestlings (Davis 1960; Morrison and Bolger 2002a), which would likely secure mobile prey and reduce force-fledging, as observed during video surveillance of the nest of a Willow Flycatcher (Paradzick et al. 2000). Egg displacement



FIGURE 15. Foraging behaviors of California Kingsnakes (*Lampropeltis californiae*) during bird nest depredations: (A) egg or nestling displacement; (B) defensive body bridging; and, (C) nestling pinning. Note all three behaviors involve the use of a body coil while simultaneously consuming an egg or nestling; all three behaviors have been observed while parent birds mobbed a kingsnake. (Illustration by Kevin Wiseman).

was seen during depredation of a Mourning Dove nest (Scott Durst, pers. comm.), similar to when a Speckled Kingsnake displaced one nestling dove inside the crook of a body coil while simultaneously consuming another (Facemire and Fretwell 1980). Perhaps this behavior also functions like pinning, to secure mobile prey while parent birds attempt to defend the nest.

Ontogenetic and individual variation in diet.—Like many serpents, including sympatric Gopher Snakes (Rodríguez-Robles 2002) and Pacific Rattlesnakes (Sparks et al. 2015), California Kingsnakes experience an ontogenetic shift in diet: juveniles consume a high proportion of lizards, eat fewer lizards and more rodents and birds as they grow to adult size, and take snakes as prey throughout their lives. That dietary shift, shown by our range-wide analysis, also characterized a Central Valley population in which California Kingsnakes < 60 cm SVL ate primarily lizards, whereas only larger

individuals often ate rodents (Hansen 1982). This overall ontogenetic pattern, including that diets are individually more diverse with increasing size (90% of snakes containing multiple prey types were > 50 cm in SVL), likely is influenced by certain effects of prey shape for a gape-limited predator.

Snake food items can be large in two ways with respect to diameter and mass, thereby defining four prey shape types, each with distinctive cost-benefit implications (Greene 1983; Cundall and Greene 2000; Vincent et al. 2006): Type I prey are relatively small in diameter and mass, therefore can be diverse in taxonomy and shape, require neither adaptations to subdue nor large gape to ingest, and provide low payoff/item; Type II prey (e.g., relatively heavy earthworms and snakes) are elongate and do not require large gape, can be large in mass if they can be subdued, and provide high payoff/item; Type III prey (e.g., relatively heavy eggs and rodents) are heavy and bulky, require large gape, and if they can

be subdued, provide high payoff/item; and Type IV prey (e.g., sunfish [Centrarchidae] and well-feathered birds) are bulky in some but not all cross-sectional dimensions, such that for a snake with equivalent gape, they are less massive, cost less to subdue, and provide less payoff/item than a heavier Type III prey.

For California Kingsnakes of all sizes, across all four major taxonomic prey categories, snakes and elongate lizards (e.g., Southern Alligator Lizards), provide the highest payoff/item and indeed are eaten throughout the lives of individuals; moreover, longitudinal extension of the esophagus and stomach, caudal displacement of the pylorus, and accordion-packing of prey facilitate ingestion of these Type II items even by juvenile California Kingsnakes (Jackson et al. 2004). Conversely, larger snakes have absolutely larger gapes and all but the smallest birds and mammals are too large for consumption by small California Kingsnakes (unlike species with relatively greater gapes, e.g., Pough and Groves 1983; Cundall and Greene 2000; Rodriguez-Robles 2002), so only larger California Kingsnakes can diversify their diet in terms of prey shapes. That adult California Kingsnakes occasionally feed on Type I items and otherwise probably take prey in proportion to encounter rates (see above) implies that handling costs are small and payoffs/item large compared to search costs (e.g., Godley 1980; Arnold 1983). Therefore, for a foraging California Kingsnake, if a potential prey item can be subdued and consumed, no matter how small, it should be taken.

