

## Food Habits of the Glossy Snake, *Arizona elegans*, with Comparisons to the Diet of Sympatric Long-nosed Snakes, *Rhinocheilus lecontei*

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**ABSTRACT.**—We studied the diet of the North American glossy snake, *Arizona elegans*, by examining stomach contents of more than 700 museum specimens, and supplemented our findings with published dietary records. Fifty percent of 107 prey were lizards and 44% were mammals; birds and snakes composed the remaining prey. Most lizard prey were diurnal, and presumably were captured when they were inactive by nocturnally wide-foraging glossy snakes. Conversely, most rodent prey were nocturnal heteromyids that we suspect were ambushed by *A. elegans*, thus raising the possibility that these snakes use alternative hunting tactics on different prey types. Ninety-five percent of the specimens with food contained a single item, and all 49 prey for which we determined direction of ingestion were swallowed head-first. Although smaller *A. elegans* consumed mammals occasionally, specimens that ate mammals were significantly larger than those that fed on lizards, and glossy snakes that took birds were larger than those that ate mammals. Larger glossy snakes ate larger prey and added birds to their diet, but they continued to eat lizards and mammals, which suggests that there is no absolute ontogenetic change in the diet of *A. elegans*. For any given body size, *A. elegans* has a longer head, and thus a larger gape than the sympatric long-nosed snake, *Rhinocheilus lecontei*. This difference in relative head length may explain why smaller *A. elegans* are capable of predation on mammals, whereas smaller *R. lecontei* feed almost exclusively on lizards, and may also account in part for the higher frequency of stout-bodied phrynosomatid lizards and of mammals in the diet of glossy snakes.

Documenting the diet and foraging behavior of a snake species is often the first step in the development of an understanding of its ecology. A detailed description of the food habits of a predator can enable subsequent users of these observations to place them in a broader ecological and evolutionary context (Greene, 1993). Dietary information can be used, for example, to evaluate hypotheses about biological diversification (cf. Futuyma, 1998), to predict aspects of the ecology of closely-related taxa, or to guide conservation efforts (Greene, 1994).

Although general accounts (e.g., Perkins, 1949; Hammerson, 1986; Collins, 1993; Degenhardt et al., 1996) state that the glossy snake, *Arizona elegans*, eats lizards and small rodents, and occasionally snakes and birds, no study has specifically addressed the diet of this species. *Arizona elegans* (adult snout-vent length [SVL] = 66–178 cm) is found from central California to southwestern Nebraska in the United States and south through Baja California and the states of

Aguascalientes, San Luis Potosí, and Sinaloa, Mexico (Dixon and Fleet, 1976). In the United States, *A. elegans* is found from below sea level (in desert sinks) to 2200 m, and in general prefers sandy grasslands and shrub lands to woodlands (Klauber, 1946). Glossy snakes are excellent burrowers, but often use crevices or rodent burrows for retreats (Degenhardt et al., 1996). *Arizona elegans* is mainly a nocturnal snake, but in some populations, especially eastern ones, crepuscular and diurnal activity occurs (Klauber, 1946). Most annual activity occurs between April and September and varies somewhat with latitude and elevation (Degenhardt et al., 1996).

As part of our ongoing analyses of the trophic ecologies of several snake species in western North America, herein we report on the diet of *Arizona elegans*. Our study is based on stomach contents of museum specimens throughout the distribution of the species and judicious use of literature records. Our goals are to evaluate variation in taxonomic composition and predator/prey size relationships in the diet of *A. elegans*. We also compare aspects of the dietary habits of glossy snakes and long-nosed snakes, *Rhinocheilus lecontei*, widely sympatric nocturnal colubrids, seeking insights into their divergent head shapes.

### MATERIALS AND METHODS

We examined 205, approximately 270, and 232 specimens of *Arizona elegans* in the Califor-

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TABLE 1. Prey eaten by *Arizona elegans*. "Frequency" refers to the number of times each prey taxon was found in the entire sample; numbers in parentheses indicate the number of snakes that ate that particular prey. "Sceloporine lizard" refers to species of *Uta*, *Urosaurus*, or *Sceloporus*; "phrynosomatid lizard" refers to species in the family Phrynosomatidae; "*Perognathus* (sensu lato) sp." refers to *Chaetodipus* or *Perognathus* (sensu stricto). \* Fide Zamudio et al., 1997.

