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Effects of Prey Type on the Feeding Behavior of *Alsophis portoricensis* (Serpentes: Colubridae)

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ABSTRACT.—*Alsophis portoricensis* can inject the secretion of its Duvernoy's gland (=venom) into its prey, constrict it, or swallow it alive. We studied the differences in prey-handling behavior of *Alsophis portoricensis* when feeding on two of its natural prey species, the lizard *Anolis cristatellus* and the frog *Eleutherodactylus coqui*. Subduing time was higher for lizards, but swallowing and handling times were longer for frogs. *Alsophis* struck *Anolis* most frequently on the trunk, whereas it attacked *Eleutherodactylus* preferentially on the head or the limbs. *Alsophis portoricensis* was equally successful in preventing both prey types from escaping after first seizing them. Snakes never constricted either prey type, but envenomated most *Anolis* and only one *Eleutherodactylus*. *Alsophis* always swallowed lizards head-first, but ingested frogs head-first or tail- or side-first indiscriminately. This diversity in *Alsophis* feeding behavior may result from differences in external morphology and retaliatory power between *Anolis cristatellus* and *Eleutherodactylus coqui*.

Predators may show variation in their feeding behavior when they encounter different prey types. These variations may be related to the antipredator mechanisms presented by the prey, microhabitat differences among prey types, or to the risk of injury or predation to the predator (Formanowicz and Brodie, 1988; Lima and Dill, 1990). Because feeding is an energy-consuming activity, a predator may minimize the amount of energy invested and/or maximize the amount of energy gained per prey item (Schoener, 1971; Stephens and Krebs, 1986; Pianka, 1988).

Some snakes exhibit variation in their feeding behavior according to prey type. In captivity, mangrove snakes (*Boiga dendrophila*, Colubridae) subdue large anoles by pressing them against the substrate, but hold large snakes in their jaws and chew them (Rocco, 1988). Pitvipers (e.g., *Crotalus* spp., *Agkistrodon piscivorus*, *Porthidium godmani*, *Bothrops jararaca*, Viperidae) usually release mammals after striking them, but retain their hold on fish, amphibians, reptiles, and birds (Klauber, 1956; O'Connell et al., 1981; Campbell and Solórzano, 1992; Hayes, 1992; Sazima, 1992). Tigersnakes (*Notechis scutatus*, Elapidae) swallow frogs after biting, but release rodents following the initial strike (Shine, 1991).

Alsophis is the most geographically widespread genus of colubrid snakes in the West Indies. Species of *Alsophis* are largely ground-dwelling, diurnal, active foragers (Henderson

and Sajdak, 1986). Although *Alsophis* is catholic in its diet, *Anolis* lizards and *Eleutherodactylus* frogs are the most common prey items found in *Alsophis* stomach contents (Henderson and Crother, 1989; Schwartz and Henderson, 1991). The Puerto Rican racer, *Alsophis portoricensis*, has a generalized diet, which is probably the main reason for its variable feeding behavior. *Alsophis* is capable of injecting the secretion of its Duvernoy's gland (=venom) into its prey, constricting it, or swallowing it while it struggles (Rodríguez-Robles, 1992). Herein we report the effects of prey type on the feeding behavior of *Alsophis portoricensis*.

MATERIALS AND METHODS

We used 20 snakes (body mass [BM] = 21.8–154.6 g) collected at the Cambalache Forest Reserve (11 snakes) and at Caja de Muertos Island Natural Reserve (9 snakes), Puerto Rico. Snakes were housed individually in plastic cages (61 cm wide × 31 cm high × 32 cm deep) with newspaper substrates and water ad libitum. Snakes were maintained at a temperature of 24–27 C with no regular light/dark regime. Animals used as prey were the polychrid (Frost and Etheridge, 1989) lizard, *Anolis cristatellus*, and the leptodactylid frog, *Eleutherodactylus coqui*, both of which are natural prey items of *Alsophis portoricensis* (Rodríguez-Robles and Thomas, 1992; M. Canals and J. Gillingham, pers. comm.). *Anolis cristatellus* is a diurnal, trunk-ground anole (Rand, 1964) usually found in open forests and fields and disturbed sites. The Puerto Rican coquí, *Eleutherodactylus coqui*, is a nocturnal frog, typically active from dusk to dawn year-round, that occurs in mesic forests where it uses all parts of the terrestrial habitat, from ground to

