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Accepted: 15 November 1991.

Journal of Herpetology, Vol. 26, No. 1, pp. 100-102, 1992
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Notes on the Feeding Behavior of the Puerto Rican Racer, *Alsophis portoricensis* (Serpentes: Colubridae)

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Colubrid snakes are able to capture and dispatch the animals they feed upon in numerous ways. During ophidian evolution, two major methods of immobilizing prey have arisen: constriction and envenomation (Gans, 1961; Shine and Schwane, 1985). A number of colubrids are constrictors (e.g., *Clelia*, *Elaphe*, *Lampropeltis*, *Pituophis*), whereas others (e.g., *Alsophis*, *Dispholidus*, *Heterodon*, *Thelotornis*) are venomous (Minton, 1990).

The primary morphological indicator of toxicity in colubrids is the presence of Duvernoy's gland (McKinstry, 1978, 1983), which is often correlated with the presence of one or more enlarged teeth on the posterior end of each maxilla. These teeth, either grooved or solid (opisthogastront), are the second-

ary morphological indicator of toxicity in colubrids (McKinstry, 1978, 1983).

The Puerto Rican racer, *Alsophis portoricensis* Reinhardt and Lütken, 1863, is an endemic, opisthogastront colubrid with a serous Duvernoy's gland (Taub, 1967), whose secretion (venom, hereafter) has a relatively mild toxicity (Heatwole and Banuchi, 1966; Thomas and Prieto-Hernández, 1985). The purpose of this work was to study the feeding behavior of *A. portoricensis* and to determine to what extent are venom and other prey-immobilizing methods employed by this snake.

The 25 snakes used for this study were collected at various sites in northern Puerto Rico (10 snakes), and at Caja de Muertos Island Natural Reserve (15 snakes). Snakes were housed individually in plastic cages (61 cm long × 31 cm high × 32 cm deep) with newspaper substrates and water ad libitum; they were maintained on a natural photoperiod at a mean diurnal temperature of 29.6 C (SD = 2.31, range = 22-34.5 C, N = 375) throughout this study. Mean body (cloacal) temperature of all snakes (pooled) was 29.0 C (SD = 2.26, range = 21.5-33.7 C, N = 375). *Anolis cristatellus* Duméril and Bibron, 1837, a lizard upon which *A. portoricensis* feeds in the wild (pers. obs.), was used as the prey item for all trials. Snakes were weighed (± 0.1 g), and anoles measured (snout-vent length to nearest mm) and weighed just before the feeding trials. Testing was conducted in the cages during daytime.

Using a stopwatch and an audio tape recorder, I recorded 70 sequences of *A. portoricensis* feeding on live prey. The 25 snakes were used two or three times each. Each trial consisted of introducing a single anole into the cage of an individual snake. If no attack occurred within 1-2 h I removed the anole. Snakes were tested not less than six days after the previous meal. The site of attack (i.e., head, body, limbs, or tail) and the final result (i.e., capture or escape) were recorded, as were subduing time (elapsed time from seizure to the commencement of ingestion), and handling time (subduing time plus time to completion of ingestion). Statistical procedures follow Sokal and Rohlf (1981). All statistical tests were performed using the STATISTIX (Version 3.0, Analytical Software, 1989) software.

Mean subduing time was 834.1 s (SD = 1058, range = 0-4672 s, N = 44), whereas average handling time was 883.4 s (SD = 777.7, range = 128-3688 s, N = 33). I plotted subduing and handling time (both variables ln-transformed) against the residuals from the linear regression of prey mass on snake mass to examine the effects of relative prey size on these variables (Fig. 1). Both subduing and handling times tended to increase relative to prey size, although the regressions were not significant at $P \leq 0.05$.

Although lizard movements commonly provoked an attack by the snakes, snakes occasionally struck lizards which had remained immobile since being introduced into the cage. Snakes watched anoles and occasionally flicked their tongues before seizing them. Snakes either moved slowly toward lizards from behind or from the side, or pursued them rapidly. Invariably, anoles jumped away as the snakes approached. The prey was seized with a quick strike, but as many as six follow-up strikes were necessary for capture when the initial strike missed the prey.

