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PREY HANDLING AND DIET OF LOUISIANA PINE SNAKES *(PITUOPHIS RUTHVENI)* AND BLACK PINE SNAKES *(P. MELANOLEUCUS LODINGI)*, WITH COMPARISONS TO OTHER SELECTED COLUBRID SNAKES

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Abstract. Diet and prey handling behavior were determined for Louisiana pine snakes *(Pituophis ruthveni)* and black pine snakes (*P. melanoleucus lodingi*). Louisiana pine snakes prey heavily on Baird's pocket gophers (*Geomys breviceps*), with which they are sympatric, and exhibit specialized behaviors that facilitate handling this prey species within the confines of burrow systems. Black pine snakes, which are not sympatric with pocket gophers, did not exhibit these specialized behaviors. For comparative purposes, prey handling of *P. sayi sayi* and *Elaphe obsoleta lindheimeri* was also examined.

Key Words. Diet; *Geomys*; *Pituophis melanoleucus lodingi*; *P. ruthveni;* Predation.

The Louisiana pine snake *(Pituophis ruthveni)* and the black pine snake (*P. melanoleucus lodingi)* are two taxa of conservation concern with limited distributions on the Gulf Coastal Plain (Sweet and Parker 1991). Both have fossorial adaptations, including thickened rostral scales and skeletal modifications of the head region (Knight 1986; Reichling 1995). *Pituophis ruthveni* is a rare species confined to eastern Texas and western Louisiana (Collins 1991; Conant 1956; Reichling 1995; Thomas et al. 1975). It is closely associated with longleaf pine (*Pinus palustris*) savannahs on sandy, well-drained soils (Rudolph and Burgdorf 1997; Young and Vandeventer 1988). These communities are maintained by frequent, low intensity ground fires (Komarek 1968; Platt et al. 1988, 1989). Data obtained in an ongoing radiotelemetry study of *P. ruthveni* (Rudolph and Burgdorf 1997; Rudolph et al. 1998) demonstrated a close association with burrow systems of Baird's pocket gophers (*Geomys breviceps*). *Pituophis m. lodingi* occupies a similarly restricted range on the lower Gulf Coastal Plain, from exlreme eastern Louisiana to extreme western Florida (Sweet and Parker 1991). The ecology of *Pituophis m. lodingi* differs substantially from that of *P. ruthveni* in that its range is allopatric with that of pocket gophers except in the extreme eastern part of its range where it intergrades with *P. m. mugitus*. In this limited area. it is sympatric with the southeastern pocket gopher (*G. pinetis*).

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Prey handling by constricting snakes is a behavioral pattern that has a long evolutionary history (Greene and Burghardt 1978). Hisaw and Gloyd (1926), Willard (1977), Greenwald (1978) and de Quciroz (1984) have described the basic patterns of constriction in the genus *Pituophis* and described variation in constriction behavior dependent on prey type and the physical setting in which constriction takes place. *Pituophis* is capable of substantial plasticity in the use of constriction to subdue a variety of prey species and, unlike many other colubrid genera, exhibits a strong tendency to use pinioning to subdue prey, especially relatively small or inactive prey (Willard 1977; de Queiroz 1984).

In an effort to better understand the ecology of these rare taxa, we obtained data on diet and observed foraging and prey handling behavior both in the field and in the laboratory. For comparative purposes we also observed prey handling behavior of *P. sayi sayi*, a closely related congener, and *Elaphe obsolete lindheimeri*, a sympatric constrictor without l'ossorial adaptations.

MATERIALS AND METHODS

Data on diet in the wild were taken from fecal samples obtained from wild caught *P. ruthveni* and *P. m. lodingi* specimens held in the laboratory for transmitter implantation or from dissection of dead animals. Hair, teeth, claw, bone, and eggshell were extracted from fecal samples and identified by comparison with a reference collection obtained from local animals. Hair samples were compared microscopically to the limited number of small mammal species occurring locally. Tooth and claw samples were compared macroscopically to available museum specimens and to remains of animals led to captive snakes. Two additional prey records for *P. ruthveni* and one for *P. m. lodingi* were obtained during field observations of radio-transmittercd animals.

