

## Feeding Ecology of the Milksnake (*Lampropeltis triangulum*, Colubridae) in the Western United States

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**ABSTRACT.**—We examined the diet of the Milksnake (*Lampropeltis triangulum*) in the western United States and evaluated predictions about ontogenetic shifts, sexual divergence, and geographic variation in diet. Identifiable prey items were found in 139 specimens, and 41 additional prey items were recorded from the literature, for 180 prey items in total from 175 individual snakes. *Lampropeltis triangulum* is a generalist predator and feeds primarily on lizards and mammals. Skinks made up a large portion of the total diet. Other lizard taxa were also important prey, whereas reptile eggs, snakes, and birds were consumed infrequently. Ontogenetic shifts in diet were documented. The upper size limit of prey increased with increasing snake size, and adult snakes continued to feed on small prey. Prey type also was related to snake size. Juveniles fed more frequently on lizards, but adults fed mainly on mammals. Although males were longer than females, there was no sexual size dimorphism in mass, and there were no differences in diet between sexes. Diet varied geographically, and the proportion of endothermic prey was greater at higher latitudes after accounting for snake size.

Snakes form a clade composed entirely of predaceous species, making them valuable study models for understanding predator and prey relationships (Greene, 1983). Research on snake diets has provided insight into various aspects of evolution (Savitzky, 1983), ecology (Reynolds and Scott, 1982), and conservation planning (Holycross and Douglas, 2007). Patterns in foraging ecology of many species are well documented, but most species have not been examined. Evaluating the foraging ecology of widespread species is important to establish the general patterns of prey–predator size relationships, ontogenetic shifts, sexual divergence, and geographic variation in diet.

Snakes are gape-limited predators, and snake size is a fundamental predictor of the upper size limit of the prey that can be consumed. Many snake species undergo ontogenetic shifts in diet, switching from smaller to larger prey with increasing size and age (Mushinsky, 1987), and excluding small prey from their diet in preference to larger, more energy-rich prey (Arnold, 1993). The ratio of prey-to-snake mass is an important response variable in quantifying ontogenetic shifts (Greene, 1983). Ingestion of proportionately heavier prey allows snakes to forage less frequently, a trade-off that may require a larger gape and larger body size. Two common patterns of prey to snake size relationships related to ontogenetic shifts with increases in snake body size are the ontogenetic telescope and the ontogenetic shift in lower prey size (Arnold, 1993).

The ontogenetic telescope describes an increase in prey size with increasing snake size, but no exclusion of smaller prey items from the diets of adult snakes (Fig. 1A). The ontogenetic shift in lower prey size describes a pattern of snakes feeding on larger prey with increasing snake size while also excluding smaller prey (Fig. 1B). Both ontogenetic shifts are qualitatively similar and require weight ratios to distinguish the two patterns (Rodríguez-Robles, 2002).

Ontogenetic shifts are often related to prey type as well as to prey size. Endothermic prey tend to be bulkier and more difficult to swallow than more slender, ectothermic prey, and snakes that prey on endotherms are larger and have a subsequently larger gape than snakes feeding primarily on ectotherms (Rodríguez-Robles et al., 1999). Ontogenetic shifts in

diet for many snake species are characterized by a shift from smaller ectothermic to larger endothermic prey with increasing snake size (Mushinsky, 1987).

Optimal foraging theory predicts that predators should either maximize energy gains or minimize time spent to obtain a fixed amount of energy (Kie, 1999). Dietary shifts in prey size and type may be related to differing energy and nutritional returns of different prey, balanced against costs of prey capture, ingestion, and digestion (Arnold, 1993). For example, larger endothermic prey may be preferred relative to smaller ectothermic prey because larger prey provide more energy relative to effort. Swallowing prey headfirst is an energetic adaptation to reduce the cost of prey handling. Most snakes swallow their prey headfirst to minimize the resistance of limbs, teeth, scales, fur, or feathers; reduce handling time; prevent abrasion of the esophagus; and allow ingestion of larger prey (Greene, 1976; Mori, 2006). Alternatively, factors such as differences in prey availability, habitat use, and thermal preferences between juveniles and adults also may be important to the optimization of energy acquisition, ultimately influencing dietary shifts (Shine, 1991b).

Sexual size dimorphism is pronounced in many snake species (Shine, 1978) and can lead to dietary divergence between the sexes (Shine, 1991a; Glaudas et al., 2008). Shine (1991a) considered dietary divergence to be an adaptation driven by body size differences related to reproductive biology. In many snake species with limited sexual dimorphism in body size, little divergence in diet is found between males and females (Holycross et al., 2002; Gardner and Mendelson, 2003). Documentation of dietary differences or similarities is important for understanding potential niche differentiation, resource partitioning, and intraspecific competition between males and females.

