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Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae)

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Studies of food relations are important to our understanding of ecology at the individual, population and community levels. Detailed documentation of the diet of large-bodied, widespread snakes allows us to assess size-dependent and geographical variation in feeding preferences of gape-limited predators. Furthermore, with knowledge of the food habits of sympatric taxa we can explore possible causes of interspecific differences in trophic niches. The feeding ecology of the North American gopher snake, *Pituophis catenifer*, was studied based on the stomach contents of more than 2600 preserved and free-ranging specimens, and published and unpublished dietary records. Of 1066 items, mammals (797, 74.8%), birds (86, 8.1%), bird eggs (127, 11.9%), and lizards (35, 3.3%) were the most frequently eaten prey. Gopher snakes fed upon subterranean, nocturnal and diurnal prey. The serpents are primarily diurnal, but can also be active at night. Therefore, gopher snakes captured their victims by actively searching underground tunnel systems, retreat places and perching sites during the day, or by pursuing them or seizing them while they rested at night. Gopher snakes of all sizes preyed on mammals, but only individuals larger than 40 and 42 cm in snout–vent length took bird eggs and birds, respectively, possibly due to gape constraints in smaller serpents. Specimens that ate lizards were smaller than those that consumed mammals or birds. Gopher snakes raided nests regularly, as evidenced by the high frequency of nestling mammals and birds and avian eggs eaten. Most (332) *P. catenifer* contained single prey, but 95 animals contained 2–35 items. Of the 321 items for which direction of ingestion was determined, 284 (88.5%) were swallowed head-first, 35 (10.9%) were ingested tail-first, and two (0.6%) were taken sideways. Heavier gopher snakes took heavier prey, but heavier serpents ingested prey with smaller mass relative to snake mass, evidence that the lower limit of prey mass did not increase with snake mass. Specimens from the California Province and Arid Deserts (i.e. Mojave, Sonoran and Chihuahuan Deserts) took the largest proportion of lizards, whereas individuals from the Great Basin Desert consumed a higher percentage of mammals than serpents from other areas, and *P. catenifer* from the Great Plains ate a greater proportion of bird eggs. Differences in prey availability among biogeographical regions and unusual circumstances of particular gopher snake populations may account for these patterns. Gopher snakes have proportionally longer heads than broadly sympatric *Rhinocheilus lecontei* (long-nosed snake), *Charina bottae* (rubber boa) and *Lampropeltis zonata* (California mountain kingsnake), which perhaps explains why, contrary to the case in *P. catenifer*, the smaller size classes of those three species do not eat mammals. *Biological Journal of the Linnean Society*, 2002, **77**, 165–183.

ADDITONAL KEYWORDS: Body size – diet – geographical dietary variation – predator/prey mass relationship – size-related dietary variation

INTRODUCTION

In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten," but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.

G. E. Hutchinson (1959: 147)

As the preceding quote indicates, studies of food relations are centrally important to our understanding of ecology at the individual, population and community levels, and can provide insight on the evolution and contemporary dynamics of biological systems (e.g.

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Losos & Greene, 1988; Madsen & Shine, 1996; Rodríguez-Robles & Greene, 1996; Ford *et al*., 1998; Luiselli, Akani & Capizzi, 1998; Caldwell & Vitt, 1999; Rodríguez-Robles & de Jesús-Escobar, 1999). By setting realistic boundaries on measures of performance, knowledge about the natural diet of an animal can also inform studies of functional and evolutionary morphology (Greene, 1986; Lorenz Elwood & Cundall, 1994; Schwenk, 2000). Even partial dietary information for extinct taxa can shed light on a variety of functions and patterns (e.g. feeding behaviour, digestive processes, habitat preferences, ecological aggregations) of ancient biotas (e.g. Chin *et al*., 1998; Poinar *et al*., 1998).

Snakes are prominent predators in many terrestrial, aquatic, and marine communities. Consequently, information about their feeding habits enhances our understanding of trophic relationships in diverse ecological assemblages. Detailed documentation of the diet of large-bodied, widespread serpents allows us to assess size-dependent and geographical variation in feeding preferences of gape-limited predators. Furthermore, with knowledge of the food habits of sympatric taxa we can explore possible causes of interspecific differences in trophic niches.

Three allopatric species of *Pituophis* are recognized in the United States, *P. catenifer* (gopher snake), *P. ruthveni* (Louisiana pinesnake), and *P. melanoleucus* (eastern pinesnake; Reichling, 1995; Rodríguez-Robles & de Jesús-Escobar, 2000). *Pituophis catenifer* has the broadest distribution, occurring from south-western Canada to northern Mexico, throughout the Baja California peninsula, and from the Pacific Coast east to the Great Plains and Great Lakes regions of the United States (Fig. 1). The taxonomic status of the Baja California populations is controversial, with one worker (Grismer, 1994, 1997, 2001) recognizing them as a different species (i.e. *Pituophis vertebralis*), and others (Rodríguez-Robles & de Jesús-Escobar, 2000) arguing that this designation, although conceivable, is premature based on available evidence.

Pituophis catenifer is found in a great variety of habitats, including woodlands, prairies, canyons, deserts and cultivated fields, but the species is generally absent from dense forests and high mountains, especially in the Pacific Northwest region of North America (Nussbaum, Brodie & Storm, 1983). Gopher snakes can grow up to 2.7 m in snout-to-vent length (SVL), but adults usually range from 0.8 to 1.5 m (Platt, 1984; Diller & Wallace, 1996; Werler & Dixon, 2000). Although they are generally terrestrial, gopher snakes are excellent excavators (Hisaw & Gloyd, 1926; Carpenter, 1982) and climbers (e.g. Marr, 1985; Eichholz & Koenig, 1992). They encounter their prey by active search, relying on olfactory and visual cues (Eichholz & Koenig, 1992; Fitch, 1999). The snakes are powerful, non-venomous constrictors (Willard, 1977; de Queiroz, 1984; Moon, 2000) and are primarily diurnal, but can become active at dusk and at night, especially in the summer (Mosauer, 1935; Stebbins, 1954; Reynolds & Scott, 1982; Degenhardt, Painter & Price, 1996; Hammerson, 1999).

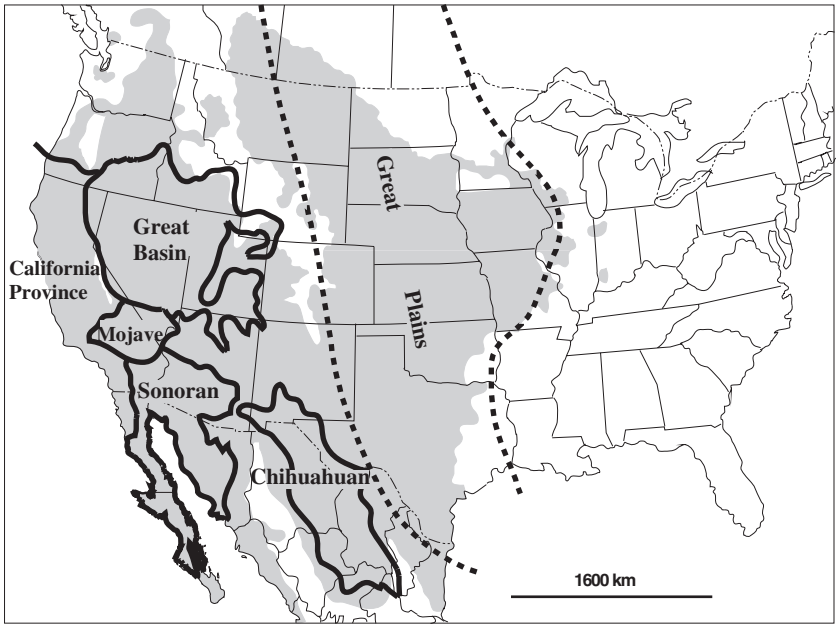

Figure 1. Approximate range of *Pituophis catenifer* (in grey) and delineation of physiographic regions used to assess geographical variation in diet in this snake.