| Prey taxon                          | Frequency | % of total<br>number of prey | Source                                                                                     |
|-------------------------------------|-----------|------------------------------|--------------------------------------------------------------------------------------------|
| AVES                                |           |                              |                                                                                            |
| Unidentified bird                   | 4 (4)     | 3.7                          | this study                                                                                 |
| MAMMALIA                            |           |                              |                                                                                            |
| Insectivora                         |           |                              |                                                                                            |
| Talpidae                            |           |                              |                                                                                            |
| <i>Scalopus aquaticus</i>           | 1 (1)     | 0.9                          | Klauber, 1946                                                                              |
| Rodentia                            |           |                              |                                                                                            |
| Heteromyidae                        |           |                              |                                                                                            |
| <i>Chaetodipus formosus</i>         | 1 (1)     | 0.9                          | this study                                                                                 |
| <i>Dipodomys merriami</i>           | 3 (3)     | 2.8                          | this study                                                                                 |
| <i>Dipodomys ordii</i>              | 1 (1)     | 0.9                          | C. Painter<br>and D. Sias,<br>unpubl. data                                                 |
| <i>Dipodomys</i> sp.                | 2 (2)     | 1.9                          | this study                                                                                 |
| <i>Perognathus inornatus</i>        | 1 (1)     | 0.9                          | this study                                                                                 |
| <i>Perognathus</i> (sensu lato) sp. | 13 (13)   | 12.1                         | this study;<br>Klauber, 1946                                                               |
| Muridae                             |           |                              |                                                                                            |
| <i>Peromyscus</i> sp.               | 3 (2)     | 2.8                          | this study                                                                                 |
| Unidentified rodent                 | 8 (8)     | 7.5                          | this study;<br>Hanley, 1943                                                                |
| Unidentified mammal                 | 14 (14)   | 13.1                         | this study                                                                                 |
| REPTILIA                            |           |                              |                                                                                            |
| Squamata                            |           |                              |                                                                                            |
| Iguanidae                           |           |                              |                                                                                            |
| <i>Dipsosaurus dorsalis</i>         | 6 (6)     | 5.6                          | this study;<br>Van Denburgh<br>and Slevin,<br>1913; Cowles<br>1941;<br>Cunningham,<br>1959 |
| Phrynosomatidae                     |           |                              |                                                                                            |
| <i>Callisaurus draconoides</i>      | 3 (3)     | 2.8                          | this study                                                                                 |
| <i>Phrynosoma cornutum</i>          | 2 (2)     | 1.9                          | this study;<br>Wright and<br>Wright, 1957                                                  |
| <i>Phrynosoma coronatum</i>         | 1 (1)     | 0.9                          | Stebbins,<br>1954                                                                          |
| <i>Phrynosoma hernandesi</i> *      | 1 (1)     | 0.9                          | this study                                                                                 |
| <i>Sceloporus magister</i>          | 1 (1)     | 0.9                          | this study                                                                                 |
| <i>Sceloporus</i> sp.               | 1 (1)     | 0.9                          | Linsdale,<br>1932                                                                          |
| cf. <i>Sceloporus</i> sp.           | 1 (1)     | 0.9                          | this study                                                                                 |
| <i>Uta stansburiana</i>             | 9 (8)     | 8.4                          | this study;<br>Klauber,<br>1931, 1946                                                      |
| Sceloporine lizard                  | 16 (16)   | 15.0                         | this study                                                                                 |
| Phrynosomatid lizard                | 2 (2)     | 1.9                          | this study                                                                                 |
| Teiidae                             |           |                              |                                                                                            |
| <i>Cnemidophorus tigris</i>         | 2 (2)     | 1.9                          | this study                                                                                 |
| <i>Cnemidophorus</i> sp.            | 1 (1)     | 0.9                          | this study                                                                                 |
| Xantusiidae                         |           |                              |                                                                                            |
| <i>Xantusia vigilis</i>             | 3 (1)     | 2.8                          | this study                                                                                 |

TABLE 1. Continued.