Some snake species are specialized predators with little geographic variability in their diets (Shine, 1984; Gardner and Mendelson, 2003), but most wide ranging species are characterized by geographic variation in diet (Rodríguez-Robles and Greene, 1999; Clark, 2002; Holycross and Mackessy, 2002; Glaudas et al., 2008). Geographic variation in diet is likely to be related to geographic variation in prey availability. Endotherm diversity increases with latitude relative to the diversity of ectotherms (Simpson, 1964; Kiestler, 1971), and endotherms are increasingly available as prey at higher latitudes. Therefore,

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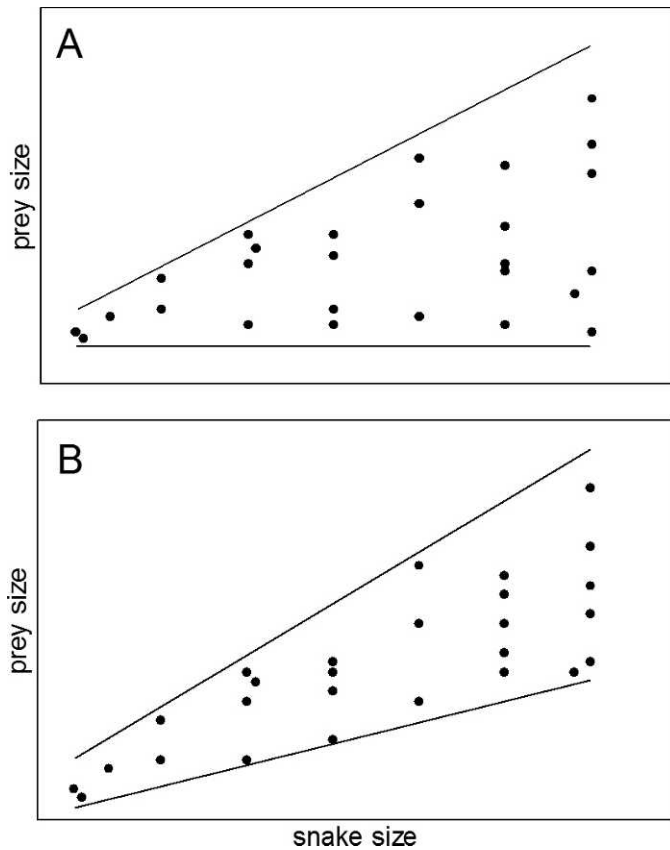


FIG. 1. Hypothetical relationships between predator and prey size. (A) Ontogenetic telescope; an increase in prey size with increasing snake size but no exclusion of smaller prey items. (B) Ontogenetic shift; an increase in prey size with increasing snake size while also excluding smaller prey (Arnold, 1993).

differential prey availability could potentially affect relationships between predator and prey size, ontogenetic shifts, and sexual divergence in diet.

The Milksnake (*Lampropeltis triangulum*) is distributed widely across a latitudinal gradient of >5,600 km, representing a variety of climates, biomes, ecoregions, and habitats that support a diverse suite of potential prey (Williams, 1988). Relative to other populations throughout the distribution of *L. triangulum*, populations in the arid western United States, are patchily distributed, more secretive and fossorial, smaller in body size, and less abundant (Williams, 1988; Conant and Collins, 1998; Stebbins, 2003). Although male *L. triangulum* are generally larger than females (Fitch and Fleet, 1970; Rodriguez and Drummond, 2000), sexual size dimorphism is less pronounced in the smaller western subspecies (Williams, 1988). In several western states, *L. triangulum* is a species of conservation priority and is either protected from collection or its collection is regulated (Hammerson, 1999; Werner et al., 2004; Brennan and Holycross, 2006; Sievert and Sievert, 2006). In these states, observations of feeding have been generally limited to anecdotal field observations and lists of prey species accepted by captive specimens (Guidry, 1953; Wright and Wright, 1957; Kamb, 1978).

We examined the diet of *L. triangulum* in the western United States using museum specimens, field observations, and literature records. Our primary objectives were to 1) test predictions about the feeding ecology of *L. triangulum* over a large geographic region and 2) provide additional dietary

information on this species. Specifically, we predicted 1) a positive relationship between prey and snake mass consistent with an ontogenetic shift in diet; 2) an ontogenetic shift in prey type with larger snakes preying on endotherms; 3) dietary divergence between males and females, with males feeding on a higher proportion of endothermic prey; and 4) geographic variation in diet, with the frequency of endothermic prey increasing with latitude.

#### MATERIALS AND METHODS

**Data Collection.**—We examined museum and field specimens of *L. triangulum* from Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, Oklahoma, South Dakota, Texas, Utah, and Wyoming. These states were chosen to cover an area of similar aridity, where primary production is limited by soil moisture, and approximately coincide with the region west of the 100th meridian (Hunt, 1967). Voucher specimens requested for this study were located on the HerpNet data base portal (<http://www.herpnet.org/herpnet/portal.html>, 16 October 2005; Appendix 1). Field samples were collected from feces of specimens palpated in the field in Navajo County, Arizona, in 2005 and 2006 as part of an inventory and monitoring program for reptiles and amphibians (E. Nowak, unpubl. data).

For each museum specimen, we made incisions (2–5 cm) into the stomach and colon and visually searched for prey items. If prey items were found after initial examination, incisions were enlarged to allow their removal. Prey items were stored in 70% ethanol after their removal. Field specimens from northern Arizona were palpated, and fecal material was collected and stored in 70% ethanol, with subsequent release of live snakes. We noted the location of prey items in the gastrointestinal tract (GI) and considered the stomach the upper gastrointestinal tract (UGI) and the intestines and colon the lower gastrointestinal tract (LGI). Prey items that occurred across both the UGI and LGI were combined into a UGI and LGI category for analysis. Because most gape-limited predators swallow their prey headfirst (Greene, 1976), when possible, we inferred the direction of ingestion (head or tail first) from orientation in the GI.

