

Food habits of the long-nosed snake (*Rhinocheilus lecontei*), a ‘specialist’ predator?

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Abstract

We explored predator specialization by examining dietary variation in the widespread North American long-nosed snake, *Rhinocheilus lecontei*. We examined the stomach contents of more than 800 museum specimens, and supplemented our findings with published dietary records. Sixty-six percent of 135 prey eaten by *R. lecontei* were lizards, 26% were mammals, and 7% were squamate eggs; teiid lizards of the genus *Cnemidophorus* comprised 72% (64 of 89) of all lizard prey. Ninety-four percent of specimens with food contained a single item, and all 79 prey for which we determined direction of ingestion were swallowed head-first. Among those specimens containing food, long-nosed snakes from Mexico were significantly larger, and ate a higher percentage of mammals, than specimens from the United States. Larger *R. lecontei* sometimes fed on larger prey, and perhaps excluded smaller prey from their diet. To assess relative trophic niche breadth for *R. lecontei*, we compared the percentage of lizards and of *Cnemidophorus* in the diet of long-nosed snakes with the percentage with which other terrestrial snakes consumed lizards as their modal prey, and with which these same snakes ate members of their preferred lizard prey genus. Although we uncovered no statistical basis for labelling *R. lecontei* a specialist, its diet may often be restricted to lizards and even to *Cnemidophorus*, and therefore recognizing long-nosed snakes as specialist predators remains a subjective decision. Our study also demonstrates that quantitative natural history can place related species in a resource use continuum, and thereby can help to elucidate the evolutionary basis for specialization.

Key words: body size, diet, geographic differences, *Rhinocheilus lecontei*, specialist predator

INTRODUCTION

Many predators are widely believed to feed on one or a few prey species, and although those with narrow diets are sometimes called ‘specialists’ (e.g. Lieberman, 1986; Simon & Toft, 1991; Gasnier, Magnusson & Lima, 1994; Thompson, 1994; Toft, 1995), criteria on which to base this judgment vary and are often not explicit (e.g. Holm, 1985; Greene, 1989a; Roper, 1994; Amundsen, 1995; Bigger & Fox, 1997; Jędrzejewska & Jędrzejewski, 1998). Resource use underlies such pervasive concepts as the niche, competitive exclusion, and optimal foraging, and ecologists often state that a specialist uses a resource out of proportion to its availability (e.g. Petraitis, 1979; Feinsinger, Spears & Poole, 1981; Jędrzejewska & Jędrzejewski, 1998). However useful, this definition entails quantitative knowledge of

resource availability that often is lacking, and for some biologists the term ‘specialist predator’ simply implies that one or a few prey types predominate in the diet (Caldwell, 1996). In contrast, for evolutionary biologists specialization usually implies modifications in organism design relative to some particular task (e.g. Greene, 1982; Futuyma & Moreno, 1988; Sherry, 1990; Thompson, 1994). Here we explore the issue of predator specialization by examining dietary variation in a widespread snake relative to the percentages with which other snake species consume their modal prey (cf. Winemiller & Pianka, 1990).

Rhinocheilus lecontei, the long-nosed snake, is found in the United States from northern California and south-western Idaho to central Oklahoma and Texas, and south in Mexico to Baja California and the states of Jalisco, San Luis Potosí, Tamaulipas, and Zacatecas. In Mexico *R. lecontei* occurs in subtropical habitats (Bogert & Oliver, 1945; Hardy & McDiarmid, 1969), but in the US it occurs mainly in shrubland, dry prairies, rocky canyons, and deserts (Klauber, 1941; Beck & Peterson, 1995; Degenhardt, Painter & Price, 1996).

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Adult body size ranges from 50 to 104 cm snout–vent length (SVL) and individuals are relatively slender. *R. lecontei* is an active forager and powerful constrictor and is largely crepuscular or nocturnal, spending the daylight hours of its active season (usually April–September in the US) hidden among rocks or debris or in mammal burrows or other underground retreats (Klauber, 1941; Medica, 1975; Beck & Peterson, 1995).

General accounts (e.g. Ditmars, 1936; Shaw & Campbell, 1974; Tennant, 1984; Degenhardt *et al.*, 1996) state that *R. lecontei* feeds on lizards and their eggs, mammals, snakes, and insects, but no study has specifically addressed the dietary habits of this species. Thus, as part of our ongoing analyses of the feeding ecologies of several snake species in western North America, we report here on dietary variation in *R. lecontei*, based on stomach contents of museum specimens and judicious use of literature records. We also review studies of the diet of certain other terrestrial snakes to assess whether *R. lecontei* specializes on particular types of prey.