| Prey taxon                       | Frequency | % of total number of prey | Source                       |
|----------------------------------|-----------|---------------------------|------------------------------|
| Unidentified lizard              | 4 (4)     | 3.7                       | this study;<br>Klauber, 1946 |
| Serpentes                        |           |                           |                              |
| Colubridae                       |           |                           |                              |
| <i>Phyllorhynchus decurtatus</i> | 1 (1)     | 0.9                       | Klauber, 1946                |
| Unidentified animal              | 2 (2)     | 1.9                       | this study                   |
| Total                            | 107       |                           |                              |

nia Academy of Sciences, San Francisco (CAS); Natural History Museum of Los Angeles County, Los Angeles (LACM); and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), respectively. We checked for stomach contents by making a midventral incision in preserved specimens, avoiding only type specimens and fragile individuals. Whenever possible, for each snake with prey we recorded locality data, body size (SVL  $\pm$  1 cm), body mass ( $\pm$  0.1 g), head length ( $\pm$  1 mm; from the tip of the rostral scale to the retroarticular process of the right mandible), and minimum number of items in the stomach. Direction of ingestion (inferred from orientation in the stomach) was recorded to the extent possible. We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly on paper towels to remove excess fluid. Weights and linear measurements of partially digested prey were estimated by comparison with complete preserved specimens in the MVZ of conspecifics of similar size from the nearest locality available.

Our data set also incorporates published dietary records of *Arizona elegans* (Table 1). We took care to account for redundancy among literature records (e.g., Van Denburgh and Slevin, 1913 with Van Denburgh, 1922; Tennant, 1984 with Tennant, 1985). We excluded records of prey taken in captivity (e.g., Cook, 1930; Reynolds, 1943). Values given are means  $\pm$  1 S.D. and *P*-values are two-tailed.

#### RESULTS

Eighty-five *Arizona elegans* (SVL =  $48.7 \pm 19.5$  cm, range = 21.3–94.5 cm, *N* = 82; body mass =  $59.3 \pm 64.9$  g, range = 5.5–351.5 g, *N* = 68), or approximately 12% of the more than 700 specimens examined, contained at least partly identifiable prey items. Including 15 literature records (from 15 snakes) and one unpublished observation (C. Painter and D. Sias, pers. comm.), 53 (49.5%) of 107 prey eaten by *A. elegans* were "lizards" (i.e., squamate reptiles other than snakes or amphisbaenians), 47 (43.9%) were mammals, four (3.7%) were birds, one

(0.9%) was a snake, and two (1.9%) were unidentified animals (Table 1; 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). Published dietary records for which we could not determine their frequency of consumption by *A. elegans* included orthopteran and coleopteran insects (probably secondarily ingested), *Cophosaurus texanus* (greater earless lizard), *Holbrookia* sp. (earless lizards), *Sceloporus occidentalis* (western fence lizard), *Uta stansburiana* (side-blotched lizard), unidentified lizards, *Dipodomys* sp. (kangaroo rats), *Perognathus* (sensu lato) sp. (pocket mice; i.e., *Chaetodipus* or *Perognathus* [sensu stricto]), and unidentified rodents and mammals (Klauber, 1946; McKinney and Ballinger, 1966; Tennant, 1984).

Ninety-five of 100 *A. elegans* with food contained single prey, whereas the remaining five had ingested two (*N* = 4) or three prey (*N* = 1); one snake had eaten two *Uta stansburiana*, one had two *Peromyscus* sp. (white-footed mice), one ate a *Cnemidophorus* sp. (whip-tailed lizard) and a sceloporine lizard, another one had a *Cnemidophorus* sp. and an unidentified bird, whereas a fifth one ate three *Xantusia vigilis* (desert night lizard). A significant difference in SVL existed among snakes that preyed on lizards (SVL =  $38.8 \pm 16.9$  cm, range = 22.1–78.4 cm, *N* = 37), mammals (SVL =  $55.3 \pm 16.5$  cm, range = 21.3–94.5 cm, *N* = 39), and birds (SVL =  $75.8 \pm 14.0$  cm, range = 55.8–87.4 cm, *N* = 4; Kruskal-Wallis single-factor ANOVA, *H* = 20.57, *df* = 2,77, *P* < 0.0001; Fig. 1), with nonparametric multiple comparison tests indicating that the differences among the three groups of snakes were significant. All 49 prey for which we determined direction of ingestion were swallowed head-first.

We have reliable estimates of prey mass for 14 items: two *Callisaurus draconoides* (zebra-tailed lizard), five *Uta stansburiana*, two *Dipodomys merriami* (Merriam's kangaroo rat), and one each *Dipsosaurus dorsalis* (desert iguana), *Phrynosoma cornutum* (Texas horned lizard), *Sceloporus magister* (desert spiny lizard), *Cnemidophorus tigris*