Sexual and morphological variation in diet.—As was the case for the Central Valley population of California Kingsnakes that Hansen (1982) studied, those with prey in our range-wide sample did not differ significantly in adult size between sexes (for males SVL, mean = 101.9 cm SVL, maximum = 131.5 cm, n = 89; for female SVL, mean = 101.1 cm, maximum = 129.5 cm, n = 64). Given lack of sexual dimorphism in body size and thus probably head length (a crude predictor of gape; Houston and Shine 1993), the lack of dietary differences between males and females is unsurprising. We expected, nonetheless, that because male California Kingsnakes have larger home ranges than females and search long distances for mates (Hansen 1982; Anguiano 2008), over short time spans they might encounter and consume a wider variety of prey types, a prediction not supported by our observations on stomachs containing multiple prey types and therefore implying that both sexes are equally opportunistic.

In some areas California Kingsnakes are polymorphic, and especially so in southern California and adjacent Baja California, where strikingly different banded and

striped color patterns co-occur with approximately equal frequencies in males and females; intermediate color patterns are rare and restricted to males (Hubbs 2009). Although color pattern polymorphisms are not uncommon among snakes (e.g., Neill 1963; Cox and Davis Rabosky 2013; Santos et al. 2017) and the genetics underlying this classic example have been reasonably well studied (e.g., Klauber 1936, 1939; Zweifel 1981), ecological mechanisms that maintain it remain incompletely understood. Both morphs occur together at some sites, and proportions of banded, striped, and intermediate snakes across San Diego County are 60%, 37%, and 3%, respectively; striped California Kingsnakes, however, increase to 50–80% in coastal (historically moister) areas, whereas relatively fewer striped individuals are found in mountains and desert foothills and they are absent from open desert (Klauber 1936; Zweifel 1982; Hubbs 2009). Because the morph frequencies vary with habitat and intermediates are rare, as well as the fact that striped vs. ringed patterns generally are associated with different locomotor escape profiles for snakes (e.g., Jackson et al. 1976; Pough 1976; Brodie 1989), disruptive selection by predators provides a plausible explanation for this polymorphism (Mather 1955; Zweifel 1982; Rueffler et al. 2006). Conversely, although syntopic California Kingsnakes of both morphs would experience similar prey availabilities and potentially could diverge in diet, feeding differences between pattern types is rare among snakes (e.g., Blood Pythons, *Python brongersmai*, Shine et al. 1998). Our data confirm that striped and banded California Kingsnakes are similar in consumption frequencies for the four main taxonomic prey types, thus strengthening the alternative hypothesis of a habitat-driven antipredator function for this polymorphism.

Seasonal and geographic variation in diet.—For snakes with generalist diets, seasonal (e.g., Klimstra 1959; Greene 1984; Rodriguez and Drummond 2000; Holycross and Mackessy 2002; Greene and Rodriguez-Robles 2003) and geographic (e.g., Rodriguez-Robles and Greene 1999; Holycross and Mackessy 2002; Rodriguez-Robles 2002; Hamilton et al. 2012) variation are likely common, albeit poorly understood. Presumably they reflect, respectively, interactions between activity patterns of snakes and their potential prey, themselves influenced by temperature and humidity (e.g., Hansen 1982; Gibbons and Semlitsch 1987; Lillywhite 1987; Brown and Shine 2002; Krysko 2002), and differences in absolute prey availability (e.g., Arnold 1993; Capizzi et al. 1995; Luiselli 2006; Halstead et al. 2008). For each type of variation, results from range-wide analyses of California Kingsnakes are consistent with more site-specific studies, suggesting that they likely are typical

for the species, and available evidence suggests some explanation for the patterns we observed.