Some authors (e.g. Imler, 1945; Fitch, 1949, 1999; Parker & Brown, 1980; Reynolds & Scott, 1982; Diller & Wallace, 1996) have studied the food habits of *P. catenifer* in different parts of its range, but a comprehensive study of the diet of this species is lacking. Herein I rely on stomach contents of museum specimens and free-ranging animals and published and unpublished accounts to determine taxonomic composition of the feeding habits of gopher snakes throughout their distribution, and use this information to investigate patterns of dietary variation in this widespread species.

METHODS

A total of 2613 specimens of *Pituophis catenifer* were examined in the California Academy of Sciences, San Francisco (CAS) and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Stomach contents were checked by making a mid-ventral incision in all alcoholic specimens, except type specimens and especially soft, brittle, or otherwise fragile individuals. Whenever possible, for each snake with prey the following were recorded: complete locality data, body size (SVL ±1 cm), body mass (±0.2 g), head length (±1 cm, from the tip of the rostral scale to the retroarticular process of the right mandible), and minimum number of items in the stomach. Taxonomic identity (cf. Whorley, 2000) and direction of ingestion of prey (inferred from orientation in the gut) were also recorded. I weighed snakes and their intact or slightly digested prey after blotting and draining them briefly in paper towel to remove excess fluid. Weights and body measurements of partially digested items were estimated by comparison with intact conspecifics of similar size from the nearest locality available in the MVZ. My data set also incorporates published and unpublished dietary reports of *P. catenifer*. I took care to account for redundancy among literature records (Klauber, 1931 with Klauber, 1947; Fitch, 1982 with Fitch, 1999; Diller & Johnson, 1982, 1988 with Diller & Wallace, 1996). I excluded from the data set dietary records of specimens fed in captivity (e.g. MVZ 50299), or under otherwise artificial circumstances (Vaughan, 1961; Zaworski, 1990).

RESULTS

I combined all dietary records of *Pituophis catenifer* (i.e. published and unpublished accounts and prey I removed from preserved specimens and free-ranging animals) to gain a more accurate estimate of the natural diet of this species (cf. Rodríguez-Robles, 1998). Seven-hundred and ninety-seven (74.8%) of 1066 prey taken by gopher snakes were mammals, 86 (8.1%) were birds, 127 (11.9%) were bird eggs, seven (0.7%) were either nestling birds or avian eggs, 35 (3.3%) were lizards, five (0.5%) were snakes, two (0.2%) were unidentified squamates, three (0.3%) were squamate eggs, and one (0.1%) each was a frog, frog eggs, turtle eggs, and an insect (see Appendix: the high number of unidentified lizards, birds, and mammals is the result of stomach contents that consisted exclusively of a few scales, feathers, or clumps of hair with no cranial material, respectively). Should future studies support the recognition of *P. vertebralis* (fide Grismer, 2001) on Baja California, 19 of the dietary records herein reported for *P. catenifer* would belong to *P. vertebralis* (i.e. 1 *Chaetodipus* sp., 4 *Perognathus* (*s.l.*) sp., 1 unidentified heteromyid, 2 *Neotoma lepida*, 1 *Neotoma* sp., 2 *Peromyscus* sp., 4 unidentified rodents, 1 unidentified bird, and 3 unidentified bird eggs (this study; Bostic (1971)).

Intra- and interspecific size-related variation in diet

The frequency distribution of number of prey per snake was markedly skewed to the right (Fig. 2). Ninety-five serpents contained 2–35 items (the 35 prey were all small mice (Pack, 1919), and thus represent actual prey, not secondarily ingested items). There was no significant difference in body size between snakes that contained single prey (mean SVL ± SD = 75 ± 27.7 cm, range = 25.5–159 cm, N = 295) and those that had multiple items (mean

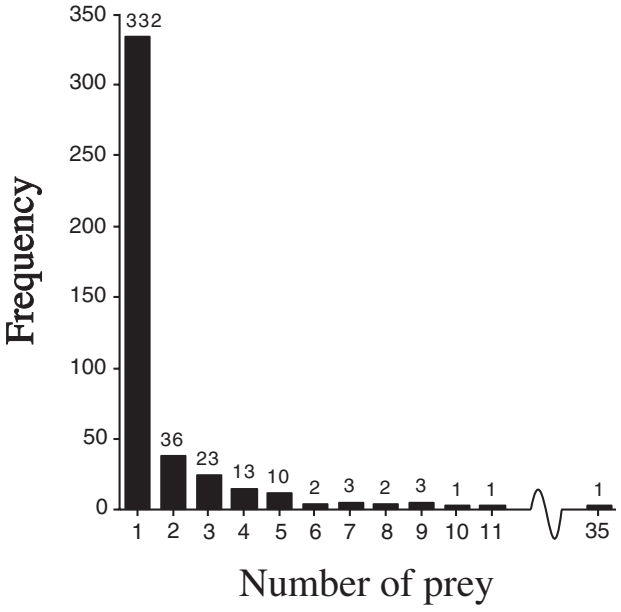

Figure 2. Frequency distribution of *Pituophis catenifer* containing different number of prey ($g_1 = 5.5$; $t_s = 46.4$, d.f. = ∞, $P < 0.0001$; $N = 427$). Numbers above bars indicate frequencies.

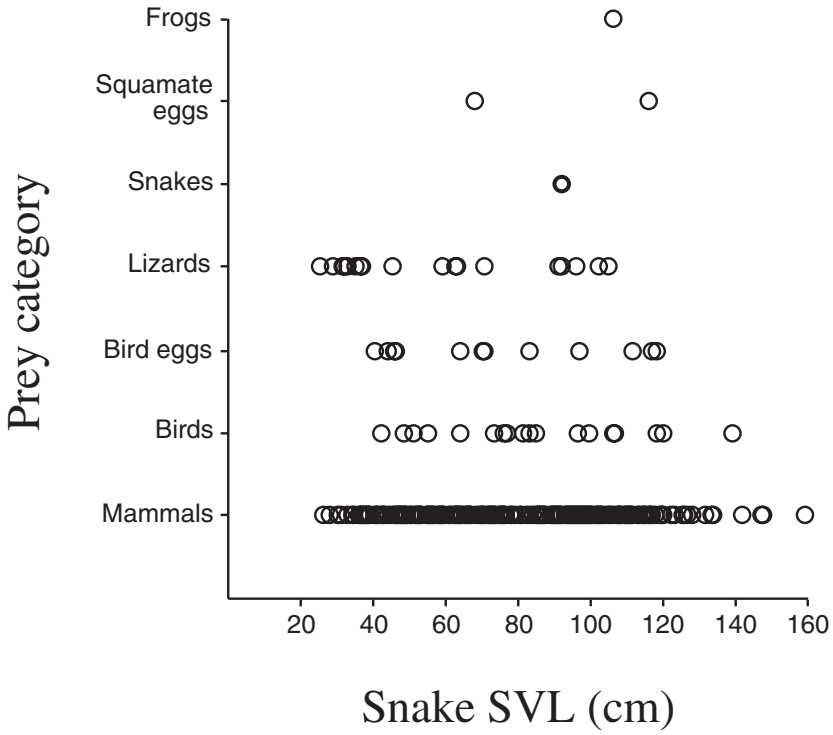

Figure 3. Relationship between prey category and snake body size (SVL) in *Pituophis catenifer* ($N = 364$).