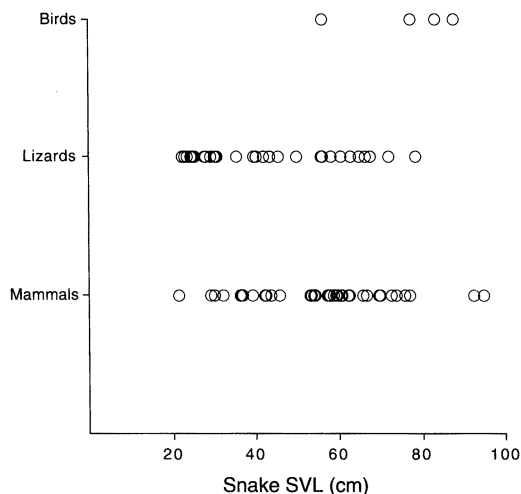


FIG. 1. Relationship between prey category (i.e., mammals, lizards, birds) and snake body size (SVL) in *Arizona elegans* (N = 81).

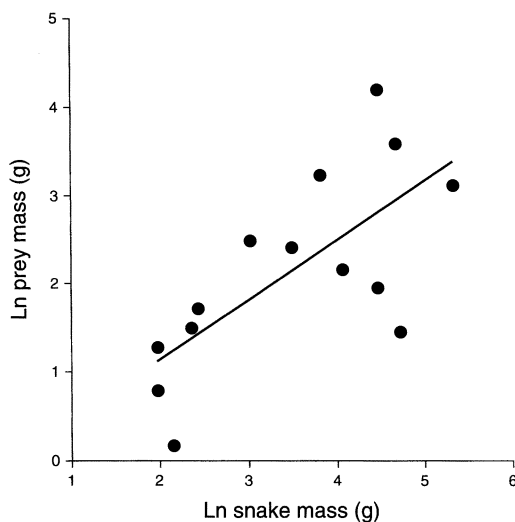


FIG. 2. (Ln-transformed) prey mass as a function of (Ln-transformed) snake mass in *Arizona elegans* (adjusted  $r^2 = 0.45$ ,  $F = 11.76$ ,  $df = 1, 12$ ,  $P = 0.005$ ).

(western whip-tailed lizard), and *Dipodomys ordii* (Ord's kangaroo rat). There was a significant relationship between snake mass and prey mass (Fig. 2). Relative prey mass (prey mass/snake mass; RPM) ranged from 0.04–0.77, with a mean =  $0.33 \pm 0.22$ ; the relatively largest item was a 67 g *D. ordii* in an 87 g *Arizona elegans* (C. Painter and D. Sias, pers. comm.). This mean RPM value is higher than those of some other colubrid snakes (e.g., *Psammodynastes pulverulentus* [Asian mock viper, 0.13; Greene, 1989a], *Boiga irregularis* [brown treesnake, 0.11; Greene, 1989b], *Thelotornis capensis* [savanna twigsnake, 0.19; Shine et al., 1996], *Coluber hippocrepis* [horseshoe racer, 0.26; Capula et al., 1997]).

*Arizona elegans* preyed significantly more on phrynosomatid iguanians (N = 37) than on teiid scleroglossan lizards (N = 3), whereas *Rhinocheilus lecontei* ate fewer phrynosomatids (N = 11) than teiids (N = 64; J. Rodríguez-Robles and H. Greene, unpubl. data; G-test of independence with Williams' correction,  $G = 71.33$ ,  $df = 1$ ,  $P < 0.00001$ ). No statistical difference in SVL existed between specimens of *A. elegans* and *R. lecontei* that contained food ( $SVL_{R. lecontei} = 50.9 \pm 14.2$  cm, range = 20.9–92.7 cm, N = 115; J. Rodríguez-Robles and H. Greene, unpubl. data; single-factor ANOVA,  $F = 0.68$ ,  $df = 1, 197$ ,  $P = 0.41$ ). We compared head lengths of *A. elegans* ( $18.4 \pm 4.8$  mm, range = 11.9–28.8 mm, N = 77) and *R. lecontei* ( $17.8 \pm 3.2$  mm, range = 10.7–25.4 mm, N = 92) with a single-factor ANCOVA, using SVL as the covariate. Because the slopes of the two regression lines of head length on SVL were indistinguishable (Student's  $t$  test,  $t = 0.56$ ,  $df = 165$ ,  $P = 0.58$ ), the results of the

ANCOVA ( $F = 45.68$ ,  $df = 1, 166$ ,  $P < 0.00001$ ) indicate that for any given body size, *A. elegans* has a longer head, and thus a larger gape (cf. Arnold, 1983; Greene, 1983), than *R. lecontei*.