The seasonal distribution of predation in our study correlates closely with surface activity patterns of California Kingsnake populations from the south coast (Anguiano and Diffendorfer 2015) and Central Valley (Hansen 1982; Fig. 16) of California, although skinks, a neonatal deer mouse, and snakes taken between December and February confirm that foraging can continue during the presumed inactive period of California Kingsnakes. Similar unimodal seasonal activity patterns pertain to Eastern Kingsnakes in the southeastern U.S. (Gibbons and Semlitsch 1987; Linehan et al. 2010; Godley et al. 2017) and Desert Kingsnakes (*L. splendida*) in New Mexico (Price and LaPointe 1990), and potential bimodal seasonal activity by California Kingsnakes and some Eastern Kingsnakes in Florida are presumably affected by changes in day length, mean high temperatures, and/or precipitation (Krysko 2002). Three of four main taxonomic prey types for California Kingsnakes are at least somewhat seasonally restricted, presumably because natural history attributes make them less vulnerable during parts of the year. As predicted by Vitt et al. (1977), predation on semi-fossorial Western and Gilbert's Skinks was greatest (65% of our records) during their March-May peak of surface breeding activity (Rodgers and Fitch 1947; Fitch 1949). Conversely, Western Fence Lizards and Southern Alligator Lizards are surface-active longer and behaviorally more conspicuous than skinks (Fitch 1940; Rodgers and Fitch 1947), thus preyed upon by California Kingsnakes with greater overall frequency and throughout a longer seasonal period. Rodent nest raids occurred primarily from April-July, with most in May, coinciding with peak California Kingsnake surface activity (Hansen 1982; Anguiano and Diffendorfer 2015). Nests of year-round-breeding California Voles were raided most often, although peak breeding in winter, when California Kingsnakes are inactive (Greenwald 1956; Hansen 1982), probably decreases effects of predation. Prairie Vole (*Microtus ochrogaster*) breeding in Illinois also peaks in winter, when Prairie Kingsnakes (*Lampropeltis calligaster*) and Fox Snakes (*Pantherophis vulpinus*) are hibernating, and experimental exclusion of snakes increased juvenile vole survival, leading to larger social groups (Klimstra 1959; Getz et al. 1990). California Kingsnake predation on birds also was strongly seasonal, and thus subject to unusual weather influences. Late-season rainfall associated with an El Niño-Southern Oscillation in 1998 delayed California Kingsnake nest predation in the south coast of California and increased reproductive success for Rufous-crowned Sparrow (Morrison and Bolger 2002b). Despite a slight increase in predation on snakes during late summer-early fall, we failed to

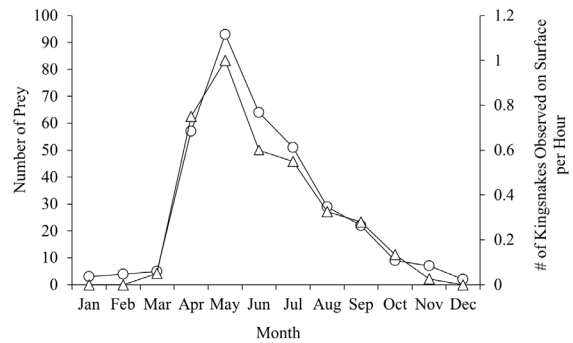


FIGURE 16. Seasonal variation in number of prey taken by California Kingsnakes, *Lampropeltis californiae* (circles), from this study and adult/subadult surface activity (triangles, from Hansen 1982).

detect an expected emphasis on recent hatchlings and neonates, perhaps due to low sample size for that period and/or increased activity of other potential prey just prior to winter inactivity.