Table 1. Relationship between prey type and direction of ingestion

	Direction of ingestion	
Prey type	Head-first	Tail-first
Mammals	257	32
Birds	9	1
Lizards	16	2
$\chi^2=0.01$, d.f. = 2, $P = 0.99$		
Nestlings	54	15
Juveniles or adults	27	2
$\chi^2=3.14$, d.f. = 1, $P = 0.077$		

SVL ± SD = 79.5 ± 27.5 cm, range = 30.4–147.4 cm, $N = 56$; single-factor ANOVA, $F_{(1,349)} = 1.24$, $P = 0.27$). In dietary studies that rely on museum specimens, evidence for intra-individual dietary variation comes from multiple prey types in the same specimen (Greene, 1989b). For gopher snakes, this variability encompasses at least mammals and birds, mammals and bird eggs, mammals, bird eggs and lizards, mammals and frogs, and birds and their eggs. Of the 321 items for which I determined direction of ingestion, 284 (88.5%) were swallowed head-first, 35 (10.9%) were ingested tail-first, and two (0.6%) were taken sideways. There was no association between prey type (i.e. mammals, birds, lizards) and direction of ingestion, but there was a trend for smaller animals (i.e. nestlings) to be swallowed tail-first with a higher frequency than juvenile or adult prey (Table 1).

There were statistically significant differences in body size between snakes that fed on mammals (mean SVL ± SD = 76.4 ± 27.5 cm, range = 26.3–159 cm, $N = 306$) and those that preyed on lizards (mean SVL ± SD = 56.9 ± 28 cm, range = 25.5–105.1 cm, $N = 19$), birds (mean SVL ± SD = 83.9 ± 25.7 cm, range = 42.3–139 cm, $N = 20$), and bird eggs (mean SVL ± SD = 77.3 ± 28.8 cm, range = 40.4–118.3 cm, $N = 13$; single-factor ANOVA, $F_{(3,354)} = 3.65$, $P = 0.01$; Fig. 3), with multiple comparison tests (i.e. Games-Howell, Scheffe's S) indicating that pairwise differences were significant between snakes that took mammals and those that ate lizards and between serpents that consumed lizards and those that fed on birds.

Head length is the best predictor of gape size in snakes (Arnold, 1983; Greene, 1983), and serpents with longer heads can eat larger prey (Shine, 1991; Forsman & Lindell, 1993). The observation that smaller gopher snakes are capable of preying on mammals (Fig. 3) suggests that these snakes may have a larger gape than individuals of similar size of other species. I tested this hypothesis by comparing head length of *P. catenifer* (mean ± SD = 2.8 ± 0.7 cm,

range = 1.3–5.1 cm, $N = 346$) with those of *Rhinocheilus lecontei* (long-nosed snake; mean ± SD = 1.8 ± 0.3 cm, range = 1.1–2.5 cm, $N = 93$), *Charina bottae* (rubber boa; mean ± SD = 1.6 ± 0.3 cm, range = 0.7–2.2 cm, $N = 38$), *Lampropeltis zonata* (California mountain kingsnake; mean ± SD = 2 ± 0.3 cm, range = 1.2–2.3 cm, $N = 28$), and *Arizona elegans* (glossy snake; mean ± SD = 1.8 ±0.5 cm, range = 1.2–2.9 cm, $N = 77$), broadly sympatric snakes in western North America that also prey on mammals (Rodríguez-Robles & Greene, 1999; Rodríguez-Robles, Bell & Greene, 1999a, b; H. W. Greene & J. A. Rodríguez-Robles, unpubl. data). To correct for differences in body size among the five species, I used the residuals from the least squares linear regression of head length on snake SVL as the dependent variable in a single-factor ANOVA ($F_{(4,577)} = 96$, $P = 0.0001$). Multiple comparison tests (i.e. Games-Howell, Scheffe's S) showed that all pairwise comparisons with *P. catenifer* were significant, indicating that after adjusting for differences in body size, gopher snakes have longer heads than *R. lecontei*, *C. bottae*, *L. zonata* and *A. elegans*.

Prey/predator mass relationship

I could reliably estimate body mass for the stomach contents of 53 *P. catenifer*. Although relative prey mass values were generally low (mean ± SD = 0.21 ± 0.26, range = 0.01–1.36, $N = 53$), gopher snakes occasionally took large prey (Fig. 4). Heavier gopher snakes took heavier prey (Fig. 5a), but the coefficient of determination of the regression of prey mass on snake mass was low (adjusted $r^2 = 0.29$), indicating that 71% of the total variation in prey mass was not explained by variation in predator mass. Indeed, heavier snakes ingested prey with relatively smaller mass (i.e. prey

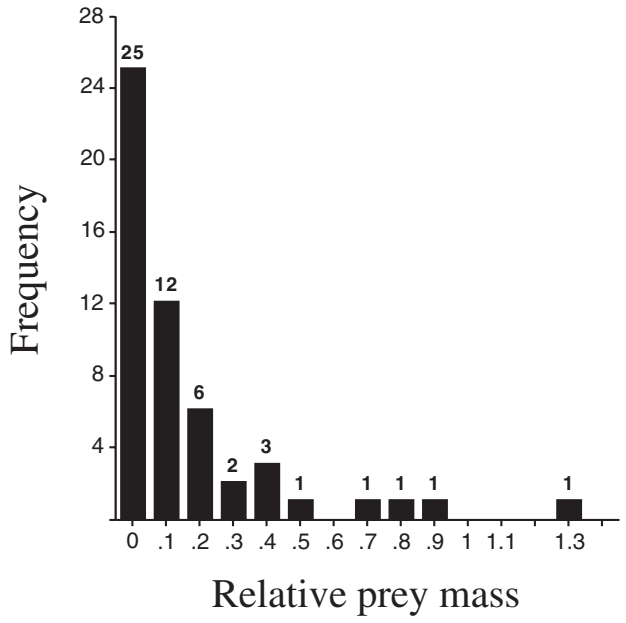

Figure 4. Frequency distribution of relative prey mass (prey mass, g / snake mass, g) in *Pituophis catenifer* ($N = 53$). Numbers above bars indicate frequencies.

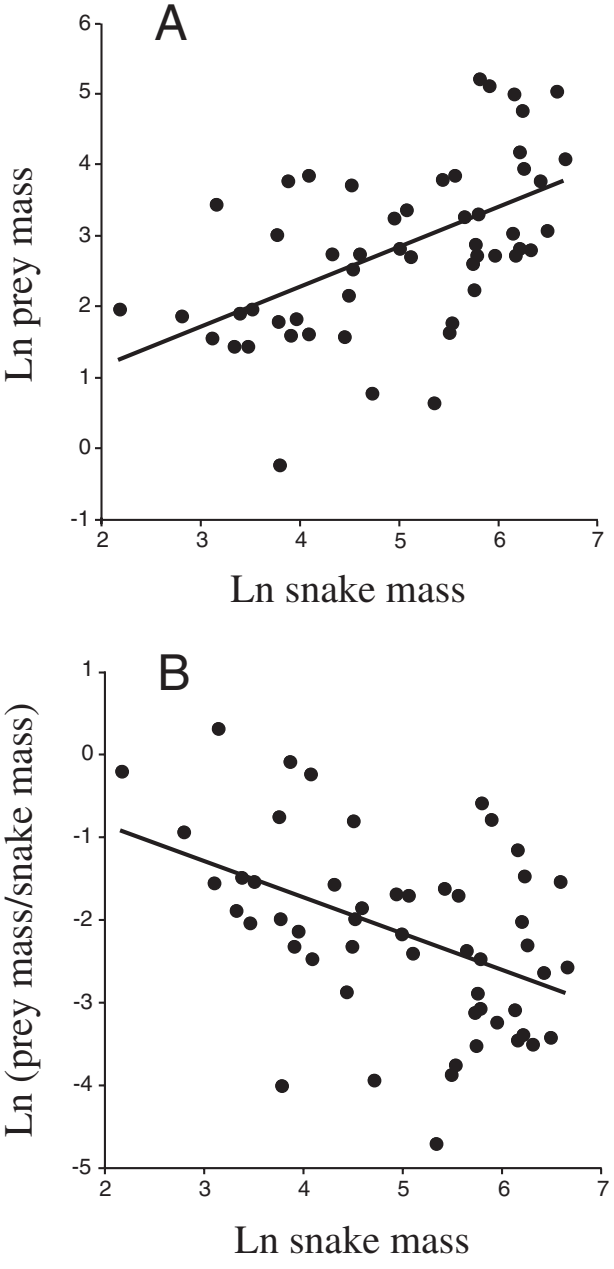

Figure 5. A. Log_n-transformed prey mass (g) as a function of $\log_n$-transformed snake mass (g) in *Pituophis catenifer* (adjusted $r^2 = 0.29$, $F_{(1,51)} = 21.7$, $P < 0.0001$). B. Log_n-transformed (prey mass, g/snake mass, g) as a function of snake mass (g) in *P. catenifer* (adjusted $r^2 = 0.19$, $F_{(1,51)} = 13.2$, $P = 0.0006$).