Prey items were examined under a  $\times 40$  magnification dissecting microscope. We identified prey items to the lowest level of taxonomic resolution possible by comparison with reference specimens, taxonomic keys, and range maps. Lower levels of taxonomic resolution were generally achieved for prey items from the UGI relative to those from the LGI. We grouped prey items into hierarchical categories consisting of endothermic (bird or mammal) and ectothermic prey. Ectothermic prey items were further classified into snakes, lizards, reptile eggs, and unknown reptiles.

We measured snout-to-vent length (SVL) by stretching a flexible tape measure along each snake's body from the tip of the rostral scale to the terminus of the anal scale ( $\pm 1$  mm). After removal of prey items from the GI, snakes and prey items were blotted dry with a paper towel, and mass was determined with a digital scale ( $\pm 0.1$  g). Sex was determined by the presence or absence of hemipenes or other reproductive structures (i.e., ova, vas deferens, or testes). However, we were unable to determine sex for many damaged and poorly preserved specimens.

To expand our sample sizes beyond museum and field specimens, we searched the literature for direct observations of feeding and prey items collected from free-ranging, wild snakes. Data from the literature were included in analyses of prey

frequencies, sexual size dimorphism, and geographic variation in diet. When snake size, sex, and GI position were not available from published sources, literature data were excluded from analyses of relationships between prey items, snake size, and sex. We excluded all literature references to prey fed to captive snakes and accounted for redundancy in literature records. In all cases, arthropod and insect parts were noted but were always very small relative to the size of the snake and were always found in association with a much larger prey item. Therefore, we classified arthropod and insect parts as a separate prey category and assumed they were ingested secondarily (sensu Fitch, 1960:209).

**Data Analysis.**—Chi-square ( $\chi^2$ ) analyses were used to test for differences in frequencies of prey items in the digestive tract, direction of ingestion, and prey categories. We used linear regression to examine the functional relationship between the natural log of snake mass and prey mass. Unless otherwise indicated, values presented are means  $\pm$  SE. *P* values were interpreted for two-tailed tests, and  $\alpha$  was set at 0.05. Statistical tests were performed using MINITAB version 14 (Minitab Inc., 2004).

**Ontogenetic Shift in Prey Size.**—We used linear regression to examine the functional relationship between snake mass and prey mass (both values natural log transformed). The ontogenetic telescope is supported when prey mass is related positively to snake mass and the weight ratio of prey:snake mass is not related to snake mass. An ontogenetic shift in lower prey size is supported when both prey mass and weight ratio are related positively to snake mass (Rodríguez-Robles, 2002). We tested for normality of the prey:predator body mass ratio.

**Ontogenetic Shift in Prey Type.**—The relationship between prey type and snake body size was examined by comparing prey categories across a range of snake body sizes. We then used a *t*-test for unequal variances to determine whether snakes preying on endotherms and mammals were larger than snakes preying on ectotherms and lizards. Large snakes were defined as individuals greater than the median SVL and small snakes as less than this value. We used  $\chi^2$  tests to determine whether larger snakes consumed mammals more frequently, and whether smaller snakes consumed lizards more frequently than expected due to chance.

**Sexual Differences in Diet.**—We used *t*-tests to assess sexual size dimorphism in SVL and body mass. Included in these tests are SVL measurements from 11 additional individuals from Utah (Tanner, 1941). We used  $\chi^2$  tests for differences in frequencies of prey types (endothermic vs. ectothermic and mammal vs. lizard) between sexes.

**Geographic Variation in Diet.**—To examine the relationship between proportion of endothermic prey and latitude, we combined prey records by state and determined the latitude of the geographic center of each state using ArcGIS 9.1 (ESRI Inc., Redlands, California). The endothermic prey proportion (ratio of endothermic/total prey number of prey items ingested per individual) was distributed normally, so we determined the Pearson product moment correlation coefficient between state latitude, snake SVL, and snake mass with prey proportion as the independent variable. Similarly, we determined correlation coefficient between SVL and latitude. We examined the influence of latitude and snake size on prey type (endothermic vs. ectothermic) using binary logistic regression. For each prey item, we used ArcMap 9.1 to determine the latitude of the geographic center of each county of collection. We then used prey type as the

dependent variable and latitude and snake size as the independent variables.

## RESULTS

We examined 955 specimens in total (947 museum specimens and eight live specimens in the field). Of these, 139 (14.5%) contained identifiable prey items. Thirty-eight prey items (4.0%) were removed but could not be identified. Identifiable prey items were more frequently found in the LGI (62.3%) than the UGI (28.3%) and least frequently in both the UGI and LGI (9.4%;  $\chi^2 = 31.2$ , *df* = 2, *P* < 0.0001). Direction of ingestion was inferred for 21 prey items and was predominantly head first (90%) and rarely tail first (10%;  $\chi^2 = 7.5$ , *df* = 1, *P* = 0.006). Prey items were generally highly digested and identifiable only to broad categories, but the presence of hair, feathers, or scales permitted identifications to mammal, bird, or squamate reptile; leathery calcareous shell to reptile egg; and scales and toe parts to lizard. Eggs were presumed to be reptile eggs based on their leathery, unbroken, folded appearance and size. It was often possible to identify lizards to more discrete categories by the presence of distinctive scales, i.e., Scincidae, *Sceloporus*, and *Aspidoscelis* (Powell et al., 1998). The single snake we found was *Tropidoclonion lineatum* (Stebbins, 2003). Arthropod parts were noted in 17 specimens. We recorded an additional 41 prey items from the literature search, for 180 prey items in total from 175 individual snakes (Appendix 2).