Geographic variation in snake diets is presumably affected by absolute availability (i.e., sympatry) of prey species, relative abundances of individual prey species, and competition with other predators (e.g., Steen et al. 2014a,b), as well as by body size variation through its influence on gape and capacity for subduing larger prey (e.g., mammals for Long-nosed Snakes, *Rhinocheilus lecontei*; Rodríguez-Robles and Greene 1999); any of those factors might plausibly influence the feeding biology of California Kingsnakes. The relative abundances of Western Fence Lizards, Southern Alligator Lizards and skinks among different California habitats, for example, might influence predation rates on them (Block and Morrison 1998). Our finding that California Kingsnakes from Sonoran, Mohave, and Great Basin deserts ate more snakes than those from other bioregions is consistent with increased predation on them in Nevada (Clark 1968) and the claim by Gates (1957) that Coachwhips made up much of the diet at a Sonoran Desert locality, as well as more generally with increased species richness of potential prey snakes at lower latitudes (Arnold 1972). In terms of potential competitors, compared to other bioregions, California Kingsnakes consumed fewer rodents in deserts, where they are sympatric with a higher diversity of mammal-eating snakes (e.g., Arnold 1972; Rodríguez-Robles and De Jesus Escobar 1999; Rodríguez-Robles et al. 1999; Rodríguez-Robles 2002).

Predator-prey size relationships.—Relative prey mass (RPM) values for California Kingsnakes (mean = 0.24 ± 0.19 ; range, 0.01–0.73) were similar to those for other lampropeltinines, including Eastern Kingsnakes (0.133 ± 0.029 ; range, 0.02–0.86; Godley et al. 2017), Glossy Snakes (0.33 ± 0.22 ; range, 0.04–0.77; Rodríguez-Robles et al. 1999), Scarlet Kingsnakes

(*Lampropeltis elapsoides*; 0.19; range, 0.11–0.38; Greene et al. 2010), Milksnakes (*Lampropeltis triangulum*; mean = 0.12 ± 0.07 ; range, 0.005–0.735; Hamilton et al. 2012), California Mountain Kingsnakes (*Lampropeltis zonata*; mean = 0.33 ± 0.23 ; range, 0.11–0.62; Greene and Rodriguez-Robles 2003), Gopher Snakes (mean = 0.21 ± 0.26 ; range, 0.01–1.36; Rodriguez-Robles 2002), and Long-nosed Snakes (mean = 0.23 ± 0.22 ; range, 0.03–0.63; Rodriguez-Robles and Greene 1999). Moreover, details for two species suggest that their maximum RPMs or upper breaking points (Arnold 1993) might be similar regardless of different gapes, modal prey shapes, and modal prey taxa. Captive California Kingsnakes regurgitated prey snakes with RPMs of 1.17 and 1.35 but successfully digested one with RPM = 1.06 (Jackson et al. 2004); our data for natural prey items, combined with findings by Jackson et al. (2004), indicate that only when taking snakes do California Kingsnakes achieve RPMs > 0.30 and that the upper breaking point for eating elongate (Type II) prey is an RPM > 0.73 and possibly > 1.06, but < 1.17. One Eastern Kingsnake had successfully consumed an Eastern Ratsnake (*Pantherophis alleghaniensis*) with an RPM of 0.86 (Godley et al. 2017). Gopher Snakes have larger gapes, typically eat bulky mammals and birds of diverse RPMs (prey Types I, III, and IV), 94% of 53 records for RPMs were < 0.80, and of three individuals with higher RPMs, two with values of 0.818 and 1.36 died from asphyxiation and/or rupturing of the stomach (Rodriguez-Robles 2002). Both species evidently can kill and ingest taxonomically acceptable prey larger than they can successfully process, with breaking points likely set by gut packaging limits, effects of increased overall mass on locomotion, reduced capacities for behavioral thermoregulation, and/or increased exposure to predators (Garland and Arnold 1983; see Repp 2002; Jackson et al. 2004). Rattlesnake prey, which may certainly account for relatively high RPM prey, did not represent the highest values of our sample of intact or estimated RPMs ($n = 23$) as most rattlesnake prey from museum specimens were digested beyond reliable estimation of mass used to determine RPM values.