Table 2. Frequency of mammals, birds, bird eggs, and lizards taken by *Pituophis catenifer* from different biogeographical regions

	Prey type			
Biogeographical region	Mammals	Birds	Bird eggs	Lizards
California Province	211	25	14	16
Great Basin Desert	151	7	2	3
Arid Deserts	50	5	1	5
Great Plains	117	14	33	2

χ^2=65.6, d.f. = 9, P <0.0001

mass/snake mass; Fig. 5b), but the coefficient of determination (adjusted $r^2 = 0.19$) of this linear regression also was low.

Geographic variation in diet

I assigned snakes with prey to one of six physiographic regions (i.e. California Province, Great Basin Desert, Mojave Desert, Sonoran Desert, Chihuahuan Desert and Great Plains; cf. Hickman, 1993; Bolen, 1998) to assess geographical variation in food habits of *P. catenifer*. However, to increase sample size, I combined snakes from the Mojave, Sonoran and Chihuahuan Deserts into a category called 'Arid Deserts.' There were significant differences in the percentage of mammals, birds, bird eggs and lizards eaten by snakes from the different biogeographical areas (Table 2). Gopher snakes from the California Province and Arid Deserts took the largest proportion of lizards, whereas specimens from the Great Basin Desert consumed a higher percentage of mammals than serpents from other areas, and *P. catenifer* from the Great Plains ate a greater proportion of bird eggs.

DISCUSSION

Mammals are the principal prey of *Pituophis catenifer*, comprising three of every four items. Birds and their eggs are also taken with some regularity, whereas lizards are eaten less frequently. Squamate eggs, frogs and their eggs, turtle eggs and insects are hardly ever consumed, and these records are likely to be the result of opportunistic feeding events. As their English common name may suggest, gopher snakes prey upon *Geomys* and *Thomomys* pocket gophers in different parts of the serpent's range (California, Nevada, Arizona, New Mexico, Nebraska, Kansas, USA), but other rodents (i.e. *Microtus* voles, *Peromyscus* white-footed mice) are eaten more frequently. Gopher snakes feed upon subterranean (i.e. *Geomys* and *Thomomys*), nocturnal (e.g. heteromyid rodents, *Neotoma* woodrats, *Peromyscus*) and diurnal prey (e.g. *Ammospermophilus* and *Spermophilus* ground squirrels, passerine (perching) birds, *Sceloporus* spiny lizards, *Cnemidophorus* whip-tailed lizards; Degenhardt *et al*., 1996; Nowak, 1999). Therefore, these serpents capture their prey by actively searching underground tunnel systems, retreat places and perching sites during the day, or by pursuing them or seizing them while they rest at night.

Across their range, gopher snakes eat a wide variety of mammals, a pattern also seen at the population level (e.g. Parker & Brown, 1980; Diller & Wallace, 1996; Fitch, 1999; Iverson & Akre, 2001). This diversity in food habits means that the reduction of one prey species should have little impact on total prey consumption by *P. catenifer*. Indeed, when *Spermophilus townsendii* (Townsend's ground squirrel), the main prey of gopher snakes, and *Crotalus oreganus lutosus* (Great Basin rattlesnake; fide Ashton & de Queiroz, 2001) at a site in south-western Idaho (USA) failed to reproduce because of a drought during the winter of 1976 and the spring of 1977, Great Basin rattlesnakes showed an almost 80% reduction in relative prey consumption in 1977, a figure similar to the proportion that Townsend's ground squirrels made up in their diet. This indicates that there was no shift to alternative prey species, and most of the rattlesnakes of this population did not feed when they could not find their preferred prey. Because *P. catenifer* had a much broader trophic niche, the reduction of Townsend's ground squirrels had little impact on its total prey consumption (Diller & Johnson, 1982).

Most *P. catenifer* contained single prey, swallowed head-first, but a large proportion of serpents (95 of 427, 22.2%; Fig. 2) had multiple prey. Of 300 items for which I determined developmental stage (i.e. juvenile vs. adult), 211 (70.3%) were nestling mammals or birds. The frequency of young endotherms in my total sample of gopher snake prey was undoubtedly higher, as most literature records of *P. catenifer* diet did not distinguish between juvenile and adult prey. One study that did (Fitch, 1949) reported that 50 of 72 (69.4%) food items were young of rodents or eggs. In

addition to the high number of juvenile prey, my records of *P. catenifer* diet include 127 bird eggs, which further supports the assertion that gopher snakes raid nests frequently (Fitch, 1949, 1999; Diller & Wallace, 1996; Shewchuk, 1996; Hammerson, 1999). One reason that gopher snakes may prey on nestlings with such high frequency is that, all else being equal, a heavier animal struggles more effectively than a lighter one, so that given the option predators may prefer to take, for example, three young mice at 10 g each, rather than one 30 g conspecific adult. In fact, total handling time may be less for three young mice than for one larger, actively struggling adult mouse that could seriously injure the snake. Adult birds can fly away from an intruding serpent, which perhaps explains their lower frequency, compared to that of avian eggs, in the diet of gopher snakes.

Pituophis catenifer has a versatile feeding behaviour. Although the species is generally terrestrial and certainly captures prey on the ground (Klauber, 1947), it is also an active and efficient burrower (Hisaw & Gloyd, 1926; Carpenter, 1982) and, unlike many other large-bodied serpents, locates and seizes a considerable fraction of its prey (*Geomys* and *Thomomys*, *Dipodomys* kangaroo rats, *Chaetodipus* and *Perognathus* pocket mice, *Microtus*, *Ammospermophilus* and *Spermophilus*) in their subterranean retreat sites and nests (Grinnell & Storer, 1924; Klauber, 1947; Gehlbach, 1965). In these underground tunnel systems, where there is rarely sufficient room for the prey to be enveloped in the coils of a constrictor snake, gopher snakes forcibly press their victims against a tunnel wall until they cease to struggle (Hisaw & Gloyd, 1926). On the other hand, *P. catenifer* preys on eggs and nestlings at ground, bank and arboreal avian nests (e.g. Cunningham, 1955; Ervin & Rose, 1973; Best, 1977; Marr, 1985; Eichholz & Koenig, 1992; McCallum, Gehlbach & Webb, 1995). After consuming large eggs, gopher snakes break the shell by forcing their body against hard objects (a rock; Gans, 1974), or by pushing the eggs against processes on the ventral surface of a few anterior vertebrae (Imler, 1945); smaller, thinner-shelled eggs (e.g. quail eggs) can be swallowed unbroken (Huey, 1942). In the absence of space constraints, *P. catenifer* is capable of simultaneously constricting up to three nestling rodents (or birds) in separate body coils (Jameson, 1956; Tennant, 1984), a behavioural trait that prevents other members of a litter or brood from escaping while the snake swallows another one. When the prey are very small (neonates), they can be seized and simply swallowed alive without being subdued first (Hisaw & Gloyd, 1926; Werler & Dixon, 2000). Thus, the diverse feeding behaviour of gopher snakes is well-suited for eating a wide variety of animals and for robbing nests.