*Lampropeltis triangulum* in the western United States consumed ectotherms (65.6%) more frequently than endotherms (34.4%;  $\chi^2 = 8.9$ , *df* = 1, *P* = 0.003; Fig. 2). Ectothermic prey (*n* = 118) were primarily squamate reptiles (91.5%) and rarely reptile eggs (8.5%;  $\chi^2 = 55.1$ , *df* = 1, *P* < 0.0001). Endothermic prey (*n* = 62) was almost entirely mammalian (98.4%), with a single bird (1.6%;  $\chi^2 = 37.1$ , *df* = 1, *P* < 0.0001). Squamate reptile prey (*n* = 108) consisted of lizards (85.2%), with snakes (4.6%) and unidentified reptiles (10.2%) forming smaller portions of the ectothermic diet ( $\chi^2 = 61.2$ , *df* = 2, *P* < 0.0001). Lizards (*n* = 92) were primarily of the family Scincidae (62.0%), *Sceloporus* (19.6%), *Aspidoscelis* (10.9%), *Ophisaurus* (2.2%), *Uta* (1.1%), and unidentified (4.3%;  $\chi^2 = 64.7$ , *df* = 5, *P* < 0.0001).

**Ontogenetic Shift in Prey Size.**—Due to the advanced stages of digestion for most prey items, reliable data on prey mass were relatively few (*n* = 21). The mean weight ratio of prey to snake mass was  $0.12 \pm 0.07$  (range, 0.005–0.735). Heavier snakes ingested heavier prey items, but snake mass explained only a small portion of the variation in this relationship (adjusted  $r^2 = 0.19$ ; Fig. 3A). There was no relationship between prey:snake weight ratio and snake weight (Fig. 3B).

**Ontogenetic Shift in Prey Type.**—When individual prey items were categorized (e.g., endotherms, ectotherm) and plotted against SVL, relatively small snakes seemed to consume mainly ectothermic vertebrates and relatively large snakes consumed mainly endothermic vertebrates (Fig. 4). Relatively long and heavy snakes tended to consume more endotherms, and conversely fewer ectotherms, than did relatively small snakes. Snakes preying on endotherms (snake SVL =  $468 \pm 22$  mm) were significantly longer than snakes that ingested ectothermic prey (snake SVL =  $360 \pm 13$  mm; *t* =  $-4.16$ , *df* = 67, *P* < 0.0001; 95% confidence interval [CI] = 63–166 mm), and this relationship held for snake mass (snake mass =  $55 \pm 7$  g, *n* = 41; snake mass =  $31 \pm 3$  g, *n* = 96; *t* =  $-3.23$ , *df* = 56, *P* = 0.002; 95% CI = 10–40 g). Snakes that ingested mammals were significantly longer and heavier than snakes that ingested lizards (*t* =  $-3.74$ , *df* = 68, *P* <

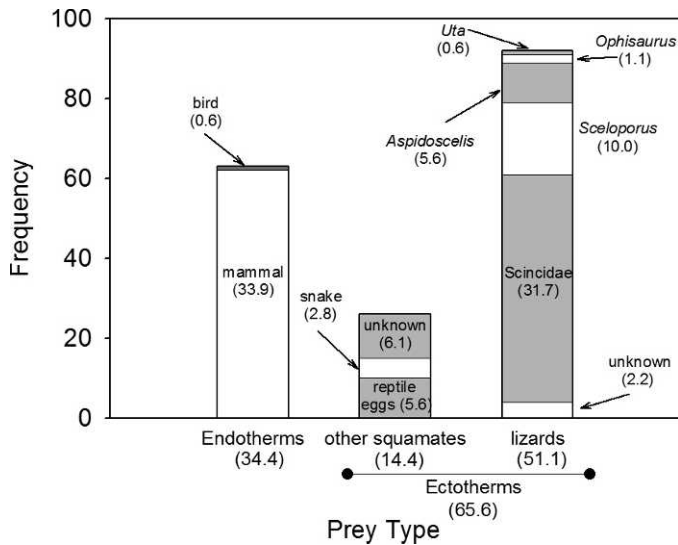


FIG. 2. Prey composition of *L. triangulum* in the western United States (total prey items  $n = 180$ ). Vertical bars represent the number of prey items identified from museum, field, and literature records; values in parentheses are percentage composition.