The outcome of the attack depended on where

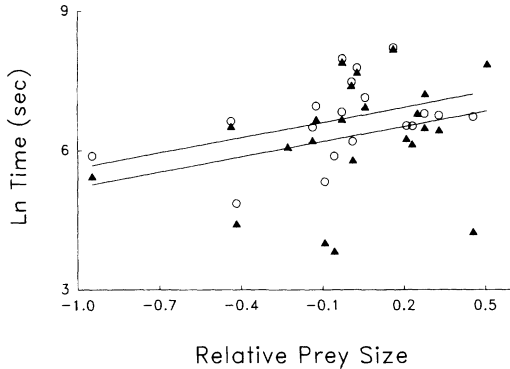


FIG. 1. Linear regression of subduing time (solid triangles; $r^2 = 0.11$, $t = 1.70$, $df = 24$, $P = 0.10$) and handling time (open circles; $r^2 = 0.17$, $t = 1.85$, $df = 17$, $P = 0.08$) on relative prey size.

snakes seized the prey. Snakes had a better chance of success striking a lizard on the body than on the head, the limbs or the tail (Table 1). Nineteen times snakes missed their strike, and on 18 occasions lizards escaped after having been seized. If the prey had not been confined in the cages, the total success rate (63.7%) would almost certainly have been lower, because anoles would probably have escaped after a missed strike.

Snakes always held their prey following successful strikes. If the anoles struggled after being captured, the snakes chewed to embed their posterior maxillary teeth. Vigorous victims were normally held firmly in this manner, the snakes chewing spasmodically and forcefully for several minutes until the lizards became still. These chewing motions did not seem to facilitate swallowing because they did not accompany a shift in the position of the bite, but instead might have helped introduce venom into the prey (Jansen and Foehring, 1983; Thomas and Prieto-Hernández, 1985). Commonly, lizards gaped and showed signs of respiratory distress a few minutes after being seized. The venom thus may act to weaken the prey, but usually does not immediately immobilize it nor kill it before ingestion. Anoles struggled 67% of the time, although not continuously, while being swallowed. The struggling consisted mainly of a lateral, sometimes violent waving of the tail, and occasional jumping. I also observed 11 anoles struggling inside the snakes for up to 414 s after they had been completely engulfed. Out of 61 trials, snakes swallowed anoles tail first on only four occasions.

Three times I observed snakes throwing two body loops around *Anolis*, but the loops appeared to be too loose for the snake to apply any strong constricting force. However, three captive *A. portoricensis* killed laboratory mice (*Mus musculus*) on several occasions solely by constriction (pers. obs.; M. Leal, pers. comm.), whereas another snake tightly restrained a large *Ameiva exsul* with constricting coils, although it is uncertain if the snake would have killed the lizard (R. Thomas, pers. comm.). Hence, the observation by Henderson and Crother (1989) that no West Indian colubrid snake uses constriction to subdue its prey is not correct. The fact that *A. portoricensis* is capable of both constricting and envenomating its prey suggests that in *Alsophis*, as in some Australian elapids (Shine

TABLE 1. Relationship between site of attack of *Alsophis portoricensis* on *Anolis cristatellus*, and outcome of the strike. Percentage of success per strike = captures/frequency. G-test of independence with Williams correction, $G = 26.68$, $df = 3$, $P < 0.0001$.

Site of attack	Frequency (%)	Captures	Escapes and missed strikes	% success per strike
Head	22 (21.6)	13	9	59.1
Body	51 (50.0)	42	9	82.4
Limbs	16 (15.7)	9	7	56.3
Tail	13 (12.7)	1	12	7.7
Total	102 (100)	65	37	63.7

and Schwaner, 1985), these strategies are not mutually exclusive answers to the problem of prey immobilization.

What cues *A. portoricensis* uses to "decide" which immobilization technique to employ are not evident. Although prey size is an obvious possibility (Willard, 1977; Kardong, 1982), instances of *A. portoricensis* using only venom to subdue *Mus musculus* (pers. obs.) and *A. exsul* (R. Thomas, pers. comm.) suggest that these snakes might also rely on other stimuli, such as prey type, or a combination of both prey size and type (Mori, 1991). Nevertheless, one possible reason for the frequent use of venom by *A. portoricensis* is that venom speeds up the prey digestion rate of this species (Rodríguez-Robles and Thomas, 1992). By accelerating digestion, venom may allow snakes to expand foraging activities (Mackessy, 1988) or to consume more prey per unit time.