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tree tops (Stewart, 1985). Both species are widespread throughout Puerto Rico and are broadly sympatric with *Alsophis portoricensis*, except for Caja de Muertos, where no frogs occur (Schwartz and Henderson, 1991). Snakes from Caja de Muertos, however, did not show any difference in prey-handling behavior of *E. coqui* when compared to snakes from mainland Puerto Rico (Rodríguez-Robles and Leal, unpubl. obs.). Snakes were used only once for each prey type. Eleven snakes were used for both prey items, whereas six snakes were used only for lizards and three only for frogs. Snakes were weighed ($BM \pm 0.1$ g) and all items measured (snout-vent length [SVL] to nearest mm) and weighed ($BM \pm 0.1$ g) immediately prior to the feeding trials.

Using a stop watch and an audio tape recorder, we recorded 17 and 14 complete sequences of *Alsophis portoricensis* feeding on *Anolis cristatellus* (SVL = 30–68 mm, BM = 0.6–10.3 g) and *Eleutherodactylus coqui* (SVL = 25–58 mm, BM = 1.4–9.5 g), respectively. Testing was conducted in completely bare cages. All trials consisted of introducing a single prey item into the cage of an individual snake. If no attack occurred within 1–3 h we removed the prey. Snakes were tested not less than three days after the previous meal. We recorded subduing time (elapsed time from first seizure of prey to commencement of ingestion), swallowing time (time from beginning to completion of ingestion), and handling time (subduing plus swallowing time), the site of the first attack (i.e., head, trunk, limbs), whether or not the prey escaped after being first grasped by the snake, and direction of ingestion (i.e., head-, tail-, or side-first). In *Alsophis portoricensis*, venom injection is dictated by a stationary bite with spasmodic and forceful chewing of the prey (Thomas and Prieto-Hernández, 1985; Rodríguez-Robles, 1992). We noted if a snake injected venom into its prey during a feeding episode. To minimize the confounding effects of variation in body mass between predators and prey when comparing handling, subduing, and swallowing times of lizards and frogs, we used an index that we called relative prey mass. Relative prey mass (RPM) was defined as the residuals (unitless) from the linear regressions of prey mass on snake mass. Because prey mass was sometimes less than the average for a given mass of predator (points below the regression line), and it was sometimes above the average (points over the regression line), RPM had both negative and positive values. We did not use the ratio of prey to snake mass to scale our data to avoid the statistical problems associated with the analysis of ratios (Packard and Boardman, 1987). We plotted (log-transformed) subduing, swallowing, and handling

times against RPM for both *Anolis* and *Eleutherodactylus* to examine the effects of RPM on these variables. Statistical procedures follow Sokal and Rohlf (1981).

RESULTS

Alsophis portoricensis took longer to subdue *Anolis cristatellus* than *Eleutherodactylus coqui*, but swallowing and handling times were higher for coquíes (Table 1). There was no relationship between subduing time and RPM for either *Anolis* or *Eleutherodactylus* (Fig. 1). Swallowing time increased linearly with RPM for *E. coqui*, but for *Anolis cristatellus* the relationship between the two variables was curvilinear (Fig. 2). Handling time was curvilinearly related to RPM for lizards, but again, the relationship was linear for frogs (Fig. 3).

We combined instances of *Alsophis* attacks on the head and limbs of *Anolis* and *Eleutherodactylus* (3 and 2, and 6 and 5 attacks, respectively) to assess differences in the site of the first attack between lizards and frogs. *Alsophis* struck *Anolis* most frequently on the trunk, whereas it attacked *Eleutherodactylus* preferentially on the head or the limbs (Table 2). Snakes were equally successful in preventing *Anolis* and *Eleutherodactylus* from escaping after first seizing them. Although *Alsophis* never constricted either prey type, it injected venom during the subduing phase of the feeding episodes into most lizards, but only into one frog (Table 2). We pooled cases of tail- and side-first ingestion (none for *Anolis* and 5 and 1, respectively, for *Eleutherodactylus*) to assess differences in the direction of swallowing between prey types. *Alsophis* always ingested *Anolis* head-first, but swallowed *Eleutherodactylus* head-first, or tail-, or side-first indiscriminately (Table 2).