Given the importance of pocket gophers in their diet, we hypothesized that *P. ruthveni* may exhibit efficient behaviors for capturing subterranean prey. To test this hypothesis, we set up a large aquarium (130 x 30 cm) with two interior plexiglas inserts that defined a 6-cm wide space around the perimeter of the aquarium. The space was filled with slightly moist sandy loam soil to a depth of 40 cm. The soil provided a space within which Baird's pocket gophers could construct a burrow system. The 6-cm soil width resulted in the interior of the burrow being visible to an observer from outside the aquarium or by looking from above through the plexiglas insert.

For each trial a pocket gopher was introduced into the aquarium and given time, 1-2 h, to construct a burrow system 2–4 m in length. A snake was then introduced onto the soil surface adjacent to an open burrow entrance left unplugged by the gopher, or opened by the observer. The resulting behavior of the gopher and snake were observed. The procedure was repeated 20 times with 14 individual *P. ruthveni* and 11 times with nine individual *P. m. lodingi*. Trials were also conducted six times with two bullsnakes (*P. sayi sayi*), and 12 times with seven Texas rat snakes (*Elaphe obsoleta lindheimeri*). All snakes, except for the *P. m. lodingi*, were from areas of sympatry with pocket gophers. These observations were compared with prey handling behaviors observed in cages (28 x 28 x 56 cm) that provided information on prey handling in conditions unrestrained by burrow walls.

A χ^2 test with Yates' correction for small sample size was used to compare predation success among selected snake taxa. To avoid a violation of independence among samples due to repeated trials of individual snakes, we statistically analyzed the data using only the first trial for each snake.

RESULTS

Baird's pocket gophers were the major prey item (10 of 22) of *P. ruthveni* represented in the data set (Table I). A minimum of 18 of the 22 prey items (pocket gophers, moles, and turtle eggs) were presumably obtained from subterranean sites. Small sample size precluded analysis of prey composition by snake size or sex. Only seven prey records were obtained for *P. m. lodingi*, predominately small mammals (Table 1).

All four taxa used coils for constriction when handling small mammalian prey in open situations (cages). In a total of 35 (11 *P. ruthveni*, 11 *P. m. lodingi*, five *P. s. sayi*, and eight *E. obsoleta*) successful trials conducted in cages lacking obstructions, all taxa exhibited similar prey handling behavior (Table 2). All four taxa struck and grasped prey in their mouths, placed one or more full coils around the prey, and maintained their grasp with mouth and coils until the prey appeared dead. In a few instances, snakes released their mouth grasp

TABLE 1. Prey of *Pituophis ruthveni* and *P. melanoleucus lodingi* as determined from field observations, analyses of fecal samples, and gastrointestinal tract contents.

Taxon	*n*
Pituophis ruthveni	
Geomys breviceps	10
Scalopus aquaticus	4
Peromyscus sp.	1
Sigmodon hispidus	1
unid. mammal	2
turtle eggs*	4
P. m. lodingi	
Sigmodon hispidus	2
Peromyscus sp.	2
Silvilagus sp.	1
Colinus virginianus (eggs)	1
spider	1

*probably *Trachemys scripta*, based on size and habitat

before the prey was dead, but only after it was immobile. Small mammal prey used in these trials were an assortment of G. *breviceps*, *Peromyscus* spp., *Rattus norvegicus*, and *Sigmodon hispidus*. All prey were readily accepted with one notable exception. Three individual l? *m. lodingi* refused *Geomys* during five of six trials.