Acknowledgments.—I thank R. Thomas, M. Leal, M. Garcia, C. Ortiz, and H. Alvarez for their help in various aspects of this project. R. Thomas, J. Ackerman, N. Fetcher, and R. Seigel greatly improved the manuscript with their suggestions. The Department of Natural Resources of Puerto Rico provided the permits necessary to carry out this work. This research was funded by the Peggy Wadsworth Memorial Award of the Natural History Society of Puerto Rico to the author, and by a grant from the Fondo Institucional para la Investigación, University of Puerto Rico, to R. Thomas. This study represents part of a thesis submitted for the M.S. degree in Biology, University of Puerto Rico, Río Piedras.

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Accepted: 15 November 1991.

Journal of Herpetology, Vol. 26, No. 1, pp. 102-105, 1992
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Parental Care in *Dendrobates granuliferus* (Anura: Dendrobatidae), with a Description of the Tadpole

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Species groups of the Neotropical frog family Dendrobatidae can be distinguished on the basis of differences in territorial and reproductive behavior

(Weygoldt, 1987; Zimmermann and Zimmermann, 1988). *Dendrobates granuliferus* Taylor 1958 is a member of the *D. histrionicus* species group (Myers and Daly, 1976, 1979; Myers et al., 1984; Zimmermann and Zimmermann, 1988). Insofar as known, all species in this group (i.e., *D. histrionicus*, *D. lehmanni*, *D. pumilio*, and *D. speciosus*) have similar advertisement calls, and social and parental behavior. Territorial behavior (Goodman, 1971; Crump, 1972), and courtship and mating behavior (Crump, 1972) have been described for *D. granuliferus*.

In captivity, females of other species in the *D. histrionicus* group act as nurse frogs and carry tadpoles individually to different water-containing axils of bromeliads. Parental care extends beyond larval transport; females regularly deposit eggs to feed the developing larvae (Weygoldt, 1980; Zimmermann and Zimmermann, 1981; Jungfer 1985).

Details of parental care are not known for *D. granuliferus*, but it could be assumed that parental care of *D. granuliferus* is similar to that of other species of the *D. histrionicus* group. We observed tadpole-carrying *D. granuliferus* and inspected potential tadpole deposition sites in the field to test this assumption. Herein, we report on some aspects of parental care in *D. granuliferus* and describe the tadpole.

Observations were made in the Quebrada Grande, about 2 km east of Palmar Norte, Puntarenas Province, Costa Rica during May-November 1987 and March-June 1988. The area is located, following the life-zone system of Holdridge, in premontane wet forest (basal belt transition; Tosi, 1969). The study site included remnants of primary and secondary rain forest along the banks of the Quebrada. Bromeliads were uncommon in this area, while other water containing plants, such as palms, *Heliconia* spp., and *Dieffenbachia longispatha* (Dumb cane) were abundant. Observations of tadpole transport and deposition by *D. granuliferus* were made between 0600 and 1300 h. Nurse frogs were sexed based on the presence (male) or absence (female) of a darkly pigmented vocal sac (Goodman, 1971). In four areas where *D. granuliferus* was abundant, small accumulations of water in the vegetation were inspected for tadpoles. The volume of water containing tadpoles was estimated by collecting the water in a 10 ml measuring cylinder using a Pasteur pipette. Tadpoles were measured to the nearest tenth of a millimeter under a stereo microscope, with an ocular micrometer. Tadpoles were deposited at the Museo de Zoología of the Universidad de Costa Rica, San José, Costa Rica (UCR 10710), and the Nationaal Natuurhistorisch Museum, Leiden, the Netherlands (RMNH 24442-8).

Larval transport by female *D. granuliferus* was observed on eight occasions. In seven of the cases the females carried a single tadpole; one female carried two tadpoles. Tadpole deposition was observed four times. Deposition sites varied: water accumulations in a broken stem of a palm tree (0.8 m above ground); a broken stem of a shrub (1.5 m above ground); a leaf-axil of a *Heliconia* sp. (0.15 m above ground); and a bromeliad 3.0 m above ground (*Guzmania* sp.). On two occasions a female nurse frog was seen inspecting leaf-axils of *Dieffenbachia longispatha*, but deposition of tadpoles in these plants was not observed. Nevertheless, water-containing axils of these plants were apparently common deposition sites. Several females