DISCUSSION

The trunk of *Anolis cristatellus* was the site of the body most commonly struck by *Alsophis portoricensis*. The possibility of retaliation increases when snakes seize their prey in posterior regions (Murphy and Campbell, 1987; pers. obs.). Preventing retaliatory bites reduces the total prey handling time of snakes, which may be adaptive because snakes may be particularly vulnerable to attack by predators during the prey-handling period (Pope, 1937). Nonetheless, two reasons why the trunk is the most common site on the anole's body struck by *Alsophis* may be that it is the longest part of the lizard or, alternatively, that snakes have better success by attacking there than at either the head, the limbs, or the tail (Rodríguez-Robles, 1992).

Average subduing time of *Anolis cristatellus* was 2.6 times that of *Eleutherodactylus coqui*. The

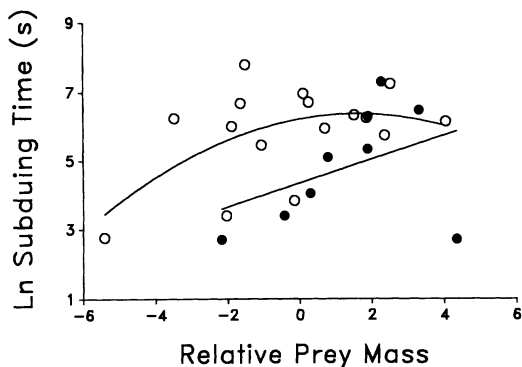


FIG. 1. Subduing time as a function of relative prey mass for *Anolis cristatellus* (open circles; $r^2 = 0.30$, $t = -1.36$, $df = 13$, $P = 0.20$) and *Eleutherodactylus coqui* (closed circles; $r^2 = 0.17$, $t = 1.18$, $df = 7$, $P = 0.28$).

difference seems to be due to the lack of retaliation by coquíes, as compared to commonly exhibited antipredator mechanisms such as biting and tail lashing (Leal and Rodríguez-Robles, unpubl. obs.) employed by *Anolis* when grasped by *Alsophis*. These defensive behaviors, or absence of them, along with visual, and probably chemical stimuli, may be signals used by *Alsophis portoricensis* to assess its prey and to "decide" if it will envenomate or not. If true, this may account for the difference in the frequency of venom use by *Alsophis* when feeding on lizards and frogs. The lack of relationship between subduing time and RPM for *Anolis* and *Eleutherodactylus* may indicate that not only prey mass, but also prey defensive behavior should be considered when examining the factors controlling subduing time in snakes. At least in the case of *Anolis cristatellus*, the longer it bit the snake, the longer it took *Alsophis* to subdue it (Leal and Rodríguez-Robles, unpubl. obs.). Furthermore, because venom of colubrid snakes is released slowly (Vest, 1981; Rosenberg et al., 1985; Vest et al., 1991) and the venom itself of *Alsophis portoricensis* does not immediately immobilize the prey (Rodríguez-Robles, 1992), envenomation by *Alsophis* results in longer subduing time. Other snakes may also rely on the retaliatory response experienced after the strike and/or seizure to employ a particular subduing strategy; *Crotalus* spp. sometimes consume nestling birds and newborn mammals without envenomating them (Klauber, 1956; Radcliffe et al., 1980), and *Pituophis melanoleucus* subdues helpless two-week old rats significantly faster than adult laboratory mice (de Queiroz, 1984).

Alsophis portoricensis could not restrain movements of anoles and coquíes with its jaws alone. After being seized, both lizards and frogs dragged snakes along whenever they struggled, jumped, or pushed themselves with the limbs.

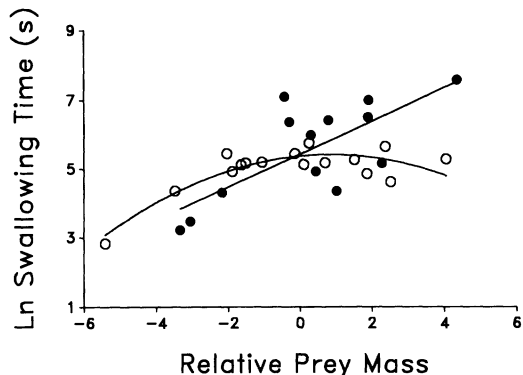


FIG. 2. Swallowing time as a function of relative prey mass for *Anolis cristatellus* (open circles; $r^2 = 0.76$, $t = -4.74$, $df = 13$, $P = 0.0004$) and *Eleutherodactylus coqui* (closed circles; $r^2 = 0.54$, $t = 3.61$, $df = 11$, $P = 0.004$).