Prey handling behavior within burrow systerns, however, varied markedly across taxa (Table 2). *Pituophis ruthveni* reacted to the occupied burrow systems immediately, presumably due to abundant prey-derived chemical cues. In all trials the snakes proceeded at a rapid rate through the burrow system until contact with the gopher. On only one of 20 trials was the gopher able to backfill the burrow sufficiently to prevent the snake's advance. *Pituophis ruthveni* confronted with a backfilled burrow initiated vigorous and powerful probing motions with its head and neck and was generally able to breach the barrier. Once contact was made with the gopher, three slightly different methods of prey handling occurred: (1) the snake rapidly proceeded past the gopher approximately a third to half of the snake's total length and pinioned the gopher by muscular kinking of its extended body (Fig. IA); (2) the snake rapidly proceeded past the gopher, doubled back, and pinioned the gopher using two lengths of its body (Fig. 1B); or (3) the snake briefly (< 2 s) grasped the gopher in its mouth until the snake positioned two lengths of its body in place as in (2) above. Only in method (3) was the snake's mouth used, and then only for 1 or 2 s. Otherwise, a snake's head was located several centimeters from the gopher until the gopher was dead, or nearly so. *Pituophis s. sayi* behaved similarly in all trials involving gophers in burrow systems (Table 2; cf. Hisaw and Gloyd 1926).

Pituophis m. lodingi reacted differently (Table 2). In nine of the 11 trials *P. m. lodingi* either refused to enter the burrow system, or entered but proceeded in a slow and deliberate manner. Individuals typ-

TABLE 2. Foraging behavior of selected snakes within burrows of Baird's pocket gophers and in open situations. Abbreviations used are Pr = *Pituophis ruthveni*, Ps = *P. sayi sayi*, Pm = *P. melanoleucus lodingi*, Eo = *Elaphe obsolete lindheimeri*.

Taxon	n	Successful Attempts		Pursuit Rate		Mouth Used		Constriction*	
		Trial 1	All Trials	Slow	Rapid	Yes	No	Yes	No
Burrow Trials									
PI	14	14 of 14	19 of 20	0	19	0	19"	0	19
Pm	9	1 of 9	2 of 11	10	1	1	1	1	1
PS	2	2 of 2	6 of 6	0	6	0	6	0	6
Eo	7	3 of 7	7of 12	12	0	7	0	7	0
Open Trials									
Pr	11	11 of 11		NA		11	0	11	0
Pm	3	2 of 3	6 of 1 I'''	NA		6	0	6	0
Ps	2	2 of 2	5 of 5	NA		5	0	5	0
Eo	7	3 of 3	8 of 8	NA		8	0	8	0

'see text for definition
"includes two trials in which month grasp was used for < 2 s.
'''Three individual *P. m. lodingi* refused *G. breviceps* a total of five times

