

Alternative Perspectives on the Diet of Gopher Snakes (*Pituophis catenifer*, Colubridae): Literature Records versus Stomach Contents of Wild and Museum Specimens

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In addition to supplementing investigations on the trophic niche of a predator, published dietary records can provide essential information to address patterns of geographic, ontogenetic, and historical variation in an animal's feeding habits (e.g., Greene, 1989; King 1993; Slowinski, 1994). During a study of the feeding ecology of gopher snakes, *Pituophis catenifer*, I noticed that the frequencies of prey types recovered from wild and preserved specimens seemed to differ from those gathered from published accounts of the diet of this snake. Thus, herein I quantitatively examine those differences and discuss their implications for studies of feeding ecology.

The number of species within the genus *Pituophis* in the United States has been a controversial issue for several decades (e.g., Smith and Kennedy, 1951; Conant, 1956; Reichling, 1995). Phylogenetic analyses of mitochondrial DNA sequences of specimens across the country (J. A. Rodríguez-Robles and J. M. De Jesús-Escobar, unpubl. data) support previous suggestions (e.g., Fugler, 1955; Wright and Wright, 1957) that *Pituophis* snakes in the United States belong to at least two species: *P. catenifer*, in the central and western parts of the country, and *P. melanoleucus* (sensu stricto) in the eastern United States (see Sweet and Parker, 1990), a taxonomic arrangement that I follow herein.

MATERIALS AND METHODS

I examined 2631 wild or preserved specimens of *P. catenifer* at the California Academy of Sciences, San Francisco (CAS), and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). I checked for stomach contents by palpating living snakes or by making a midventral incision in museum specimens, avoiding only type specimens and especially soft, brittle, or otherwise fragile individuals. I recorded minimum number of items in each stomach and, for this analysis, identified them to general categories [i.e., insects, amphibians, mammals, birds, "lizards" (squamate reptiles other than snakes and amphisbaenians), snakes, frog eggs, turtle eggs, bird eggs, and squamate eggs]. Frog eggs, turtle eggs, or squamate eggs in a single stomach were counted as one item

because sometimes the exact number of items was impossible to determine. I excluded prey from specimens that I suspected were fed in captivity (e.g., MVZ 23973, MVZ 50299). I also surveyed the literature for reports on the diet of *P. catenifer*, taking care to account for redundancy between literature records (e.g., Klauber, 1931, 1947; Diller and Johnson, 1988; Diller and Wallace, 1996). I limited my survey to accounts reporting number of prey in digestive tracts, omitting vague statements (e.g., Gordon, 1939; Gates, 1957) about diet. All *P*-values are two-tailed.

RESULTS

I assigned 463 items recovered from wild ($n = 3$) and museum ($n = 358$) specimens of *P. catenifer* to one of the 10 prey type categories. Using published accounts, I compiled a list of 445 prey taken from an undetermined number of snakes (Table 1). Relative frequencies of lizards as prey of *P. catenifer* were significantly higher in wild and museum specimens than in literature records (24/463: 9/445 *G*-test of independence with Williams' correction, $G = 6.12$, $df = 1$, $P = 0.01$), whereas those of birds (21/463: 56/445, $G = 16.61$, $df = 1$, $P = 0.00005$) and bird eggs (28/463: 59/445, $G = 11.55$, $df = 1$, $P = 0.0001$) were significantly lower. There were no significant differences in relative frequencies of mammals (387/463: 312/445, $G = 2.88$, $df = 1$, $P = 0.09$), squamate eggs (2/463: 0/445, Fisher's exact test, $P = 0.50$), snakes (1/463: 3/445, Fisher's exact test, $P = 0.37$), amphibians (0/463: 3/445, Fisher's exact test, $P = 0.12$), and frog eggs, turtle eggs, and insects (0/463: 1/445, Fisher's exact test, $P = 0.49$) between both data sources. I repeated the comparison for lizards, birds, and bird eggs after removing from the published accounts all records ($n = 26$) of *P. catenifer* predation on birds and bird eggs that were published by ornithologists or in avian journals. The differences between wild and preserved specimens and literature records in relative frequencies of these prey types remained significant (lizards, 24/463: 9/419, $G = 5.32$, $df = 1$, $P = 0.02$; birds, 21/463: 43/419, $G = 9.44$, $df = 1$, $P = 0.002$;

TABLE 1. FREQUENCIES OF DIFFERENT TYPES OF PREY CONSUMED BY *Pituophis catenifer*, AS DETERMINED FROM STOMACH CONTENTS OF WILD AND MUSEUM SPECIMENS VERSUS A SURVEY OF SPECIFIC LITERATURE RECORDS. "Lizards" refers to squamate reptiles other than snakes and amphisbaenians.

Prey category	Frequency (percentage)		
	Prey items from wild and museum specimens (n = 463)	Prey items from literature records* (n = 445)	Combined (n = 908)
Mammals	387 (83.6)	312 (70.1)	699 (77.0)
Bird eggs	28 (6.0)	59 (13.3)	87 (9.6)
"Lizards"	24 (5.2)	9 (2.0)	33 (3.6)
Birds	21 (4.5)	56 (12.6)	77 (8.5)
Squamate eggs	2 (0.4)	0	2 (0.2)
Snakes	1 (0.2)	3 (0.7)	4 (0.4)
Amphibians	0	3 (0.7)	3 (0.3)
Frog eggs	0	1 (0.2)	1 (0.1)
Turtle eggs	0	1 (0.2)	1 (0.1)
Insects	0	1 (0.2)	1 (0.1)