Nevertheless, *Alsophis* never constricted or used its body to restrain movements of either prey type. Despite the sometimes violent struggling of *Anolis*, only 2 out of 17 lizards escaped after being first captured by *Alsophis*, but both were recaptured a few seconds later. Although *Eleutherodactylus coqui* >18 mm SVL are able to escape from predatory *Olios* spiders (Sparassidae) by kicking free after being captured (Formanowicz et al., 1981), none of them could do so after being grasped by *Alsophis*.

Only two frogs gave release calls when seized by *Alsophis*. However, *Eleutherodactylus coqui* commonly gives aggressive calls, followed by an attack, while defending retreat sites from conspecifics, and male *E. coqui* give aggressive calls after human disturbances of their shelters or in response to the intruding predator *Anolis gundlachi* (Stewart and Rand, 1991). Hence, the reasons why coquíes do not vocalize more often

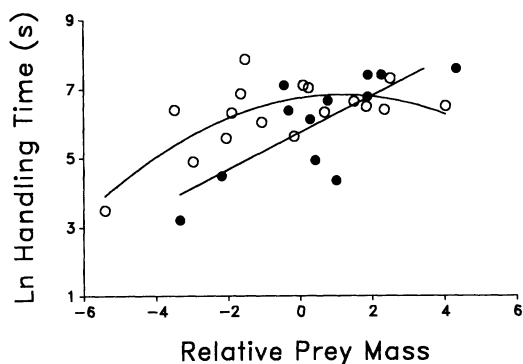


FIG. 3. Handling time as a function of relative prey mass for *Anolis cristatellus* (open circles; $r^2 = 0.55$, $t = -2.66$, $df = 14$, $P = 0.019$) and *Eleutherodactylus coqui* (closed circles; $r^2 = 0.57$, $t = 3.63$, $df = 10$, $P = 0.005$).

TABLE 1. Differences in subduing, swallowing, and handling times of *Alsophis portoricensis* when feeding upon *Anolis cristatellus* and *Eleutherodactylus coqui*. ANCOVA analyses were performed on log-transformed handling, subduing, and swallowing times using relative prey mass as the covariate in all comparisons (see text for further details). Reported means are unadjusted.

	Mean (\pm 1 SE)	Range	n
Subduing time (sec)			
<i>Anolis cristatellus</i>	623.1 (151.0)	16–2411	16
<i>Eleutherodactylus coqui</i>	242.2 (117.9)	0–1461	13
ANCOVA, $F = 4.90$, $df = 1,22$, $P = 0.038$.			
Swallowing time (sec)			
<i>Anolis cristatellus</i>	174.3 (18.6)	17–317	16
<i>Eleutherodactylus coqui</i>	538.2 (159.2)	25–1930	13
ANCOVA, $F = 16.57$, $df = 1,26$, $P = 0.0004$.			
Handling time (sec)			
<i>Anolis cristatellus</i>	758.3 (147.6)	33–2587	17
<i>Eleutherodactylus coqui</i>	788.4 (196.8)	25–1945	12
ANCOVA, $F = 16.85$, $df = 1,26$, $P = 0.0004$.			

TABLE 2. Differences in feeding behavior of *Alsophis portoricensis* when preying on *Anolis cristatellus* and *Eleutherodactylus coqui* in terms of site of first attack, escapes after first seizure, venom injection, and direction of swallowing.

	Site of first attack	
	Head or limbs	Trunk
<i>Anolis cristatellus</i>	5	12
<i>Eleutherodactylus coqui</i>	11	3
G-test of independence with Williams' correction, $G = 7.18$, $df = 1$, $P = 0.007$.		
	Escapes after first seizure	
	Escaped	Did not escape
<i>Anolis cristatellus</i>	2	15
<i>Eleutherodactylus coqui</i>	1	13
Two-tailed Fisher's exact test of independence, $P = 1.00$.		
	Venom injection	
	Yes	No
<i>Anolis cristatellus</i>	13	4
<i>Eleutherodactylus coqui</i>	1	13
G-test of independence with Williams' correction, $G = 16.13$, $df = 1$, $P < 0.0001$.		
	Direction of swallowing	
	Head-first	Tail-first or side-first
<i>Anolis cristatellus</i>	17	0
<i>Eleutherodactylus coqui</i>	8	6
Two-tailed Fisher's exact test of independence, $P = 0.004$.		

during encounters with snakes are not apparent.