METHODS

We examined 248, 175, 253, *c.* 100, and *c.* 50 specimens of *Rhinocheilus lecontei* in the California Academy of Sciences, San Francisco (CAS); Los Angeles County Museum of Natural History, Los Angeles (LACM); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Arizona, Tucson (UAZ); and Collection of Vertebrates, University of Texas, Arlington (UTA), respectively. We checked for stomach contents by making a midventral incision in preserved specimens, avoiding only soft, brittle, or otherwise fragile individuals. Whenever possible, for each snake with prey we recorded locality data, SVL (± 1 cm), body mass (± 0.1 g), and minimum number of items in the stomach. All squamate eggs in a single stomach were counted as one item because they are likely to represent a single feeding event and because their exact number was sometimes impossible to determine. Direction of ingestion (inferred from orientation in the stomach) and order of ingestion of multiple items were recorded where possible. We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly on paper towels to remove excess fluid. Mass and linear measurements of partially digested items were estimated by comparison with complete preserved specimens in the MVZ of conspecifics of similar size from the nearest available locality.

Our data set also incorporates published dietary records of *R. lecontei*. We took care to account for redundancy among literature records (Klauber, 1941 with Stebbins, 1954) and between literature records and museum specimens (Banks & Farmer, 1962; Grismer, 1990; CAS 98095). We excluded prey from specimens that we suspected were fed in captivity before being preserved. Values given are means ± 1 SD. Unless otherwise indicated, *P*-values are 2-tailed.

We surveyed the literature for studies of snake diets that reported the exact number of prey found in the animal's digestive tract. We limited our survey to accounts that dealt with terrestrial snakes and that recovered ≥ 20 items.

RESULTS

One-hundred and sixteen *Rhinocheilus lecontei* (SVL = 50.9 ± 14.1 cm, range = 20.9–92.7 cm, $n = 116$; body mass = 66.6 ± 49.3 g, range = 4.1–319.5 g, $n = 104$), *c.* 14% of all specimens examined by us, contained at least partly identifiable prey items. Including 14 items (from 12 snakes) from the literature, 89 of 135 (65.9%) prey eaten by *R. lecontei* were lizards (i.e. squamate reptiles other than snakes and amphisbaenians), 35 (25.9%) were mammals, nine (6.7%) were squamate eggs, one (0.7%) was an unidentified squamate, and one was a grasshopper (Table 1; the high number of unidentified lizards and mammals is the result of stomach contents that consisted only of a few scales or clumps of mammalian hair with no cranial material). Teiids of the genus *Cnemidophorus* (whip-tailed lizards and racerunners) composed 71.9% (64 of 89) of all lizard prey. Published dietary records for which we could not determine the frequency of consumption by *R. lecontei* included *Dipodomys merriami* (Merriam's kangaroo rat) and other unidentified rodents (Klauber, 1941), *Cnemidophorus* sp. (Gates, 1957), *Uta stansburiana* (side-blotched lizard), *Sceloporus* sp. (spiny lizards), and *Cnemidophorus* sp. (McKinney & Ballinger, 1966), and *C. sexlineatus* (six-lined racerunner), which long-nosed snakes have been observed rooting out after dark (Tennant, 1984). Excluding the six snakes that only had ingested squamate eggs, 115 of 122 (94.3%) *R. lecontei* with food contained single prey, and the remaining seven snakes had ingested two prey (Table 2). All 79 prey for which we determined direction of ingestion were swallowed head-first.

In the absence of detailed habitat data for many of the snakes in our sample, we used the border between the US and Mexico as a surrogate for temperate *vs* subtropical localities, respectively, and thereby assessed geographic differences in the food habits of *R. lecontei*. Adult Mexican *R. lecontei* that contained food (SVL = 63.7 ± 9.9 cm, range = 50.7–92.7 cm, $n = 18$) were larger than those from the US (SVL = 59.0 ± 7.4 cm, range = 50.4–86.5 cm, $n = 49$; one-way ANOVA, performed on ln-transformed SVL, $F_{(1,65)} = 4.64$, $P = 0.035$). Mexican long-nosed snakes showed a strong trend to eat a higher proportion of mammals and a lower proportion of lizards than snakes from the US, (11/15: 23/72, *G*-test of independence with Williams' correction, $G = 3.05$, 1 d.f., $P = 0.08$). (Because the number of *R. lecontei* from Mexico [$n = 3$] and the US [$n = 5$] that ate squamate eggs was similar, we only compared the frequencies of lizards and mammals eaten by snakes from both countries.) Eleven of 15 (73.3%) and 51 of 72 (70.8%) lizards eaten by *R. lecontei* from Mexico

Table 1. Prey eaten by *Rhinocheilus lecontei*. ‘Sceloporine lizard’ refers to species of *Uta*, *Urosaurus*, or *Sceloporus*; ‘*Perognathus* (*sensu lato*) sp.’ refers to *Chaetodipus* or *Perognathus* (*sensu stricto*). ‘Frequency’ refers to the number of times each prey taxon was found in the entire sample (as no more than one individual of any prey type was found in any snake, it is also the frequency of snakes that ate that prey)