Intra- and interspecific size-related variation in diet

Gopher snakes of all sizes prey on mammals (Fig. 3). Although there are exceptions (e.g. Luiselli & Angelici, 1998; Shine *et al*., 1998b; Rodríguez-Robles *et al*., 1999a), the common pattern for mammal-eating ophidian species is for smaller individuals to eat lizards (and sometimes invertebrate prey as well), and only to add mammals to their diet after reaching a larger body size (e.g. Henderson *et al*., 1987; Savidge, 1988; Greene, 1989b; Shine & Slip, 1990; Henderson, 1993a, b; Shine *et al*., 1998a; Webb & Shine, 1998; Rodríguez-Robles & Greene, 1999; Rodríguez-Robles *et al*., 1999b). The finding that gopher snakes have proportionally longer heads than broadly sympatric *Rhinocheilus lecontei*, *Charina bottae* and *Lampropeltis zonata* may explain why the smaller size classes of the latter species do not prey on mammals, instead relying exclusively on squamate eggs and slender-bodied lizards (Rodríguez-Robles & Greene, 1999; Rodríguez-Robles *et al*., 1999b; H. W. Greene & J. A. Rodríguez-Robles, unpubl. data). Like gopher snakes, *Arizona elegans* of all sizes prey on mammals, but they do so less frequently and on smaller species (e.g. *Dipodomys* kangaroo rats, *Perognathus* pocket mice, *Peromyscus* white-footed mice; Rodríguez-Robles *et al*., 1999a) than *P. catenifer*, whose longer heads allow them to take a larger size range of mammalian prey that includes *Lepus* jack rabbits, *Sylvilagus* cottontail rabbits, *Geomys* and *Thomomys* pocket gophers and *Neotoma* woodrats. Hence, variation in head length can result in marked differences in the kind and size of prey eaten by smaller and larger conspecifics and by different sympatric taxa.

Contrary to the situation with mammals, gopher snakes did not feed on birds until the serpents were larger than 42 cm in SVL. Birds are relatively bulky, and snakes that eat avian prey require a larger gape than those that take mammals or lizards of similar body mass (Greene, 1983), which may explain why only larger *P. catenifer* feed on birds. Similarly, gopher snakes smaller than 40 cm in SVL did not ingest bird eggs, possibly due to constraints in gape size as well. This size-dependent pattern of predation is seen in several other snake species (e.g. *Epicrates striatus* (Henderson *et al*., 1987), *Boiga irregularis* (brown treesnake; Savidge, 1988; Greene, 1989b), *Arizona elegans* (Rodríguez-Robles *et al*., 1999a), *Dendroaspis jamesoni* (Jameson's green mamba; Luiselli, Angelici & Akani, 2000)). However, smaller specimens of large-bodied boas and pythons (e.g. *Corallus hortulanus* (common tree boa; Henderson, 1993b), *Python regius* (ball python; Luiselli & Angelici, 1998), *Python reticulatus* (reticulated python; Shine *et al*., 1998b)) also take birds, probably because even smaller specimens of

these taxa have proportionally longer heads than those of adults of most other snake species.

General statements in the literature (e.g. Stebbins, 1954; Miller & Stebbins, 1964; Nussbaum *et al*., 1983) assert that only juvenile *P. catenifer* eat lizards. Indeed, gopher snakes that consumed lizards were significantly smaller than those that took mammals and birds, but larger gopher snakes occasionally ate lizards. Only *P. catenifer* larger than *c*. 115 cm in SVL stopped eating lizards altogether (Fig. 3). Perhaps serpents this size cease to encounter relatively small ectotherms, or undergo a real change in prey preference.

Prey/predator mass relationship

Relative prey mass for *P. catenifer* was lower on average and encompassed a wider range of values than those of other snake species for which similar data are available (Table 3). Nevertheless, *P. catenifer* occasionally eat very heavy items. Gopher snakes that have recently eaten a large prey in the wild may preferentially expose the stomach region to sunlight while keeping the rest of the body concealed (Ashton, 1998). This behaviour, called regional heterothermy (cf. Peterson, Gibson & Dorcas, 1993), may enhance digestion and reduce exposure to predators, which is advantageous because large food items impede movement and locomotory escape in serpents (Garland & Arnold, 1983).

There was a significant, positive association between *P. catenifer* body mass and that of its prey, which indicates that heavier snakes eat heavier animals. However, there was considerable variation in this relationship. In fact, heavier snakes ingested prey with smaller mass relative to snake mass (Fig. 5b), evidence that in gopher snakes the lower limit of prey mass does not increase with snake mass (Shine, 1991). In other words, *P. catenifer* does not exclude lighter (= smaller) items from its diet as it grows larger (= heavier), as some snake species do (Arnold, 1993).

Why do larger gopher snakes continue to eat small prey? For many snakes the rates of prey encounter and the costs of handling (finding, capturing, ingesting and digesting a prey item) are low relative to the predator's energy needs, whereas the payoff for each food item is high. For example, for a *Thamnophis elegans* (western terrestrial gartersnake) the energetic costs of attacking and ingesting a *Plethodon jordani* (Jordan's salamander) are less than 1% of the energy assimilated from the prey (Feder & Arnold, 1982), so even if most prey escape following detection, they are still worth attacking in view of the potentially huge ener-

Table 3. Relative prey mass of various snake species

Species (common name)	Mean relative prey mass (±SD)	Range	*N*	Source
ANILIIDAE				
Anilius scytale (red pipesnake)	0.32 (?)	0.11–0.82	7	Greene (1983)
COLUBRIDAE				
Arizona elegans (glossy snake)	0.33 (0.22)	0.04–0.77	14	Rodríguez-Robles *et al*. (1999a)
Boiga irregularis (brown treesnake)	0.11 (?)	0.004–0.24	13	Greene (1989b)
Bothrophthalmus lineatus (red-lined snake)	0.39 (?)	0.21–0.58	8	Luiselli *et al*. (1999)
Coluber hippocrepis (horseshoe racer)	0.26 (?)	0.05–0.56	11	Capula *et al*. (1997)
Hypsiglena torquata (desert nightsnake)	0.24 (0.19)	0.03–0.5	9	Rodríguez-Robles, Mulcahy & Greene (1999)
Lampropeltis zonata (California mountain kingsnake)	0.33 (0.23)	0.11–0.62	6	H. W. Greene & J. A. Rodríguez-Robles, unpubl. data
Pituophis catenifer (gopher snake)	0.21 (0.26)	0.01–1.36	53	This study
Psammodynastes pulverulentus (Asian mock viper)	0.13 (?)	0.06–0.26	12	Greene (1989a)
Rhinocheilus lecontei (long-nosed snake)	0.23 (0.22)	0.03–0.63	10	Rodríguez-Robles & Greene (1999)
Thelotornis capensis (savanna twigsnake)	0.19 (0.16)	0.01–0.5	21	Shine *et al*. (1996)
ELAPIDAE				
Micrurus fulvius (harlequin coralsnake)	0.42 (?)	0.02–1.31	6	Greene (1984)
VIPERIDAE				
Crotalus oreganus oreganus[1] (northern Pacific rattlesnake)	0.40 (?)	0.035–1.23	20	Fitch & Twining (1946)

[1]fide Ashton & de Queiroz (2001).

getic reward for a successful attack. In addition to eating heavier prey, larger specimens of *P. catenifer* take prey as small as that which smaller individuals eat, presumably because for those larger snakes small prey are nutritious yet energetically inexpensive to handle, without the additional costs of finding a more energetically rewarding item (Shine, 1991; Greene, 1997). In other ophidian species larger individuals continue to feed on small prey as well (e.g. *Crotalus atrox* (western diamond-backed rattlesnake; Beavers, 1976), *Enhydrina schistosa* (beaked seasnake; Voris & Moffett, 1981), *Nerodia clarkii compressicauda* (salt marsh watersnake; Miller & Mushinsky, 1990), *Acrochordus arafurae* (filesnake; Houston & Shine, 1993), *Hoplocephalus bungaroides* (broad-headed snake; Webb & Shine, 1998)), and this pattern, sometimes referred to as 'ontogenetic telescope' (Arnold, 1993), may be more common than previously realized. Perhaps the diets of gopher snakes and other serpents are determined by intrinsic constraints (e.g. limitations of sensory capabilities, maximum gape size) and relative availability of different prey species, rather than by 'optimal foraging' decisions to pursue or ignore a particular item (Greene, 1984).