0.0001, 95% CI = 62–170 mm;  $t = -3.41$ ,  $df = 56$ ,  $P < 0.001$ , 95% CI = 11–42 mm). The frequencies of prey item types ingested varied over a range of snake body sizes. Relatively “large” and “small” snakes were defined as individuals longer or shorter than

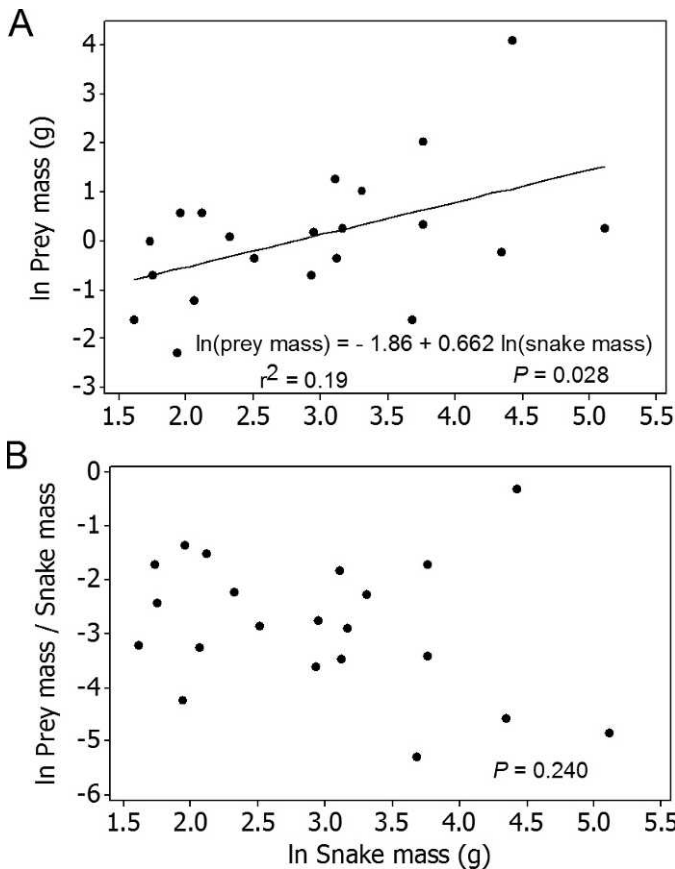


FIG. 3. Relationships between prey and predator mass for *L. triangulum* in the western United States. (A) Prey mass vs. snake mass. (B) Prey:snake mass vs. snake mass. Values on both axes were natural log transformed, and each circle represents a single prey item.

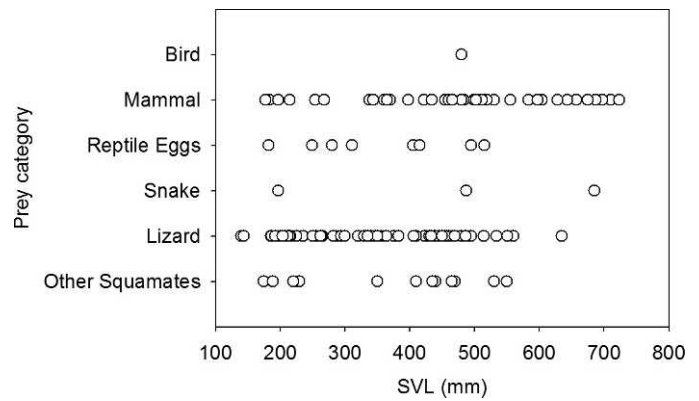


FIG. 4. Relationship between prey type and snake size (SVL) of *L. triangulum* in the western United States ( $n = 138$ ). Each circle represents a single prey item.

the median SVL of 410 mm, respectively. Large snakes consumed mammals more frequently (50.1%), and lizards less frequently (49%), than did small snakes (22.6 and 77.4%, respectively;  $\chi^2 = 9.2$ ,  $df = 1$ ,  $P = 0.002$ ).

**Sexual Size Dimorphism.**—Adult *L. triangulum* were sexually dimorphic in length but consumed similar frequencies of ectotherms and endotherms. Males were longer than females (male SVL =  $449 \pm 17$  mm; female SVL =  $387 \pm 18.0$  mm;  $t = -2.52$ ,  $df = 97$ ,  $P = 0.013$ ; 95% CI = 13–111 mm), but males and females did not differ in mass (male mass =  $49 \pm 5$  g; female mass =  $38 \pm 5$  g;  $t = -1.48$ ,  $df = 88$ ,  $P = 0.142$ ). Male and female snakes did not differ in the frequency of ectotherms or endotherms in their diets ( $\chi^2 = 0.637$ ,  $df = 1$ ,  $P = 0.423$ ) or in the frequency of mammals and lizards ( $\chi^2 = 0.008$ ,  $df = 1$ ,  $P = 0.929$ ).

**Geographic Variation in Diet.**—The proportion of endothermic prey was correlated positively with latitude (degrees), SVL (millimeters), and mass (grams; Fig. 5A, C, D). Although the scatterplot of snake SVL vs. latitude (Fig. 5B) seemed to indicate a positive relationship, the regression coefficient was not significant ( $P = 0.118$ ). The coefficients for both latitude and snake length were significant under a logistic regression model; however, the effect of latitude (coefficient = 0.166;  $P = 0.001$ ) was greater than SVL (coefficient = 0.007;  $P < 0.0001$ ).

DISCUSSION

*Lampropeltis triangulum* in the western United States fed primarily on lizards and mammals. Skinks made up a large portion of the total diet. Other lizard taxa also were important prey, whereas reptile eggs, snakes, and birds were infrequently consumed. The *L. triangulum* of our study in the western United States displayed an ontogenetic telescope in prey size vs. predator size and shifted from ectothermic to endothermic prey as they grew. We did not find evidence of sexual dimorphism in dietary composition, but we did see geographic variation in the prey items (ectothermic vs. endothermic) included in the diet.