Alsophis took 3.1 times longer to swallow *Eleutherodactylus* than *Anolis*. The anole's body is cylindrical, whereas *E. coqui* has a triangular shape, the head being the widest area. In addition, some coquíes inflated their lungs to full capacity while they were being swallowed. These sudden increases in prey diameter, rather than absolute girth, may represent critical obstacles to ingestion and require more time and energy to overcome (Gans, 1953; Diefenbach and Emslie, 1971).

Swallowing prey items from the front is advantageous to snakes because both the front and hind limbs of the prey fold against the body, offering less resistance during ingestion (Klauber, 1956; Diefenbach and Emslie, 1971). Sharply pointed imbricate scales may also impede swallowing from the rear. One possible cue for head-first ingestion of reptiles is scale overlap (Greene, 1976). The ventral scales of *Anolis cristatellus* overlap somewhat, which can be a signal that cues *Alsophis* as to which end of the body to begin the swallowing process. If true, this signal is absent when *Alsophis* preys on *Eleutherodactylus*, and the snake may simply start to consume the frog by the end closest to that portion of the body grasped initially (Cooper, 1981).

Natural selection may favor optimal feeding strategies for animals (Griffiths, 1980). The time for handling both *Anolis* and *Eleutherodactylus* increases with their body mass, as presumably do energy costs. Nonetheless, after the intersection of the regression curves, handling time of *Anolis* decreased (Fig. 1). Thus, on the basis of optimal foraging theory (Stephens and Krebs, 1986; Krebs and Kacelnik, 1991), if *Anolis cris-*

tatellus and *Eleutherodactylus coqui* have the same caloric and nutritional content and the same "catchability" (Pianka, 1988), *Alsophis* should feed on coquíes up to a certain body mass and then switch to anoles. We doubt such a strategy evolved in *Alsophis portoricensis* because this snake is an opportunistic feeder that takes almost any small vertebrates encountered, which probably results from lack of a choice among prey species. This hypothesis, however, can be tested by presenting *Alsophis* with choices between *Anolis cristatellus* and *Eleutherodactylus coqui*.

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NOTE ADDED IN PROOF: On March 3, 1993 the junior author recovered a freshly ingested (tail-first) *Eleutherodactylus antillensis* from an *Alsophis portoricensis* at the Cambalache Forest Reserve. The frog was still alive four days later. On March 21 he collected another *A. portoricensis* at Ranchos de Guayama, Guayama, Puerto Rico, that had swallowed two *E. antillensis*, one head-first and one tail-first. One frog escaped after the snake was forced to regurgitate and the other was still alive on March 23. These findings support our conclusions that *A. portoricensis* usually does not envenomate *Eleutherodactylus*.

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The Reproductive Cycle of the Viviparous Mexican Lizard *Sceloporus torquatus*

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ABSTRACT.—The reproductive cycle of the lizard *Sceloporus torquatus* was determined using data obtained from field caught and museum specimens. Males exhibit testicular recrudescence during late summer and maximal testicular volumes occur during September and October. Similarly, females begin vitellogenesis in late summer, culminating in ovulation during November or December. Females are pregnant throughout the winter months with birth in April or early May. Average clutch size is 9.7 young. Neonates of both sexes are born early in summer, achieve adult size within five months and are thus capable of reproductive activity the first fall after birth. This study adds to the data that indicate that fall reproductive activity is the common reproductive strategy among viviparous lizards of the genus *Sceloporus*.

The timing of reproductive activity is an important aspect of a species' reproductive strategy. Since the classic work of Fitch (1970), a substantial literature has developed demonstrating that lizards exhibit a number of differing reproductive activity patterns. Early work suggested that temperate lizards showed spring gonadogenesis, ovulation, fertilization, and oviposition associated with increasing ambient temperature. In contrast, tropical species were either seasonal, dependent on rainfall and food availability, or aseasonal breeders, exhibiting

reproductive activity throughout the year (Fitch, 1970, 1982). Data from several early studies examining viviparous lizards of the genus *Sceloporus* demonstrated that a different pattern of seasonal activity was possible for temperate species, as gametogenesis, courtship, mating, and fertilization occurred during the fall months. Embryos developed throughout the winter months with parturition the following spring (*Sceloporus cyanogenys*: Crisp, 1964; Callard et al., 1972; *Sceloporus jarrovi*: Goldberg, 1970, 1971; Ballinger, 1973; *Sceloporus poinsetti*: Ballinger,