Prey taxon	Frequency	Percentage total number of prey	Source
Insecta			
Orthoptera			
Grasshopper	1	0.7	Klauber, 1941
Mammalia			
Rodentia			
Heteromyidae			
<i>Chaetodipus hispidus</i>	1	0.7	Fouquette & Lindsay, 1955
<i>Dipodomys ordii</i>	1	0.7	Fouquette & Lindsay, 1955
<i>Dipodomys</i> sp.	2	1.5	This study
<i>Perognathus</i> (<i>sensu lato</i>) sp.	6	4.4	This study
Unidentified rodent	8	5.9	This study
Unidentified mammal	17	12.6	This study
Reptilia			
Squamata			
Eublepharidae			
<i>Coleonyx variegatus</i>	1	0.7	This study
Iguanidae			
<i>Dipsosaurus dorsalis</i>	1	0.7	Banks & Farmer, 1962
Phrynosomatidae			
<i>Holbrookia maculata</i>	2	1.5	This study
<i>Sceloporus occidentalis</i>	2	1.5	This study
<i>Sceloporus undulatus</i>	1	0.7	This study
<i>Sceloporus</i> sp.	1	0.7	This study
<i>Uta stansburiana</i>	3	2.2	This study
Sceloporine lizard	2	1.5	This study
Scincidae			
<i>Eumeces gilberti</i>	1	0.7	Fitch, 1949
Teiidae			
<i>Cnemidophorus ceralbensis</i>	1	0.7	This study
<i>Cnemidophorus marmoratus</i>	1	0.7	Minton, 1958
<i>Cnemidophorus sexlineatus</i>	3	2.2	Miller, 1987; Gubanyi, 1992; This study
<i>Cnemidophorus tessellatus</i>	2	1.5	Klauber, 1941
<i>Cnemidophorus tigris</i>	21	15.6	This study
<i>Cnemidophorus</i> cf. <i>C. tigris</i>	2	1.5	This study
<i>Cnemidophorus uniparens</i>	2	1.5	This study
<i>Cnemidophorus</i> sp.	32	23.7	This study; Klauber, 1924; Woodin, 1953; Fouquette & Rossman, 1963
Unidentified lizard	11	8.1	This study
Unidentified squamate	1	0.7	This study
Squamate eggs			
1	1	0.7	This study
2	1	0.7	Klauber, 1941
4	2	1.5	This study
5	1	0.7	This study
6	1	0.7	This study
8	1	0.7	This study
10	1	0.7	This study
10–12	1	0.7	This study
TOTAL	135		

and the U.S.A., respectively, were *Cnemidophorus*. Smaller *R. lecontei* from the U.S.A., and perhaps from Mexico as well, fed almost exclusively on lizards, but snakes that ate mammals (SVL = 54.2 ± 10.6 cm, range = 38.1–73.8 cm, *n* = 32) were not significantly larger than those that took lizards (SVL = 49.4 ± 15.1 cm, range = 20.9–92.7 cm, *n* = 78; Kruskal–

Wallis one-way ANOVA, $H_{(1,108)} = 1.97$, $P = 0.16$). Mammals occurred only in snakes > 38 cm SVL, but many larger individuals continued to eat lizards and squamate eggs (Fig. 1).

We have reliable estimates of prey mass for two *Cnemidophorus uniparens* (desert grassland whip-tailed lizard), and one each *Dipsosaurus dorsalis* (desert

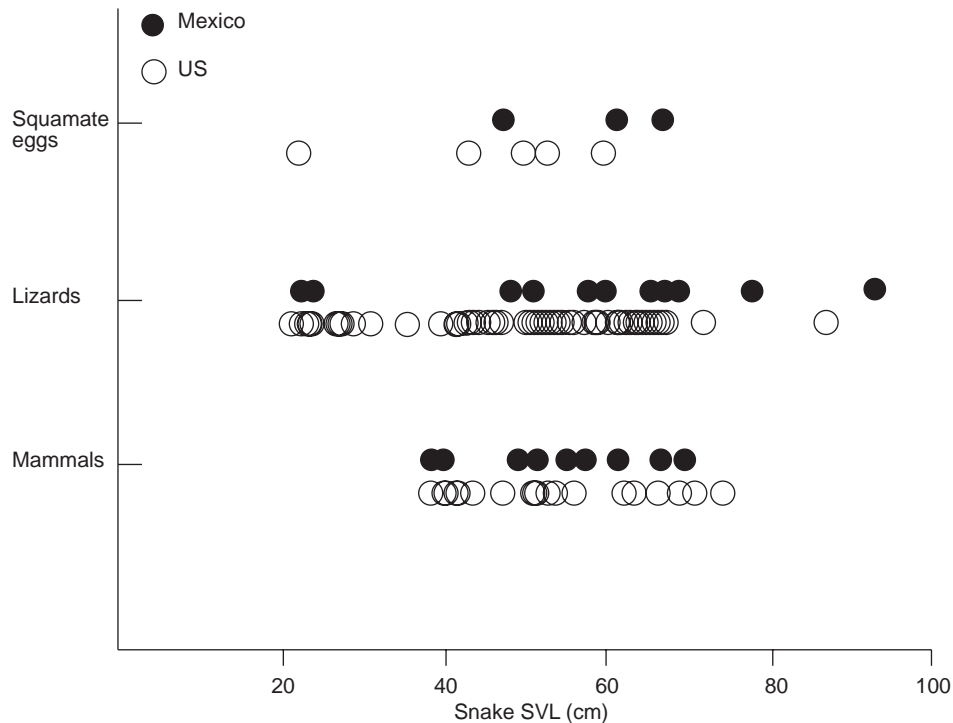


Fig. 1. Relationship between prey category and snake body size (SVL) in *Rhinoceros lecontei* from Mexico ($n = 27$) and the United States ($n = 91$).