Our data demonstrate that California Kingsnakes exhibit some ontogenetic telescoping (Arnold 1983), in that although larger individuals often ate absolutely heavier prey than did smaller snakes, they took relatively lighter prey with increasing snake size and continued to consume small items. This latter pattern, which contrasts with one of more tightly rising lower prey size limit (Arnold 1993), also characterizes some other lampropeltinines (e.g., Gopher Snakes, Rodriguez-Robles 2002; Milksnakes, Hamilton et al. 2012; Eastern Kingsnakes, Godley et al. 2017) as well as numerous other snake species (e.g., Greene 1984; Arnold 1993; Bilcke et al. 2007; Halstead et al. 2008), presumably

because small items are energetically inexpensive to capture and process relative to search costs and payoffs (Shine 1977; Godley 1980; Arnold 1993).

Methodological, evolutionary, and conservation implications.—Our study was descriptive and comprehensive, initially motivated by curiosity regarding the feeding biology of a widespread, often common, yet poorly studied western North American serpent. We used multiple data sources, primarily stomach contents of museum specimens, supplemented with various sorts of unpublished information. We were aware of potential biases arising from using multiple sources of data (Rodriguez-Robles 1998) including the prevalence of snake prey from personal communications and unpublished field notes (likely due to increased prey handling times making them more likely to be observed), while all records of squamate egg raids resulted from museum specimens. Clearly additional techniques (e.g., stable isotopes, Willson et al. 2010; videography, Putman and Clark 2015; Glaudas et al. 2017) and increased reliance on social media (Layloo et al. 2017) should lead to further insights regarding California Kingsnakes and other snake species. This organism-focused approach notwithstanding, we conclude here by emphasizing that recording and analyzing the widest possible range of parameters, with reasonably large sample sizes, will maximize future applicability of snake diet studies for more conceptually oriented questions (Greene 2005).

As an example of broader implications, only because we obtained a large data-set on diverse aspects of feeding biology can we address Liem's Paradox, whereby organisms exhibit specializations for rare prey in this case, although species in the *Lampropeltis getula* complex are immune to pitviper venoms, rattlesnakes constitute only 7% by frequency for California Kingsnakes (for general discussions and other examples, see, e.g., Robinson and Wilson 1998; Binning et al. 2009; Mohammadi et al. 2016). Our results demonstrate that compared to the other three main prey types taken by California Kingsnakes, only snakes are commonly taken by individuals of all sizes, are seasonally reliable prey, and, because of their elongate shape, on average provide higher payoff/item. Moreover, among all serpents taken, rattlesnakes are the most nutritionally valuable prey. The ability to safely subdue even a single rattler per year might thus be highly significant in the lives of California Kingsnakes (Fig. 17), an insight worthy of emphasis in educational materials about both predator and prey (e.g., Nowak and Greene 2016).

In terms of conservation implications, on the one hand the California Kingsnake is geographically widespread, occupies diverse habitats, and is individually responsive to shifting prey availability across a range of diet types, which are all reasons to regard this species