The 'upper breaking point' is the largest size of prey that a snake is capable of ingesting (Arnold, 1982). Two juvenile *P. catenifer* (MVZ 232802–232803) from north-western California were found dead in the wild after having swallowed rodents representing 136 and 81.8% of their respective body masses (Fig. 6). In both snakes the skin was markedly distended around the prey, and was ruptured in the area of the stomach in MVZ 232802, which probably caused this animal's death. MVZ 232803 did not present any external lesion, and I believe this individual died of asphyxiation because its mouth was wide open and the mouse it had eaten still was in its oesophagus. Aside from predation, field observations of death are rare for many vertebrates. The fortunate discovery of these two specimens suggests that mammalian prey that amount to 136% and 81.8% of the body mass of *P. catenifer* (23.2 g and 8.8 g, respectively) are in the immediate vicinity of the upper breaking point of these ophidians (where their energetic costs of prey transport dramatically increase; B. E. Dial, pers. comm. to Cundall & Greene, 2000). This finding also suggests that the breaking point of gopher snakes increases as the serpents grow larger.

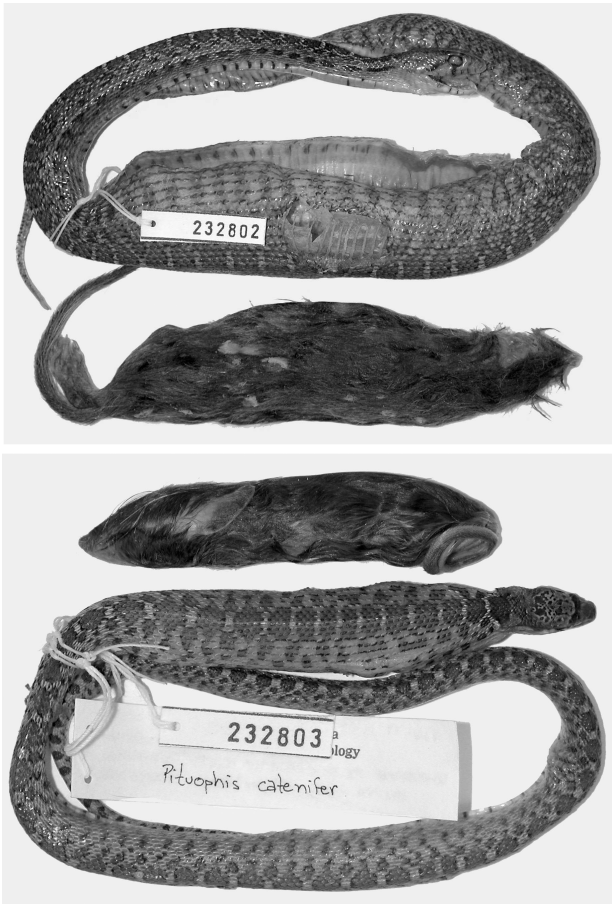

Figure 6. Top. *Pituophis catenifer* (MVZ 232802), snout–vent length 39.5 cm, 23.2 g, from Mendocino County, California (USA), with the 31.5 g *Clethrionomys californicus* (California red-backed vole) it ate. Bottom. *P. catenifer* (MVZ 232803), snout–vent length 31.2 cm, 8.8 g, from the same locality with its prey, a 7.2 g *Peromyscus maniculatus* (deer mouse). Both food items were in the immediate vicinity of the 'breaking point' of their respective predators (see main text).

Geographic variation in diet

The proportion of various prey types comprising the diet of *P. catenifer* varied across physiographic regions, but the reasons for these differences are not apparent. If lizards are more abundant in the California Province and the Arid Deserts, and mammals more so in the Great Basin Desert, *P. catenifer* from these regions may encounter those prey more frequently, which may explain why snakes from the former two areas took the largest proportion of lizards and serpents from the Great Basin Desert consumed a higher percentage of mammals. Similarly, if ground-nesting birds are more abundant in predominantly grassland regions such as the Great Plains, gopher snakes may experience more opportunities to prey on avian eggs. Alternatively, *P. catenifer* from the California Province and the Arid Deserts, the Great Basin Desert and the Great Plains may have a real preference for lizards, mammals and bird eggs, respectively, but evidence supporting this hypothesis is lacking. On the other hand, local circumstances could account for some of the broader geographical differences in food habits that I discovered.

Most (115 of 168, 68.5%) of my dietary records for gopher snakes from the Great Plains came from the Crescent Lake National Wildlife Refuge in western Nebraska (Imler, 1945; Iverson & Akre, 2001). Some *P. catenifer* from this population became so accustomed to eating bird eggs during the avian nesting season that they ate little else (Imler, 1945), and it is unknown whether other gopher snake populations from the Great Plains would have shown a similar, temporal preference for bird eggs.

The findings herein presented have provided a better understanding of taxonomic composition of the diet of *Pituophis catenifer*, and allowed me to examine patterns of dietary variation and make inferences about the foraging behaviour of this wide-ranging snake. This information, together with knowledge of the food habits of sympatric species, can be used, for example, to formulate testable hypotheses regarding the organization of predatory vertebrate assemblages (e.g. Cadle & Greene, 1993; Jaksic, Feinsinger & Jiménez, 1993), or to design studies of physiological responses to feeding (e.g. Secor & Diamond, 2000). Clearly, natural history studies continue to supply crucial data for elucidating ecological and evolutionary processes.

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APPENDIX

Prey eaten by *Pituophis catenifer*. '*Perognathus (s. l.)* sp.' refers to *Chaetodipus* sp. or *Perognathus (s. s.)* sp. 'Frequency' refers to the number of times each prey taxon was found in the entire sample; instances in which the exact frequency was unknown are indicated with a question mark and were counted as one for the purpose of calculating the total number of prey. Numbers in parentheses indicate the number of snakes that ate that particular prey, but when that number was impossible to determine from literature records, the range of possibilities is indicated

Prey taxon	Frequency	Percentage of total number of prey	Source
Mammalia			
CARNIVORA			
Mustelidae			
cf. *Mustela frenata*	1 (1)	0.1	Mulaik (1938)
CHIROPTERA			
Vespertilionidae			
Plecotus townsendii	1 (1)	0.1	Galen & Bohn (1979)
INSECTIVORA			
Soricidae			
Sorex trowbridgii	1 (1)	0.1	This study
Talpidae			
Scalopus aquaticus	1 (1)	0.1	Fitch (1999)
LAGOMORPHA			
Leporidae			
Lepus californicus	3 (2–3)	0.3	Burt & Hoyle (1934); Reynolds & Scott (1982)
Sylvilagus audubonii	6 (3–6)	0.6	Fitch (1949); Howard (1949); Reynolds & Scott (1982)
Sylvilagus bachmani	3 (3)	0.3	This study
Sylvilagus floridanus	1 (1)	0.1	Fitch (1999)
Sylvilagus nuttallii	12 (2–12)	1.1	Diller & Wallace (1996)
Sylvilagus sp.	5 (4)	0.5	This study; Parker & Brown (1980); Iverson & Akre (2001)
Unidentified rabbits	7 (4)	0.7	Ruthven (1907); Klauber (1947)
RODENTIA			
Geomyidae			
Geomys bursarius	6 (4–5)	0.6	This study; Imler (1945); Wellstead (1981); Iverson & Akre (2001)
Geomys sp.	1 (1)	0.1	This study
Thomomys bottae	26 (19–20)	2.4	This study; von Bloeker (1942); Fitch (1949); Cunningham (1959)
Unknown no. of *Thomomys bottae*	1 (?)	0.1	Gehlbach (1965)
Thomomys sp.	11 (3)	1.0	This study
Unidentified gophers	1 (1)	0.1	Klauber (1947)
Heteromyidae			
Chaetodipus penicillatus	1 (1)	0.1	Reynolds & Scott (1982)
Chaetodipus sp.	7 (7)	0.7	This study; von Bloeker (1942)