iguana), *Holbrookia maculata* (lesser earless lizard), *Sceloporus occidentalis* (western fence lizard), *Uta stansburiana*, *C. tigris* (western whip-tailed lizard), *C. cf. C. tigris*, *Cnemidophorus* sp., and an unidentified nestling mammal. Mean relative prey mass (prey mass/snake mass) was 0.23 ± 0.22 (range = 0.03–0.63, $n = 10$); the relatively largest item was a 3.5 g *S. occidentalis* in a 5.6 g *R. lecontei*. Larger *R. lecontei* sometimes fed on larger prey, but the relationship was not statistically significant (one-way ANOVA, performed on ln-transformed mass, $F_{(1,8)} = 3.65$, $P = 0.09$). However, the strong trend and limited sample size indicate a likely Type II error (accepting a false null hypothesis).

Literature accounts that met our criteria for inclusion in this study dealt with 55 snake species for which lizards were the modal prey category (Appendix). Sixty per cent (33 of 55) of the snake species in this sample occur in Australia and the West Indies, and may feed predominantly on lizards because these are the only relatively abundant prey. Nevertheless, at many habitats in the West Indies frogs are just as abundant, if not more so, than lizards (R. Thomas, pers. comm.) and at least one snake from the island of Hispaniola feeds predominantly on anurans (i.e. *Darlingtonia haetiana*; Henderson & Schwartz, 1986), whereas other species eat frogs at least occasionally (Henderson & Crother, 1989; Henderson & Sajdak, 1996). Similarly, although over most of Australia lizards are more abundant than anurans (R. Shine, pers. comm.), some Australian serpents mainly eat frogs (e.g. *Dendrelaphis punctulata*, *Denisonia devisi*, *Hemiaspis damelii*, *Hoplocephalus bitorquatus*, *Pseudechis porphyriacus*, *Tropidonophis*

mairii; Shine, 1977, 1983a,b, 1987b, 1991). Thus, for most West Indian and at least for some Australian snakes, suitable prey types other than lizards are available, and the frequencies of lizards in the diets of these snakes are more likely to reflect their dietary preferences. The percentages of lizards in the diets of the 55 species in our survey ranged from 42.1 to 100%, with a mean = 74.6 ± 18.2 and a median (M) = 72.7 (Fig. 2; species towards the right end of the frequency distribution have increasingly narrower trophic niches), whereas the percentages of the modal lizard genus preyed upon by 51 of these 55 snakes ranged from 7.5 to 100%, with mean = 46.6 ± 29.6 and $M = 41.8$ (Fig. 3). *Rhinoceros lecontei* falls within the narrower diet cluster of snakes that emphasize lizards in their diets, but short of the mean and median for the overall data set. Long-nosed snakes also fall just within the narrower diet cluster with respect to use of prey genera, and substantially to the right of the mean and median for the overall data set.

Different operational criteria might be used to assess whether *R. lecontei* is considered a specialist predator. For example, one could require that frequency of lizards in the diet of a 'lizard specialist' lies within the upper two-thirds of the sample, upper three-quarters of the sample, or three positive standard deviations above the mean for the entire sample. Such criteria depend on what researchers consider distinctive enough to be 'specialized', and therefore are arbitrary to some extent, and the 'three standard deviations rule' for distinctiveness can be misleading, as the critical number of standard deviations above or below the mean necessary for a particular value to be discordant depends heavily

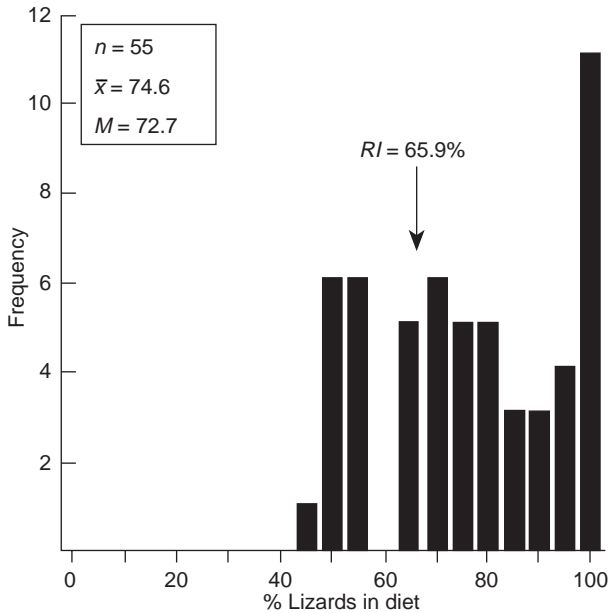


Fig. 2. Frequency distribution of percentage of lizard prey in the diet of terrestrial alethinophidian snakes whose most common prey category was lizards (see Appendix 1 for data; M = median; RI = percentage of lizard prey in the diet of *Rhinocheilus lecontei*).