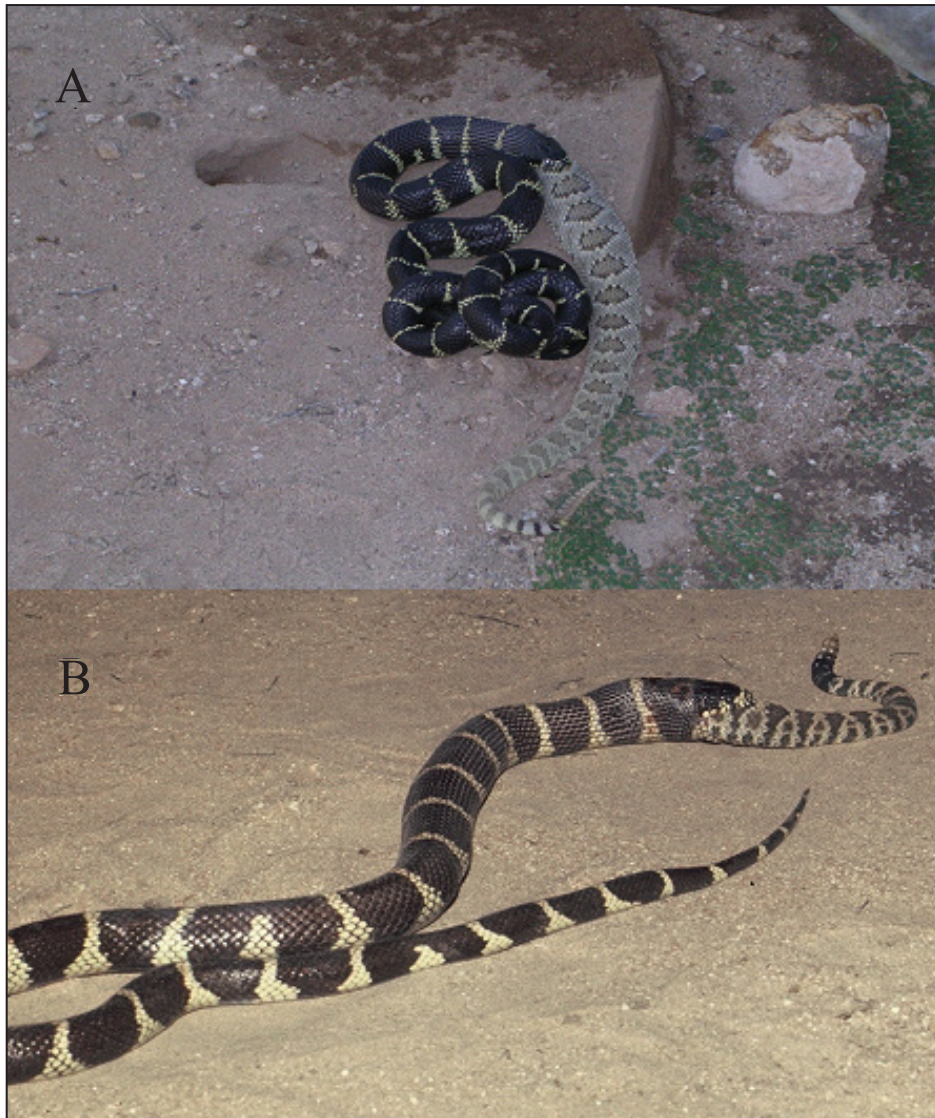


FIGURE 17. The huge potential caloric payoff for California Kingsnakes (*Lampropeltis californiae*) that consume relatively massive snakes likely promoted the evolution of venom immunity: (A) a Mohave Rattlesnake (*Crotalus scutulatus*) from Graham County, Arizona (Photographed by Richard White); (B) a Northern Pacific Rattlesnake (*Crotalus oreganus*) from the San Joaquin Experimental Range in Madera County, California, where Henry Fitch conducted his pioneering snake studies. (Photographed by Stanley Westfall).

as relatively secure in the face of increasing human impact. Indeed, populations of California Kingsnakes sometimes persist despite urbanization and habitat fragmentation (Anguiano and Diffendorfer 2015), in contrast to enigmatic declines of a closely related species in parts of the eastern U.S. (Winne et al. 2007; Steen et al. 2014a; Godley et al. 2017). On the other hand, those same characteristics might prove relevant to managing introduced California Kingsnakes in the Canary Islands (Monzon-Arguello et al. 2015) and in South Africa (Maritz 2018), where, as has been the case for Old World tree snakes (*Boiga* sp.) with some similar natural history attributes (Greene 1989: 202-203), they could have devastating effects on an endemic fauna

(e.g., Rodda et al. 1999). The efforts to solve the Canary Islands problem have until now preceded in the absence of detailed knowledge of the invader within its native range (Fisher et al. 2019), which emphasizes the need for additional species-focused studies of snake diets, as well as the core importance of museum collections (Suarez and Tsutsui 2004; Pyke and Erlich 2010) for securing that knowledge.

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