Appendix *Continued*

Prey taxon	Frequency	Percentage of total number of prey	Source
Dipodomys heermanni	2 (2)	0.2	This study; Fitch (1949)
Dipodomys merriami	10 (7–9)	0.9	This study; Miller & Stebbins (1964); Reynolds & Scott (1982)
Dipodomys ordii	12 (4–12)	1.1	This study; Diller & Wallace (1996); Iverson & Akre (2001)
Dipodomys venustus	1 (1)	0.1	This study
Dipodomys sp.	6 (6)	0.6	This study; Fautin (1946); Klauber (1947)
cf. *Dipodomys* sp.	2 (2)	0.2	This study
Perognathus apache	1 (1)	0.1	This study
Perognathus longimembris	1 (1)	0.1	von Bloeker (1942)
Perognathus parvus	6 (1–6)	0.6	Diller & Wallace (1996)
Perognathus (s. l.) sp.	20 (18–19)	1.9	This study; Fitch (1949); Parker & Brown (1980); Iverson & Akre (2001)
Unknown no. of *Perognathus* (*s. l.*) sp.	1 (1)	0.1	Imler (1945)
Unidentified heteromyids	2 (2)	0.2	This study
cf. unidentified heteromyids	3 (3)	0.3	This study
Muridae			
Baiomys taylori	1 (1)	0.1	This study
Clethrionomys californicus	1 (1)	0.1	This study
Lemmiscus curtatus	4 (1)	0.4	Hammerson (1999)
Microtus californicus	72 (45–51)	6.8	This study; von Bloeker (1942); Fitch (1949)
Microtus longicaudus	2 (2)	0.2	This study; Parker & Brown (1980)
Microtus montanus	18 (5–14)	1.7	This study; Parker & Brown (1980); Diller & Wallace (1996)
Microtus ochrogaster	9 (2–8)	0.8	This study; Fitch (1999)
Microtus sp.	80 (18–56)	7.5	This study; Imler (1945); Iverson & Akre (2001)
Unknown no. of *Microtus* sp.	1 (1)	0.1	Imler (1945)
cf. *Microtus* sp.	5 (5)	0.5	This study
Mus musculus	17 (8–14)	1.6	This study; Diller & Wallace (1996)
Neotoma albigula	2 (2)	0.2	Douglas (1966); D. Caldwell, pers. comm.
Neotoma cinerea	1 (1)	0.1	This study
Neotoma fuscipes	4 (2–4)	0.4	This study; Fitch (1949)
Neotoma lepida	7 (7)	0.7	This study
Neotoma sp.	3 (3)	0.3	Gloyd (1937); Miller & Stebbins (1964); Bostic (1971)
Unknown no. of *Neotoma* sp.	1 (?)	0.1	Gehlbach (1965)
cf. *Neotoma* sp.	1 (1)	0.1	This study
Ondatra zibethicus	1 (1)	0.1	Diller & Wallace (1996)
Onychomys torridus	3 (1)	0.3	This study
cf. *Onychomys leucogaster*	1 (1)	0.1	Marr (1944)
Peromyscus californicus	1 (1)	0.1	von Bloeker (1942)
Peromyscus cf. *P. californicus*	1 (1)	0.1	Grinnell & Storer (1924)
Peromyscus leucopus	2 (2)	0.2	Fitch (1999)

Appendix *Continued*

Prey taxon	Frequency	Percentage of total number of prey	Source
Peromyscus maniculatus	58 (12–54)	5.4	This study; von Bloeker (1942); Marr (1944); Reynolds & Scott (1982); Diller & Wallace (1996)
Peromyscus cf. *P. maniculatus*	1 (1)	0.1	This study
Peromyscus sp.	60 (31–35)	5.6	This study; Fitch (1949); Parker & Brown (1980); Iverson & Akre (2001)
Unknown no. of *Peromyscus* sp.	1 (?)	0.1	Gehlbach (1965)
cf. *Peromyscus* sp.	3 (3)	0.3	This study
Reithrodontomys megalotis	19 (17)	1.8	This study; von Bloeker (1942)
cf. *Reithrodontomys megalotis*	1 (1)	0.1	This study
Sigmodon arizonae	3 (2)	0.3	This study
Sigmodon hispidus	2 (2)	0.2	This study; Fitch (1999)
Unidentified murids	14 (9)	1.3	This study
cf. unidentified murids	1 (1)	0.1	This study
Sciuridae			
Ammospermophilus leucurus	7 (3)	0.7	This study; Fautin (1946); Parker & Brown (1980)
Ammospermophilus nelsoni	1 (1)	0.1	Jennings *et al.* (1996)
Spermophilus beecheyi	5 (1–5)	0.5	Fitch (1949)
Spermophilus lateralis	2 (1)	0.2	Hammerson (1999)
Spermophilus mexicanus	1 (1)	0.1	Bailey (1905)
Spermophilus mollis	2 (2)	0.2	Richardson (1915); Fautin (1946)
Spermophilus spilosoma	1 (1)	0.1	Reynolds & Scott (1982)
Spermophilus townsendii	16 (4–14)	1.5	This study; Diller & Wallace (1996)
Spermophilus tridecemlineatus	2 (2)	0.2	Webb (1970); Hammerson (1999)
Spermophilus sp.	7 (5)	0.7	This study
cf. *Spermophilus* sp.	2 (2)	0.2	This study
Unidentified ground squirrels	2 (2)	0.2	Ruthven (1907); Turner (1955)
Unknown no. of ground squirrels	2 (2)	0.2	Klauber (1947)
Unidentified sciurids	2 (2)	0.2	This study
cf. unidentified sciurids	1 (1)	0.1	This study
Unidentified rodents	103 (55)	9.7	This study, Pack (1919); Woodbury (1928); Klauber (1947); Fitch (1949)
Unknown no. of rodents	2 (2)	0.2	Klauber (1947)
Unidentified mammals	75 (49–72)	7.0	This study; Parker & Brown (1980); Iverson & Akre (2001)
Unknown no. of unidentified mammals	1 (1)	0.1	McKinney & Ballinger (1966)
Aves			
ANSERIFORMES			
Anatidae			
Anas acuta eggs	1 (1)	0.1	Rockwell (1911)
Anas crecca	1 (1)	0.1	Glup & McDaniel (1988)
Unknown no. of *Anas platyrhynchos* eggs	1 (1)	0.1	Hammerson (1999)
Anas strepera eggs	7 (2)	0.7	Imler (1945)
Aythya americana eggs	1 (1)	0.1	Imler (1945)