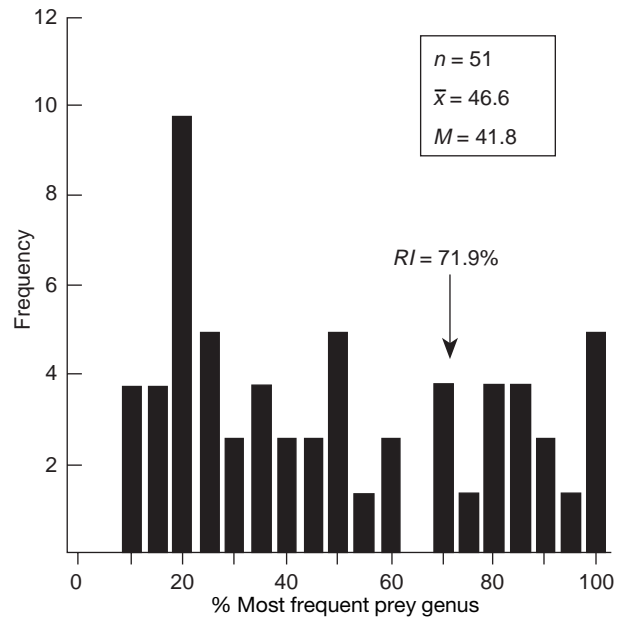


Fig. 3. Frequency distribution of percentage of most commonly eaten lizard genera in the diet of terrestrial alethinophidian snakes whose most common prey category was lizards (see Appendix 1 for data; M = median; RI = percentage of all lizard prey in the diet of *Rhinocheilus lecontei* comprised by *Cnemidophorus* spp.).

on sample size (Barnett & Lewis, 1994). Even a simple criterion of 'greater than the sample mean' results in the paradoxical conclusion that long-nosed snakes are specialized predators on *Cnemidophorus*, but not on lizards!

In search of a more objective criterion to identify specialist predators, we compared percentages of lizards and of *Cnemidophorus* in the diet of *R. lecontei* with diet samples for other snakes that mainly preyed on lizards. We found no statistical difference between the percentage of lizards in the diet of *R. lecontei* (65.9%) and the sample mean of the percentages of lizards in the diets of other terrestrial snakes (74.6%; Student's t -test, $t = -0.47$, 54 d.f., one-tailed $P = 0.32$; Sokal & Rohlf, 1995), or between the percentage of *Cnemidophorus* in the diet of long-nosed snakes (71.9%) and the sample mean of the percentages with which other snakes ate their modal prey (lizard) genus (46.6%; $t = 0.89$, 50 d.f., one-tailed $P = 0.19$). Because the frequency with which *R. lecontei* ate *Cnemidophorus* differed greatly from the mean of the frequency distribution with which other snakes ate their modal prey genus, we also conducted a discordancy test for outliers in univariate samples (Barnett & Lewis, 1994; Sokal & Rohlf, 1995), and the differences were still not significant (square root-transformed data, test statistic = 0.88, $n = 52$, one-tailed $P \gg 0.05$).

DISCUSSION

Our findings support general literature statements that *Rhinocheilus lecontei* is mainly a lizard-eating snake,

and that it also eats mammals and, rarely, squamate eggs. Excluding specimens that contained squamate eggs, most snakes contained a single prey, which suggests that *R. lecontei* does not commonly raid mammalian nests, as does the larger sympatric gopher snake, *Pituophis catenifer* (J. A. Rodríguez-Robles, pers. obs.). None the less, multiple prey items in stomachs of *R. lecontei* demonstrate that within-individual dietary variability (cf. Greene, 1984) encompasses at least lizards and rodents, squamate eggs and mammals, squamate eggs and lizards, and insects and squamate eggs (Table 2). Most lizard prey were *Cnemidophorus* teiids, which are common and syntopic with *R. lecontei* throughout its range (Wright, 1993). That we did not find grasshoppers, *Dipsosaurus dorsalis*, *Eumeces gilberti* (Gilbert's skinks), or snakes (Perkins, 1949; Tennant, 1984; Collins, 1993) in more than 800 specimens from most of *R. lecontei*'s range suggests that those prey types are at most rarely eaten by long-nosed snakes.