**Ontogenetic Shift in Prey Size.**—The *L. triangulum* in our study showed an ontogenetic shift in diet consistent with an ontogenetic telescope (Arnold, 1993). The upper limit of prey size increased with increasing snake size, but larger snakes continued to feed on small prey. Rodriguez-Robles (2002) suggested that the ontogenetic telescope represents a general pattern in snakes, because it occurs in multiple species across

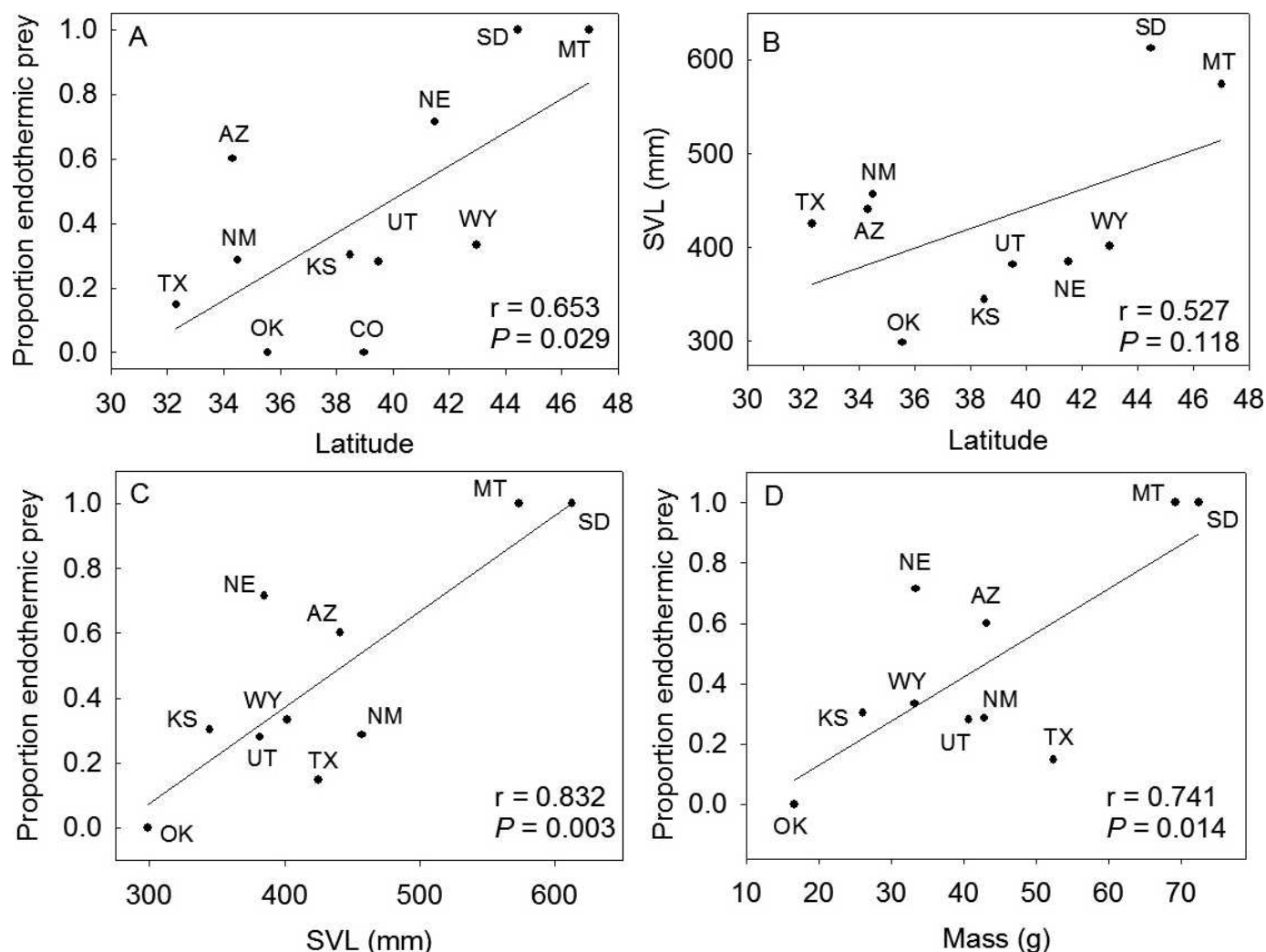


FIG. 5. Relationships between (A) endothermic prey and latitude, (B) SVL and latitude, (C) endothermic prey and SVL, and (D) endothermic prey and mass for *L. triangulum* in the western United States. State abbreviations are AZ = Arizona (3/5), CO = Colorado (0/1), KS = Kansas (26/85), MT = Montana (7/7), NE = Nebraska (5/7), NM = New Mexico (2/7), OK = Oklahoma (0/9), SD = South Dakota (2/2), TX = Texas (4/27), UT = Utah (7/25), and WY = Wyoming (1/3). Values in parentheses are the number of endothermic prey over the total number of prey items identified from museum and field specimens and literature records per state.

several families (e.g., *Crotalus atrox*, *Enhydryna schistosa*, *Acrochordus arafurae*, *Pituophis catenifer*).