Appendix *Continued*

Prey taxon	Frequency	Percentage of total number of prey	Source
Oxyura jamaicensis	1 (1)	0.1	Imler (1945)
Unidentified ducks	2 (2)	0.2	Imler (1945); Iverson & Akre (2001)
Unknown no. of duck eggs	2 (2)	0.2	Imler (1945); Glup & McDaniel (1988)
CHARADRIIFORMES			
Recurvirostridae			
Recurvirostra americana eggs	7 (1)	0.7	Imler (1945)
Scolopacidae			
Unknown no. of *Numenius* americanus eggs	1 (1)	0.1	Hammerson (1999)
COLUMBIFORMES			
Columbidae			
Zenaida macroura	2 (1)	0.2	Marr (1944)
Unknown no. of *Zenaida macroura*	1 (1)	0.1	D. Caldwell, pers. comm.
Unknown no. of *Zenaida* macroura eggs	1 (1)	0.1	D. Caldwell, pers. comm.
GALLIFORMES			
Odontophoridae			
Callipepla californica eggs	20 (4)	1.9	Fitch (1949)
Callipepla gambelii eggs	8 (1)	0.8	Huey (1942)
Unidentified quails	1 (1)	0.1	Klauber (1947)
Quail eggs	11 (2)	1.0	Klauber (1947)
Phasianidae			
Gallus gallus	1 (1)	0.1	Klauber (1947)
Gallus gallus eggs	1 (1)	0.1	Klauber (1947)
cf. *Numida meleagris* eggs	1 (1)	0.1	Klauber (1947)
Unidentified pheasants	1 (1)	0.1	Iverson & Akre (2001)
PASSERIFORMES			
Aegithalidae			
Psaltriparus minimus	3 (1)	0.3	Ervin & Rose (1973)
Alaudidae			
Eremophila alpestris eggs	3 (1)	0.3	This study
Cardinalidae			
Unknown no. of cf. *Spiza americana* eggs	1 (1)	0.1	Fitch (1999)
Corvidae			
Cyanocitta stelleri	4 (1)	0.4	Klauber (1947)
Emberizidae			
Unknown no. of *Junco hyemalis oreganus*	1 (1)	0.1	Cunningham (1959)
Unknown no. of *Pipilo crissalis* nestlings or eggs	1 (1)	0.1	Eichholz & Koenig (1992)
Hirundinidae			
Unknown no. of *Hirundo rustica*	1 (1)	0.1	Parker & Brown (1980)
Unknown no. of *Petrochelidon pyrrhonota* nestlings or eggs	1 (1)	0.1	Thompson & Turner (1980)
Stelgidopteryx serripennis	1 (1)	0.1	Hammerson (1999)
Stelgidopteryx serripennis eggs	4 (1)	0.4	Best (1977)
Unknown no. of *Stelgidopteryx serripennis* eggs	1 (1)	0.1	Strecker (1929)
Icteridae			
Unknown no. of *Euphagus cyanocephalus* nestlings or eggs	1 (1)	0.1	Eichholz & Koenig (1992)

Appendix *Continued*

Prey taxon	Frequency	Percentage of total number of prey	Source
Icterus galbula	3 (1)	0.3	Marr (1985)
Unknown no. of *Icterus galbula* nestlings or eggs	1 (1)	0.1	Eichholz & Koenig (1992)
Quiscalus quiscula eggs	1 (1)	0.1	Niedrach (1971)
Unknown no. of *Sturnella* sp.	1 (1)	0.1	Imler (1945)
Unknown no. of cf. *Sturnella* sp. eggs	1 (1)	0.1	Fitch (1999)
Unknown no. of icterids	1 (1)	0.1	Imler (1945)
Sturnidae			
Unknown no. of *Sturnus vulgaris* nestlings or eggs	1 (1)	0.1	Eichholz & Koenig (1992)
Troglodytidae			
Unknown no. of cf. *Troglodytes aedon* eggs	1 (1)	0.1	Fitch (1999)
Turdidae			
Sialia currucoides	1 (1)	0.1	E. D. Brodie III, pers. comm.
Unknown no. of *Sialia currucoides* eggs	1 (1)	0.1	Hammerson (1999)
Sialia mexicana	15 (4)	1.4	J. L. Dickinson, pers. comm.
Unknown no. of *Sialia mexicana*	1 (1)	0.1	J. L. Dickinson, pers. comm.
Sialia mexicana eggs	1 (1)	0.1	J. L. Dickinson, pers. comm.
Unknown no. of *Sialia mexicana* nestlings or eggs	2 (2)	0.2	Eichholz & Koenig (1992); J. L. Dickinson, pers. comm.
Unknown no. of *Sialia sialis*	1 (1)	0.1	Howitz (1986)
Turdus migratorius	2 (2)	0.2	Maxson (1981); Hammerson (1999)
Turdus migratorius eggs	1 (1)	0.1	Maxson (1981)
Tyrannidae			
Myiarchus cinerascens	1 (1)	0.1	J. L. Dickinson, pers. comm.
Unknown no. of passerines	1 (1)	0.1	Gehlbach (1965)
PICIFORMES			
Picidae			
Colaptes auratus	5 (1)	0.5	Hammerson (1999)
Unknown no. of *Melanerpes formicivorus* eggs	1 (1)	0.1	Eichholz & Koenig (1992)
STRIGIFORMES			
Strigidae			
Asio flammeus	2 (1)	0.2	Imler (1945)
Unknown no. of *Otus flammeolus* eggs	1 (1)	0.1	McCallum, Gehlbach & Webb 1995
Unidentified birds	31 (27–28)	2.9	This study; Cunningham (1959); Klauber (1947); Hulse (1973); Reynolds & Scott (1982); Diller & Wallace (1996); Fitch (1999)
Unknown no. of unidentified birds	1 (1)	0.1	McKinney & Ballinger (1966)
Bird eggs	46 (16–30)	4.3	This study; Fitch (1999); Iverson & Akre (2001)
Unknown no. of bird eggs	2 (2)	0.2	McKinney & Ballinger (1966); Diller & Wallace (1996)
Reptilia			
SQUAMATA			
Crotaphytidae			
Gambelia wislizenii	1 (1)	0.1	This study

Appendix *Continued*

Prey taxon	Frequency	Percentage of total number of prey	Source
Phrynosomatidae			
Sceloporus occidentalis	7 (4–5)	0.7	This study; Fitch (1949)
Sceloporus cf. *S. occidentalis*	2 (2)	0.2	This study
Sceloporus undulatus	3 (1)	0.3	This study
Unknown no. of *Sceloporus undulatus*	1 (?)	0.1	Gehlbach (1965)
Sceloporus sp.	1 (1)	0.1	Klauber (1947)
Urosaurus ornatus	1 (1)	0.1	Hulse (1973)
Uta stansburiana	7 (6–7)	0.7	This study; Fitch (1949); Parker & Brown (1980)
Sceloporine lizards	2 (2)	0.2	This study
Teiidae			
Cnemidophorus sexlineatus	2 (1–2)	0.2	Fitch (1999)
Cnemidophorus tessellatus	1 (1)	0.1	Klauber (1947)
Cnemidophorus tigris	1 (1)	0.1	This study
Cnemidophorus sp.	2 (2)	0.2	This study; Klauber (1947)
Unidentified lizards	4 (4)	0.4	This study
SERPENTES			
Colubridae			
Pituophis catenifer	1 (1)	0.1	Klauber (1947)
Viperidae			
Crotalus oreganus cerberus[1]	1 (1)	0.1	K. Diehl, pers. comm.
Crotalus oreganus lutosus[1]	2 (1)	0.2	Klauber (1972)
Unidentified snakes	1 (1)	0.1	This study
Unidentified squamates	2 (2)	0.2	This study
Squamate eggs	3 (2)	0.3	This study
Testudines			
Unknown no. of turtle eggs	1 (1)	0.1	McKinney & Ballinger (1966)
Amphibia			
ANURA			
Pelobatidae			
Scaphiopus couchii	1 (1)	0.1	This study
Unknown no. of anuran eggs	1 (1)	0.1	McKinney & Ballinger (1966)
Insecta			
ORTHOPTERA			
Unidentified orthopterans	1 (1)	0.1	Parker & Brown (1980)
Total	**1066**		

[1]fide Ashton & de Queiroz (2001).