Our data confirm that Mexican *R. lecontei* attain larger body sizes than specimens from the US (Grismer, 1990), and those snakes showed a strong trend to include more mammals in their diet than did *R. lecontei* from the US. Specimens <38 cm SVL did not eat mammals, presumably because as gape-limited predators, the smaller snakes are physically incapable of swallowing even small rodents (cf. Shine, 1980c; Greene, 1989b; Shine & Slip, 1990; Henderson, 1993; Henderson & Sajdak, 1996; Luiselli, Capula & Shine, 1997; Rodríguez-Robles, Bell & Greene, 1999). Like many other predators, larger *R. lecontei* feed on larger prey, and perhaps exclude smaller prey from their diet

Table 2. Records of *Rhinocheilus lecontei* that consumed multiple prey. Except for the records from MVZ 97123 and Klauber (1941), first prey listed represents the item first eaten by the snake

Museum catalogue number/source	Snake SVL (cm)	Snake mass (g)	Prey
CAS 98095	92.7	319.5	<i>Dipsosaurus dorsalis</i>
CAS 190421	41.7	31.9	<i>Cnemidophorus ceralbensis</i> <i>Cnemidophorus</i> sp.
LACM 102740	61.2	–	Unidentified rodent 6 squamate eggs
MVZ 97123	42.9	34.1	Unidentified mammal Unidentified lizard
MVZ 193319	62.8	118.5	8 squamate eggs <i>Dipodomys</i> sp.
UTA 2626	44.5	32.9	Unidentified rodent <i>Cnemidophorus sexlineatus</i>
Klauber 1941	–	–	<i>Cnemidophorus</i> sp. Grasshopper 2 squamate eggs

(Arnold, 1993; see also Reynolds & Scott, 1982; Greene, 1984; Seib, 1985; Henderson *et al.*, 1987b; Pleguezuelos & Moreno, 1990; Capizzi & Luiselli, 1997), but there is no distinct ontogenetic shift in prey type.

A cursory inspection of papers in *American Naturalist*, *Canadian Journal of Zoology*, *Ecology*, *Ecological Monographs*, *Journal of Animal Ecology*, *Journal of Zoology (London)*, *Oecologia*, and *Oikos* since 1990 indicates that ecologists often refer to many species as dietary or habitat specialists, and in the introductory remarks to a symposium on the evolution of specialization, Berenbaum (1996: S78) stated that 'specialization for particular diets or habitats is a remarkably widespread biological phenomenon'. Nevertheless, the operational challenges in identifying specialization are considerable (Holm, 1985; Sherry, 1990). For example, ecologists dealing exclusively with contemporary phenomena treat specialization as a matter of resource use relative to abundance. That approach, however useful, has severe limitations for broader questions in evolutionary biology (Caldwell, 1996) because most investigations of prey population densities (e.g. Godley, 1980; Houston & Shine, 1993; Capizzi *et al.*, 1995) are only possible for relatively small areas and no more than a few years, whereas available dietary data must often reflect records from distant localities and span many years (e.g. our earliest record of *R. lecontei* containing *Cnemidophorus* was collected in Nevada in 1932, and the most recent came from Arizona in 1996). Because population densities vary over space and time (see Milstead, 1965; Pianka, 1970; Whitford & Creusere, 1977 for examples of *Cnemidophorus*), the relevance of *Cnemidophorus* densities in southwestern Texas in the mid-1960s (e.g. Degenhardt, 1966) for addressing specialization in *R. lecontei* would be uncertain.

Our comparisons of the percentages of lizards and of *Cnemidophorus* in the diet of *R. lecontei* with those of diet samples for other snakes that mainly preyed on lizards uncovered no statistical basis for considering long-nosed snakes as specialized predators. Defining a

specialist based strictly on patterns of resource utilization does not, however, distinguish between 'ecological' and 'evolutionary' specialization. If specialization on certain resources arose early in the evolutionary history of a lineage, then members of those lineages would be expected to mainly use those resources (Caldwell, 1996), independent of patterns of use of similar resources by other species. *R. lecontei* belongs to the tribe Lampropeltini, a monophyletic group composed of *c.* 25 species (Keogh, 1996; Rodríguez-Robles & De Jesús-Escobar, 1999). To consider long-nosed snakes specialist predators on lizards and on *Cnemidophorus* under an 'evolutionary specialist' concept, most other members of Lampropeltini would have to not emphasize lizards and *Cnemidophorus* in their diets, so that predation upon these taxa would not simply represent the retention of an ancestral trait. In fact, most lampropeltinines mainly feed on mammals or have more generalized diets (Rodríguez-Robles & De Jesús-Escobar, 1999). For evolutionary biologists specialization might also imply possession of functional modifications for particular biological roles. Long-nosed snakes, which hunt by extracting sleeping lizards from their holes (Tennant, 1984), are characterized by a long snout with a large, pointed rostral scale (Grismer, 1990) and an underslung lower jaw, traits which are often considered adaptations for burrowing. If these characters indeed evolved to facilitate predation on lizards in general and upon *Cnemidophorus* in particular, then long-nosed snakes may be considered specialist predators because these two morphological traits would represent structures evolved for a particular task. Nevertheless, because many authors consider arguments supporting these adaptationist scenarios teleological (Rose & Lauder, 1996), labelling *R. lecontei* an evolutionary specialist remains problematic.

Despite all these arguments, the fact remains that two-thirds of all prey taken by *R. lecontei* throughout its range are lizards, and *Cnemidophorus* constituted 72% of all lizard prey. Moreover, long-nosed snakes

everywhere feed almost exclusively on lizards (mostly *Cnemidophorus*) until they reach 38 cm SVL, so some workers might claim that there are biological reasons for regarding *R. lecontei* a specialized predator on lizards and even on *Cnemidophorus*. Thus, as aptly summarized by Futuyma & Moreno (1988:208) 'often specialization must lie in the eye of the beholder'.