Compared with other snake species (Rodríguez-Robles, 2002), the average ratio of prey to snake mass was low (0.12), indicating that *L. triangulum* fed on relatively small prey. Although the tendency of larger snakes to feed on large prey is related strongly to gape size, other factors may override this relationship. For example, Shine (1991b) found that foraging mode (active vs. ambush), encounter rates, ingestion efficiency, and prey choice were more important than gape limitations in predicting the upper limit of prey size under field conditions for Australian Blacksnakes (*Pseudechis porphyriacus*).

**Ontogenetic Shift in Prey Type.**—*Lampropeltis triangulum* also showed an ontogenetic shift in prey type, feeding more frequently on lizards as juveniles and on mammals as adults. Similar shifts from ectothermic to endothermic prey occur in many snake species. Shifts in prey type are related to prey size as well as shape. Compared with ectotherms, endotherms are generally larger and less cylindrical and therefore more difficult to ingest. In the western United States, *L. triangulum* is an active, nocturnal forager and likely captures most prey in burrows at

night (Fitch and Fleet, 1970; Fitch, 1999). Although most mammals were highly digested, several were neonates and these are smaller and more elongate than adults (Loop and Bailey, 1972; Morrison et al., 1977). Small snakes that fed on mammals likely captured and ingested these prey as neonates in their nests.

**Intersexual Differences in Body Size and Diet.**—The *L. triangulum* of our study were sexually dimorphic in body length but not mass. Although females were on average 14% shorter than males, diets were similar between the sexes. Although similar patterns in sexual size dimorphism are seen in other colubrids, such as *Pituophis catenifer* and *Rhinocheilus lecontei* (Shine, 1994), dietary divergence between sexes has not been examined explicitly in studies of their feeding ecology (Rodríguez-Robles and Greene, 1999; Rodríguez-Robles, 2002). Dietary divergence is driven primarily by body size differences, and the sexual size dimorphism in *L. triangulum* may not be large enough to allow the development of dietary divergence.

**Geographic Variation in Diet.**—As predicted, the diet of *L. triangulum* varied geographically, and the proportion of endothermic prey increased with latitude. As one of the most widely distributed snake species in the Western Hemisphere (Williams,

1988), this result was expected. Given that reptile diversity decreases at a greater rate than mammal diversity with increasing latitude (Simpson, 1964; Kiestler, 1971), our result may reflect an increase in the availability of mammalian prey at higher latitudes relative to endothermic prey, rather than a preference for endotherms at northern latitudes.

The seven subspecies in our study region are differentiated weakly; intergrade extensively; and occur in wide variety of grassland, woodland, and forest habitats (Tanner and Loomis, 1957; Williams, 1988). Geographically, we examined a greater number of individuals from intergrade zones than from areas within the established range of each subspecies. Although we were unable to address questions about feeding ecology by subspecies or habitat types, a finer grained sampling scheme could reveal additional geographic variation in diet.

The diet of *L. triangulum* populations in the west differed from eastern U.S. populations in several respects. Two well defined subspecies exist in the east, *L. t. triangulum* and *L. t. elapsoides*. *Lampropeltis t. triangulum* feeds primarily on mammals (Uhler et al., 1939; Surface, 1906; Dyrkacz, 1977; Brown, 1979) but also includes birds, snakes, lizards, and eggs (bird and squamate) in its diet (Medsker, 1922; Brown, 1979). *Lampropeltis t. elapsoides* feeds primarily on lizards (particularly skinks) and snakes (Williams, 1988; Lee, 2006). Our observed subspecific differences in diet are likely related to differences in body size and gape. We note that *L. t. triangulum* is one of the larger subspecies and *L. t. elapsoides* is the smallest (Williams, 1988), and the *L. triangulum* subspecies that we examined are intermediate in size (e.g., *annulata*, *amaura*, *syspila*, *celanops*, *taylori*, *gentilis*, and *multistriata*). Our results show that variation in body size seems to be related to dietary preference, and the studies cited above reveal an overall pattern in which the largest subspecies prey primarily on mammals, the smallest on slender ectothermic prey. Those included in this study fed on a mixture of the two prey types.

The proportion of *L. triangulum* with identifiable prey items (0.147) in this study was low relative to that of other studies (Shine, 1986; range, 0.05–1.00) and was particularly low considering that many studies used only UGI prey items (Gardner and Mendelson, 2003; Greene and Rodriguez-Robles, 2003; Glaudas et al., 2008; but see Taylor, 2001; Holycross and Mackessy, 2002; Weatherhead et al., 2009). Had we used only UGI prey items, identifiable prey would have fallen to 6%, one of the lowest yet reported in snakes (Shine, 1986) and much lower than reported in other *Lampropeltis* species (Klimstra, 1959; Greene and Rodriguez-Robles, 2003). The low percentage of prey items found may simply reflect infrequent feeding (sensu Shine, 1986) or extended intervals between collection and preservation, allowing digestion of prey and defecation prior to preservation (Greene and Rodriguez-Robles, 2003).

Stable nitrogen and carbon isotopes can provide integrated information about diet (Kelly, 2000), such as trophic level, prey proportions, and fasting; yet, they are rarely applied to studies of snake feeding ecology. Incorporation of stable isotopes into future studies of snake feeding ecology could provide alternative perspectives complementary to traditional GI analyses.

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APPENDIX 1. Natural history collections and number of specimens of *Lampropeltis triangulum* examined. The number of specimens is given in parentheses. Museum initialisms follow Sabaj Pérez (2010).