* Taken from Ruthven, 1907; Richardson, 1915; Pack, 1919; Van Denburgh and Slevin, 1921; Grinnell and Storer, 1924; Woodbury, 1928; Burt and Hoyle, 1934; Gloyd, 1937; Mulaik, 1938; Huey, 1942; von Bloeker, 1942; Marr, 1944; Imler, 1945; Fautin, 1946; Klauber, 1947, 1972; Fitch, 1949, 1982; Howard, 1949; Cunningham, 1959; Vaughan, 1961; Miller and Stebbins, 1964; Douglas, 1966; McKinney and Ballinger, 1966; Webb, 1970; Bostic, 1971; Niedrach, 1971; Ervin and Rose, 1973; Hulse, 1973; Best, 1977; Galen and Bohn, 1979; Parker and Brown, 1980; Thompson and Turner, 1980; Maxson, 1981; Wellstead, 1981; Reynolds and Scott, 1982; Tennant, 1984; Marr, 1985; Howitz, 1986; Glup and McDaniel, 1988; Eichholz and Koenig, 1992; McCallum et al., 1995; Diller and Wallace, 1966; Jennings et al., 1996.

bird eggs, 28/463; 46/419; $G = 5.97$, $df = 1$, $P = 0.01$).

Detailed studies of the diet of a species at a particular site presumably are as reliable as museum records. I compared relative frequencies of mammals, lizards, birds, and bird eggs in the diet of *P. catenifer*, as determined from studies of the feeding habits of this snake conducted in central California (San Joaquín Experimental Range; Fitch, 1949) and in southwestern Idaho (Snake River Birds of Prey Area; Diller and Wallace, 1996), with frequencies from wild and museum specimens from throughout the species' range. The differences were highly significant (Table 2). The relative frequencies with which mammals, lizards, birds, and bird eggs were eaten by snakes from the aforementioned two sites also differed significantly ($\chi^2 = 35.7$, $df = 3$, $P < 0.0001$).

DISCUSSION

There are marked differences between wild and museum specimens and literature records regarding the relative frequencies with which lizards, birds, and bird eggs are eaten by *P. catenifer*. The wide range of *P. catenifer* (from the

TABLE 2. FREQUENCIES OF MAMMALS, BIRD EGGS, LIZARDS, AND BIRDS IN SPECIMENS OF *Pituophis catenifer* FROM CENTRAL CALIFORNIA (FITCH, 1949) AND SOUTHWESTERN IDAHO (DILLER AND WALLACE, 1996), COMPARED WITH THOSE FROM WILD AND MUSEUM SPECIMENS FROM THROUGHOUT THE SPECIES' RANGE.

Prey category	Frequency (percentage)	
	Prey items from specimens from central California (n = 72)	Prey items from wild and museum specimens (n = 460)
Mammals	48 (66.7)	387 (84.1)
Bird eggs	20 (27.8)	28 (6.1)
"Lizards"	4 (5.6)	24 (5.2)
Birds	0	21 (4.6)
$\chi^2 = 38.1$, $df = 3$, $P < 0.0001$		
Prey category	Prey items from specimens from southwestern Idaho (n = 100)	Prey items from wild and museum specimens (n = 460)
Mammals	98 (98.0)	387 (84.1)
Bird eggs	1 (1.0)	28 (6.1)
"Lizards"	0	24 (5.2)
Birds	1 (1.0)	21 (4.6)
$\chi^2 = 13.8$, $df = 3$, $P = 0.003$		

Pacific coast to Indiana in the United States, and from southwestern Canada to northern Mexico, including the Baja California peninsula) raises the possibility that these discrepancies may reflect geographic differences in the feeding habits of this snake. My separate analysis of dietary records of *P. catenifer* from particular sites in central California and southwestern Idaho support this hypothesis. In southern California, Kansas, Utah, and Idaho, zero of 19 (Von Bloeker, 1942), six of 18 (Fitch, 1982), two of 22 (Parker and Brown, 1980), and two of 100 prey (Diller and Wallace, 1996), respectively, were birds or bird eggs. These field studies also indicate possible geographic differences in the diet of *P. catenifer* (perhaps as a consequence of differences in prey availability among sites); they suggest as well that birds and bird eggs are seldom commonly eaten by this species.

Why do literature records and wild and museum specimens provide such a different account of the frequency with which *P. catenifer* preys on lizards, birds, and bird eggs? I suggest a bias in the frequency with which field observations of *P. catenifer* predation on bird and bird eggs are published, which also would indirectly affect the relative frequencies of lizards recorded for the diet of this species. With some exceptions (e.g., Mulaik, 1938; Galen and Bohn, 1979; Jennings et al., 1996), ornithologists traditionally have been more diligent than other verte-

brate biologists in publishing field observations of predation on their study animals, perhaps in part because predation events on birds and bird nests may be more visible and/or audible to observers. In fact, most recent records of *P. catenifer* eating birds and bird eggs were published almost exclusively by ornithologists or in avian journals (i.e., *Auk*, *Condor*, *Loon*, *Murrelet*, *Wilson Bulletin*; see references in Table 1). Removal of the latter data indicates that a bias in the frequency of published records of predation by *P. catenifer* on birds and bird eggs accounts in part for differences between literature records and wild and museum specimens (as indicated by the lower value of the *G*-statistic), but other factors, such as opportunistic predation, also might play a significant role. Faced with this situation, one may analyze stomach contents and literature records separately, carefully seeking insights in each dataset, or preferably, combine all dietary records of *P. catenifer* in hopes of gaining a more accurate estimate of the natural diet of this snake. In any case, I recommend caution when inferring the importance of different prey types in a predator's diet using literature records alone.

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