The literature abounds with examples of performance advantages associated with particular phenotypes (e.g. for birds, Grant, 1986; for snakes, Scanlon & Shine, 1988; Greene, 1989a; for rodents, Dayan & Simberloff, 1994; for frogs, Caldwell, 1996), but relatively little evidence of why such innovations accompany narrow niches in some circumstances and not others (see Greene, 1982; Futuyma & Moreno, 1988; Caldwell, 1996; Robinson & Wilson, 1998). For evolutionary biologists, defining specialization and addressing such issues is an intriguing problem that is ultimately likely to be solved by comparisons of detailed phylogenetic, ecological, morphological, and physiological studies of several species, rather than by adopting statistical criteria. Our study demonstrates that understanding levels of variation is critical to a robust analysis of resource use because niche specializations may fluctuate across life stages and geographic ranges. We also show that quantitative natural history, expressed through Winemiller & Pianka's (1990) frequency distribution method, provides a straightforward means for placing related species in a resource use continuum, and thereby can help to elucidate the evolutionary basis for specialization.

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Appendix Percentages and frequencies (in parentheses) of lizards and of the most common lizard genus in the diet of 55 snake species

Species	Percentage (frequency) of lizards in the diet	Most frequent prey genus	Percentage (frequency) of most frequent lizard genus eaten	Source
Boidae				
<i>Candoia aspera</i>	78.0 (32/41)	—	—	Harlow & Shine, 1992
<i>Candoia bibroni</i>	68.2 (15/22)	—	—	Harlow & Shine, 1992
<i>Candoia carinata</i>	86.0 (80/93)	<i>Emoia</i>	11.3 (9/80)	Harlow & Shine, 1992
<i>Corallus grenadensis</i>	67.9 (53/78)	<i>Anolis</i>	98.1 (52/53)	Henderson, 1993, pers. comm.
Colubridae				
<i>Alsophis cantherigerus</i>	62.7 (42/67)	<i>Anolis</i>	78.6 (33/42)	Henderson & Sajdak, 1996
<i>Alsophis portoricensis</i>	84.8 (67/79)	<i>Anolis</i>	65.7 (44/67)	Rodríguez-Robles & Leal, 1993; Henderson & Sajdak, 1996
<i>Alsophis rufiventris</i>	55.0 (11/20)	<i>Anolis</i>	90.9 (10/11)	Henderson & Sajdak, 1996
<i>Alsophis vudii</i>	70.1 (61/87)	<i>Anolis</i>	68.9 (42/61)	Henderson & Sajdak, 1996
<i>Antillophis parvifrons</i>	83.9 (146/174)	<i>Anolis</i>	84.9 (124/146)	Henderson <i>et al.</i> , 1987a
<i>Arizona elegans</i>	49.5 (53/107)	<i>Uta</i>	17.0 (9/53)	Rodríguez-Robles, Bell & Greene, 1999
<i>Boiga ceylonensis</i>	61.8 (21/34)	<i>Calotes</i>	23.8 (5/21)	Greene, 1989b
<i>Boiga irregularis</i>	47.9 (313/653)	—	—	Savidge, 1988; Greene, 1989b; Shine, 1991
<i>Coluber viridiflavus</i>	49.2 (29/59)	<i>Podarcis</i>	93.1 (27/29)	Capizzi <i>et al.</i> , 1995
<i>Coronella austriaca</i>	87.7 (142/162)	<i>Lacerta</i>	59.9 (85/142)	Rugiero <i>et al.</i> , 1995; Luiselli, Capula & Shine, 1996
<i>Elaphe quadrivirgata</i>	77.5 (124/160)	<i>Eumeces</i>	96.8 (120/124)	Hasegawa & Moriguchi, 1989
<i>Hypsiglena torquata</i>	52.7 (49/93)	<i>Uta</i>	16.3 (8/49)	Schmidt & Owens, 1944; Rodríguez-Robles, Mulcahy & Greene, 1999
<i>Hypsirhynchus ferox</i>	100.0 (49/49)	<i>Ameiva</i>	49.0 (24/49)	Henderson, 1984
<i>Lampropeltis triangulum</i>	61.9 (13/21)	<i>Eumeces</i>	100.0 (13/13)	Fitch, 1982