ASU (Arizona State University; 20), BYU (Monte L. Bean Museum, Brigham Young University; 104), CAS (California Academy of Sciences; 9), CM (Carnegie Museum of Natural History; 41), KUNHM (University of Kansas Natural History Museum and Biodiversity Research Center; 218), LACM (Natural History Museum of Los Angeles County; 65), LSU (Louisiana Museum of Natural History, Louisiana State University; 16), MCZ (Museum of Comparative Zoology, Harvard University; 17), MHP (Museum of the High Plains-Fort Hays State University, Sternberg Museum of Natural History; 123), MSB (Museum of Southwestern Biology, University of New Mexico; 31), MVZ (Museum of Vertebrate Zoology University of California-Berkeley; 23), OMNH (Sam Noble Oklahoma Museum, University of Oklahoma; 40), TCWC (Texas Cooperative Wildlife Collection, Texas A&M University; 87), UMMZ (University of Michigan Museum of Zoology; 38), UNSM (University of Nebraska State Museum; 104), UMNH (Utah Museum of Natural History; 11).

APPENDIX 2. Frequency of prey items in the diet of *L. triangulum* in the western United States, summarized by state. Prey item frequencies represent 180 prey items from 175 individual snakes.

ARIZONA ( $n = 19$ ): unknown mammal (3)<sup>1</sup>, unknown reptile (2)<sup>1</sup>; COLORADO ( $n = 19$ ): squamate eggs (1)<sup>2</sup>; KANSAS ( $n = 382$ ): *Blarina hylophaga* (2)<sup>6</sup>, *Cryptotis parva* (4)<sup>3,5,6</sup>, *Microtus ochrogaster* (9)<sup>6</sup>, *Perognathus* ssp. (1)<sup>1</sup>, *Peromyscus maniculatus* (1)<sup>3,5,6</sup>, unknown mammal (14)<sup>1</sup>, *Aspidoscelis sexlineata* (7)<sup>1,4</sup>, *Carphophis vermis* (1)<sup>3,5,6</sup>, *Diadophis punctatus* (2)<sup>3,5,6</sup>, *Ophisaurus attenuatus* (1)<sup>1</sup>, *Plestiodon fasciatus* (12)<sup>1,3,5,6</sup>, *Plestiodon obsoletus* (4)<sup>3,5,6</sup>, *Sceloporus consobrinus* (2)<sup>1,4</sup>, *Sceloporus* ssp. (3)<sup>1</sup>, unknown Scincidae (20)<sup>1</sup>, *Tropidoclonion lineatum* (1)<sup>1</sup>, squamate eggs (3)<sup>1,5</sup>; MONTANA ( $n = 11$ ): unknown bird (1)<sup>1</sup>, unknown mammal (6)<sup>1</sup>;

NEBRASKA ( $n = 103$ ): unknown mammal (5)<sup>1</sup>, *Aspidoscelis sexlineata* (1)<sup>1</sup>, *Sceloporus consobrinus* (1)<sup>1</sup>; NEW MEXICO ( $n = 34$ ): unknown mammal (3)<sup>1</sup>, *Arizona elegans* (1)<sup>9</sup>, *Sceloporus* ssp. (1)<sup>1</sup>, unknown reptile (2)<sup>1</sup>, *Uta stansburiana* (1)<sup>1</sup>; OKLAHOMA ( $n = 54$ ): *Sceloporus* ssp. (1)<sup>1</sup>, unknown Scincidae (4)<sup>1</sup>, unknown reptile (1)<sup>1</sup>, squamate eggs (3)<sup>1</sup>; SOUTH DAKOTA ( $n = 29$ ): unknown mammal (2)<sup>1</sup>; TEXAS ( $n = 163$ ): unknown mammal (4)<sup>1</sup>, *Ophisaurus attenuatus* (1)<sup>7</sup>, *Sceloporus* ssp. (4)<sup>1</sup>, Scincidae (10)<sup>1</sup>, unknown lizard (3)<sup>1</sup>, unknown reptile (5)<sup>1</sup>; UTAH ( $n = 90$ ): unknown mammal (6)<sup>1</sup>, *Aspidoscelis tigris* (2)<sup>1</sup>, *Plestiodon skiltonianus* (7)<sup>1</sup>, *Sceloporus graciosus* (1)<sup>8</sup>, *Sceloporus* ssp. (4)<sup>1</sup>, unknown lizard (1)<sup>1</sup>,

squamate eggs (3)<sup>1</sup>; WYOMING ( $n = 5$ ): unknown mammal (1)<sup>1</sup>, *Sceloporus* ssp. (1)<sup>1</sup>, unknown reptile (1)<sup>1</sup>.

\* *Lampropeltis triangulum* may not occur in North Dakota, because only a single specimen has been collected from the state (UMMZ 74338) in 1932 and is not included in most range maps (Williams, 1988; Stebbins, 2003). The species was recently described from eastern Nevada (Mulks, 2005), but no specimens were examined. Superscript numbers indicate the following source: 1, this study; 2, Hahn (1968); 3, Fitch and Fleet (1970); 4, Knight and Collins (1977); 5, Fitch (1982); 6, Fitch (1999); 7, Werler and Dixon (2000); 8, Tanner (1941); 9, Cotten et al. (2008).