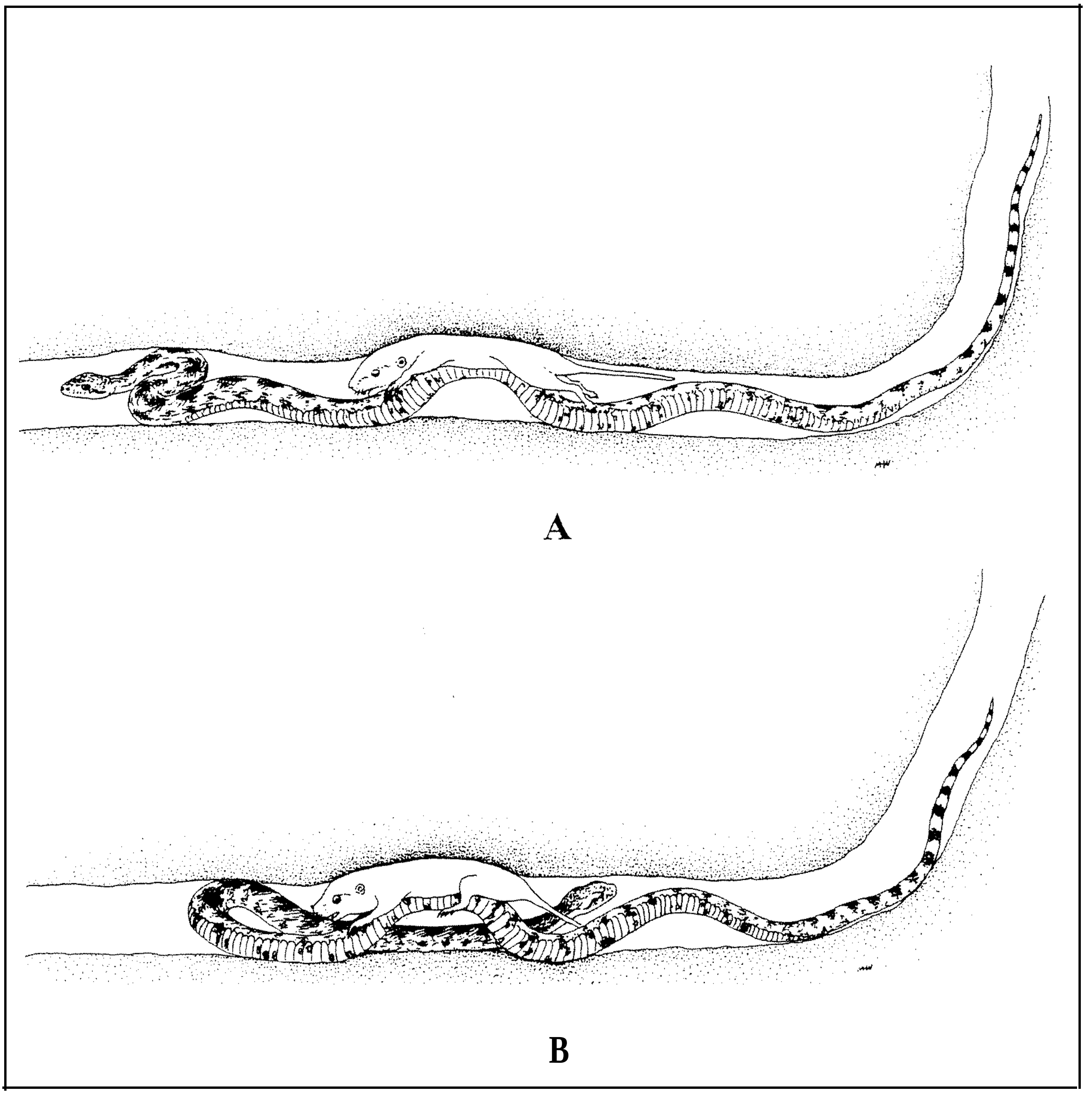

Figure 1. Prey handling behavior of *Pituophis ruthveni* during trial interactions with *Geomys breviceps* showing gopher pinioning (A) by muscular kinking of the extended body and (R) by using two lengths of' body.

ically doubled back either before or after contact with the gopher, returning to the surface or to an unoccupied portion of the burrow system. Often, the gopher had detected the advancing snake and backfilled the burrow with soil, preventing actual contact by the time the slowly advancing snake arrived. In none of these trials did the snake initiate a predatory attack on the gopher or attempt to breach the backfill barriers. Two trials, both by the same snake that had previously eaten a *Geomys* in the cage trials, were successful. The first successful trial resembled that of an E. *obsoleta* (see below). However, the second successful trial resembled that of a *P. ruthveni*. The *P. m. lodingi* moved fairly rapidly through the burrow system, did not use its mouth to grasp the *Geomys*, and made no attempt to use coils to constrict the prey. Subjectively, this individual seemed less proficient than *P. ruthveni* throughout the prey handling sequence.

Elaphe o. lindheimeri behaved differently from *all Pituophis* (Table 2). *Elaphe o. lindheimeri* readily entered the burrow systems in apparent pursuit of the gopher. Movements were slow and deliberate, in marked contrast to those of *P. ruthveni* and *P. s. sayi*. The gophers had often detected the advancing snake prior to its arrival and initiated vigorous backfilling of the burrow. Backfilling was often successful (five of 12 trials), and the snake was unable to penetrate the blockage and attack the gopher. If the snake arrived prior to backfilling, or was able to penetrate the blockage and attack the gopher (seven of 12 trials) the snake then grasped the gopher in it's mouth and maintained this hold while attempting to constrict the gopher in the confines of the burrow system. These attempts, although always successful, appeared awkward. The snakes eventually succeeded in killing the gopher by obtaining a partial coil and/or pinioning the gopher against the burrow wall, typically at the end of a burrow or at a sharp bend in the passage, with the anterior portion of its body.

Based on the first trial for each snake, *P. ruthveni* was more successful than either l? *m. lodingi* ($\chi^2 = 24.15$, $P < 0.001$) or *E. o. lindheimeri* ($\chi^2 = 6.38$, $P < 0.025$) in capturing *G. breviceps* within the confines of a burrow system. Sample size was loo small lo compare *P. s. sayi* success.