<i>Macrotodon cucullatus</i>	46.7 (21/45)	<i>Psammmodromus</i>	47.6 (10/21)	Pleguezuelos, Honrubia & Castillo, 1994
<i>Masticophis flagellum</i>	63.3 (31/49)	—	—	Hamilton & Pollack, 1956
<i>Masticophis taeniatus</i>	64.3 (18/28)	<i>Uta</i>	66.7 (12/18)	Parker & Brown, 1980
<i>Mastigodryas melanolomus</i>	70.6 (24/34)	<i>Anolis</i>	50.0 (12/24)	Seib, 1984
<i>Oxybelis aeneus</i>	100.0 (21/21)	<i>Anolis</i>	76.2 (16/21)	Henderson, 1982
<i>Philodryas chamissonis</i>	42.1 (16/38)	<i>Liolaemus</i>	100.0 (16/16)	Greene & Jaksic, 1992
<i>Philodryas natterei</i>	75.0 (24/32)	<i>Cnemidophorus</i>	45.8 (11/24)	Vitt, 1980
<i>Psammodynastes pulverulentus</i>	70.8 (80/113)	<i>Sphenomorphus</i>	7.5 (6/80)	Greene, 1989a
<i>Thelotornis capensis</i>	54.8 (57/104)	<i>Mabuya</i>	21.1 (12/57)	Shine <i>et al.</i> , 1996
<i>Uromacer catesbyi</i>	51.6 (33/64)	<i>Anolis</i>	87.9 (29/33)	Henderson, Schwartz & Noeske-Hallin, 1987c
<i>Uromacer frenatus</i>	100.0 (108/108)	<i>Anolis</i>	70.4 (76/108)	Henderson <i>et al.</i> , 1987c
<i>Uromacer oxyrhynchus</i>	100.0 (44/44)	<i>Anolis</i>	81.8 (36/44)	Henderson <i>et al.</i> , 1987c
Elapidae				
<i>Acanthophis antarcticus</i>	52.9 (18/34)	<i>Pseudemoia</i>	22.2 (4/18)	Shine, 1980c
<i>Austrelaps superbus</i>	70.0 (147/210)	<i>Lampropholis</i>	25.9 (38/147)	Shine, 1987a
<i>Cacophis harriettae</i>	87.8 (36/41)	<i>Lampropholis</i>	30.6 (11/36)	Shine, 1980a
<i>Cacophis krefftii</i>	100.0 (23/23)	<i>Anomalopus</i>	8.7 (2/23)	Shine, 1980a
<i>Cacophis squamulosus</i>	79.7 (55/69)	<i>Lampropholis</i>	43.6 (24/55)	Shine, 1980a
<i>Demansia atra</i>	72.7 (16/22)	<i>Carlia</i>	37.5 (6/16)	Shine, 1980b
<i>Demansia psammophis</i>	90.5 (67/74)	<i>Lampropholis</i>	41.8 (28/67)	Shine, 1980b
<i>Drysdalia coronoides</i>	83.9 (52/62)	<i>Pseudemoia</i>	38.5 (20/52)	Shine, 1981b
<i>Echiopsis curta</i>	51.9 (28/54)	<i>Hemiergis</i>	17.9 (5/28)	Shine, 1982
<i>Furina diadema</i>	100.0 (50/50)	<i>Lampropholis</i>	88.0 (40/50)	Shine, 1981a
<i>Hemiaspis signata</i>	66.3 (69/104)	<i>Limnodynastes</i>	53.6 (37/69)	Shine, 1987b
<i>Pseudonaja inframacula</i>	68.6 (24/35)	<i>Lerista</i>	25.0 (6/24)	Shine, 1989
<i>Pseudonaja modesta</i>	91.6 (87/95)	<i>Ctenotus</i> , <i>Diplodactylus</i>	12.6 (11/87)	Shine, 1989
<i>Rhinoplocephalus nigrescens</i>	93.5 (87/93)	<i>Lampropholis</i>	55.2 (48/87)	Shine, 1984b
<i>Simoselaps bertholdi</i>	100.0 (27/27)	<i>Lerista</i>	33.3 (9/27)	Shine, 1984a
<i>Suta flagellum</i>	100.0 (29/29)	<i>Lampropholis</i>	27.6 (8/29)	Shine, 1988
<i>Suta gouldii</i>	99.3 (138/139)	<i>Menetia</i>	17.4 (24/138)	Shine, 1988

Appendix (continued)

Species	Percentage (frequency) of lizards in the diet	Most frequent prey genus	Percentage (frequency) of most frequent lizard genus eaten	Source
<i>Suta nigriceps</i>	93.2 (41/44)	<i>Menetia</i>	12.2 (5/41)	Shine, 1988
<i>Suta spectabilis</i>	98.1 (52/53)	<i>Ctenotus</i>	7.7 (4/52)	Shine, 1988
<i>Suta suta</i>	69.0 (40/58)	<i>Amphibolorus</i>	17.5 (7/40)	Shine, 1988
Pythonidae				
<i>Aspidites melanocephalus</i>	79.6 (39/49)	<i>Varanus</i>	30.8 (12/39)	Shine & Slip, 1990
<i>Aspidites ramsayi</i>	46.9 (15/32)	<i>Varanus</i>	20.0 (3/15)	Shine & Slip, 1990
Viperidae				
<i>Bitis caudalis</i>	75.3 (113/150)	<i>Mabuya</i>	19.5 (22/113)	Shine <i>et al.</i> , 1998
<i>Vipera ammodytes</i>	50.0 (52/104)	<i>Podarcis</i>	80.8 (42/52)	Luiselli, 1996