#### DISCUSSION

Lizards and mammals, which were consumed with similar frequency, constituted more than 93% of all prey recovered from *Arizona elegans*. Birds and snakes composed the remaining prey. Diurnal lizards (i.e., iguanids, phrynosomatids, teiids; Table 1), composed most (46 of 49, 94%) of the reptilian prey, and presumably were captured when they were inactive by nocturnally wide-foraging glossy snakes. Conversely, 21 of 24 (88%) identified rodents were nocturnal heteromyids. We suspect these were ambushed by *A. elegans*, thus raising the possibility that these snakes use alternative hunting tactics on different prey types. Most snakes contained a single item, which suggests that *A. elegans* does not commonly raid mammalian nests, as does the larger syntopic gopher snake, *Pituophis catenifer* (J. Rodríguez-Robles, unpubl. data). Nonetheless, multiple prey items in stomachs of glossy snakes demonstrate that individual variability (cf. Greene, 1984) in feeding preferences encompasses at least lizards and birds.

Literature records of the diet of *Arizona elegans* agree well with our findings, but some differences exist. C. B. Perkins stated that "[g]eckos surely are its [*A. elegans*'] natural food" (Reynolds, 1943:196), whereas Macey and Papenfuss (1991:325) asserted that the food of *A. elegans* "consists of small rodents, lizards, and reptile

eggs." However, we have found no specific records of wild *A. elegans* feeding on geckos (*Coleonyx*, *Phyllodactylus*) or reptile eggs; the absence of *Coleonyx* from the diet of *A. elegans* may reflect chemosensory detection of and avoidance of predatory snakes by these geckos (Dial et al., 1989; Dial and Schwenk, 1996).

We follow traditional taxonomy in regarding *Arizona* as monotypic, although Collins (1991, 1992) recognized eastern (*A. elegans*, sensu stricto) and western (*A. occidentalis*) species within *A. elegans* (sensu lato). Our data do not indicate dietary differences between eastern and western populations of *A. elegans*, but 90 of 100 *A. elegans* with food in our sample were from western North America (Baja California, California, Nevada, western Arizona) and additional studies of the more diurnally active eastern glossy snakes (Klauber, 1946) clearly would be of interest.

Larger specimens of *Arizona elegans* fed on larger prey, which may suggest that larger *A. elegans* exclude smaller items from their diet (see Arnold, 1993). Despite the fact that smaller glossy snakes took mammals at least occasionally (Fig. 1), specimens of *A. elegans* that ate mammals were significantly larger than those which fed on lizards. Although larger snakes added birds to their diet, they continued to eat lizards and mammals, thus implying only a modest ontogenetic shift in emphasis rather than an abrupt change in feeding preferences. 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 *A. elegans* fed on birds.

*Arizona elegans* consumed lizards and mammals with similar frequency, whereas lizards and mammals composed 66.4 and 26.1%, respectively, of the diet of *Rhinocheilus lecontei* (J. Rodríguez-Robles and H. Greene, unpubl. data). For gape-limited predators such as snakes that swallow their prey whole and do not experience a size-specific trophic specialization or change in shape in their feeding apparatus, specimens with larger heads relative to their body size can eat larger prey than specimens with relatively smaller heads (Pough and Groves, 1983; Shine, 1991b; Forsman and Lindell, 1993; Houston and Shine, 1993). At a given body size, *A. elegans* has a longer head than *R. lecontei*, which probably explains why smaller *A. elegans* are capable of predation on mammals, whereas smaller *R. lecontei* feed almost exclusively on lizards (J. Rodríguez-Robles and H. Greene, unpubl. data). The difference in relative head length between *A. elegans* and *R. lecontei* may also account in part for the higher frequency of mammals in the diet of glossy snakes. Although at least two

glossy snakes died while trying to swallow horned lizards (*Phrynosoma*; see photographs in Stebbins, 1954; Wright and Wright, 1957), greater gape presumably facilitates feeding on stout-bodied phrynosomatid lizards as well.

*Arizona elegans*, *Rhinocheilus lecontei*, and *Pituophis catenifer* are sympatric throughout much of their ranges, and they eat lizard and mammalian prey with different frequencies (mammals and lizards constitute 77 and 3.6%, respectively, of the diet of *P. catenifer*; Rodríguez-Robles, 1998). Our ongoing studies will assess the extent to which these three species and other largely sympatric western North American serpents (e.g., species of *Crotalus*, *Lampropeltis*, *Masticophis*) partition prey resources, as is the case in some other snake assemblages (e.g., Brown and Parker, 1982; Fitch, 1982; Vitt, 1983; Voris and Voris, 1983; Shine, 1991a).

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