A field observation of *P. ruthveni* capturing a pocket gopher, although representing only a partial sequence, is consistent with the above trials. On 16 August 1996 a 1.4 m female *P. ruthveni* was located with 15 cm of its tail protruding from a pocket gopher burrow. Its tail was subsequently retracted into the burrow. Several minutes later a portion of the snake's body broke through the soil surface approximately 1.5 m from the burrow entrance. A struggling *G. breviceps* was held in a loop, not a full coil, of the snake's body. The surface breach was presumably a result of the pressure of the snake's kinked body breaking through the relatively thin (5 cm) overburden. The snake did not have a secure coil around the gopher and the snake's head was not visible. After approximately 5 min the snake was able to retract its body and the gopher underground. Both anterior and posterior portions of the snake were intermittently observed for an additional 22 min. The gopher was not observed again.

DISCUSSION

The prey of *Pituophis* spp. consists primarily of small mammals (Sweet and Parker 199 1). The data reported here for *P. ruthveni* and *P. m. lodingi* are consistent with these reports. The prominence of pocket gophers in the diet of F! *ruthveni* is consistent with the close association of *P. ruthveni* with pocket gopher burrow systems. Telemetry studies (Rudolph and Burgdorf 1997; Rudolph et al. 1998) have demonstrated that *P. ruthveni* present on the surface are most frequently in the immediate vicinity of a pocket gopher burrow system. Pocket gopher burrow systems are the main shelters during the active season, hibernation, and escape from fire.

The importance of pocket gophers in the diet of *P. ruthveni* may be associated with the small clutch size (mean = 4) and large hatchling size (mean = 54.4 cm) of this species (Reichling 1990). Remarkably large hatchling size may be an adaptation to reduce the amount of time and growth necessary to reach a size sufficient to allow predation on pocket gophers. This strategy might have a selective benefit because of the paucity of small mammals in sandy upland sites in west Gulf Coastal Plain longleaf pine savannahs.

The reluctance of *P. m. lodingi* to prey on pocket gophers in this study may be due to the lack of sympatry between these two taxa. The relative contribution of genetic and learned components to this behavior is unknown. Comparable data from *P. m. mugitus* from areas to the east of *P. m. lodingi*, where it is sympatric with *Geomys pinetis*, would be of interest.

The efficiency with which *P. ruthveni* and *P. s. sayi* handle pocket gophers in burrow systems has two critical components lacking in *P. m. lodingi* and *E. o. lindheimeri*. First, the rapid searching through burrow systems reduces the probability of pocket gophers backfilling the burrow and precluding successful predation. In the loose soil of the experimental system. pocket gophers could backfill and pack the burrow, creating a burrow plug 4-X cm in length in less than 1 min. *Pituophis ruthverzi* and *P. s. sayi*, which possess substantial excavating abilities (Carpenter 1982; Reichling 1995). were delayed for a minute or more. In a natural situation this might allow critical time for pocket gopher escape. *Elaphe o. lindheimeri*, lacking specialized excavating abilities, were completely stopped by a completed burrow plug.

Second, the lack, or minimal, use of the mouth to grip the pocket gopher, combined with pinioning the prey using a kink in the snake's extended body rather than coils, reduces the risk of injury during prey handling in a confined space (Hisaw and

Gloyd 1926). Efficient prey handling potentially reduces the time required to subdue dangerous prey species. In addition, the snake's vulnerable head and neck are a considerable distance from the prey, further reducing the probability of injury.

Our results support the previous hypothesis of a close association of l? *ruthveni* and G. *breviceps*, and the near restriction of *P. ruthveni* to longleaf pine savannahs (Rudolph and Burgdorf 1997). Our results are also consistent with the hypothesized cause of the apparent population declines and range contractions of *P. ruthveni* in recent decades (Rudolph and Burgdorf 1997). We suggest that alteration of the fire regime has resulted in successional loss of herbaceous vegetation and consequent declines in G. *breviceps* populations, the primary prey species of *P. ruthveni.*

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