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On the Diet of the Boa *Epicrates striatus* on Hispaniola, with Notes on *E. fordi* and *E. gracilis*

Robert W. Henderson[1], Teresa A. Noeske-Hallin[1], José A. Ottenwalder[2], Albert Schwartz[3]

Abstract. The stomach contents of 214 specimens of Hispaniolan *Epicrates* (Serpentes: Boidae) were examined for prey remains. The largest species, *E. striatus*, exhibits a sharp ontogenetic shift in diet: snakes < 60 cm SVL ate predominantly *Anolis* lizards; snakes 60-80 cm SVL took anoles and small rodents; and snakes > 80 cm SVL ate birds and rats (*Rattus rattus*). *Epicrates fordi* preyed on anoles and small rodents, and *E. gracilis* took only *Anolis*. *E. striatus* ate larger individuals of the same species of *Anolis* consumed by Hispaniolan colubrids. Before the arrival of Europeans on Hispaniola, large *Epicrates striatus* most likely preyed upon birds and now-extict rodents (*Brotomys, Isolobodon* and *Plagiodontia*) and insectivores (*Nesophontes*). The diet of *E. striatus* would have gradually shifted from native to introduced mammals, and by the early 20th century, when most native, non-volant mammals had become extinct on Hispaniola, the shift would have become nearly complete, with the exotics *Mus musculus* and *Rattus rattus* becoming the predominant prey species.

Introduction

The island of Hispaniola has the richest snake fauna in the Antilles, including three species (of which two are endemic) of the boid genus *Epicrates*; no other West Indian island has more than a single species. The three species differ in size, distribution and habitat. *Epicrates striatus* is by far the largest of the Hispaniolan boas: the longest measured by us was a female with a snout-vent length (SVL) of 193 cm and a total length of 222 cm; of those containing prey remains the mean SVL was 95.8 ± 7.3 cm, and mean midbody circumference (MBC) was 99.0 ± 10 mm. *Epicrates striatus* is the most widespread of the Hispaniolan boids, occurring throughout main island Hispaniola and some of its satellite islands in a variety of habitats (Sheplan and Schwartz, 1974); the species also occurs in the Bahama Islands. *Epicrates fordi* is the

[1] Section of Vertebrate Zoology, Milwaukee Public Museum, Milwaukee, WI 53233 USA
[2] Florida State Museum and School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611 USA; Permanent Address: Parque Zoologico Nacional, P.O. Box 2449, Santo Domingo, Dominican Republic
[3] Biology Department, Miami-Dade Community College-North Campus, Miami, FL 33167 USA

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smallest (= shortest) of the three species ($\bar{x}$ SVL = 45.5 ± 4.9 cm; $\bar{x}$ MBC = 41 ± 2.9 mm), and the most geographically restricted. Most specimens have come from the Cul de Sac-Valle de Neiba plain, plus some associated areas and at least three satellite islands (Sheplan and Schwartz, 1974). It has generally been taken in xeric habitats. *Epicrates gracilis* is the most morphologically specialized *Epicrates*. Although it reaches a greater length than *E. fordi*, it is more slender (mean SVL = 56.7 ± 6.5 cm; $\bar{x}$ MBC = 39.0 ± 5.0 mm). It is more widespread than *E. fordi*, but it is nowhere very common. *Epicrates gracilis* is almost invariably found in mesic situations.

Surprisingly little is known about the natural history of West Indian *Epicrates*, including trophic ecology; most references to prey preference have been very general (e.g. Reagan, 1984) or fortuitous observations (Sheplan and Schwartz, 1974). Greene (1983b) summarized dietary diversity in boids, including *Epicrates*, but specific information on West Indian *Epicrates* diets has dealt largely with their proclivity for eating bats (Hardy, 1957b; Rodriguez and Reagan, 1984), and Ottenwalder (1980) reported a somewhat artificial situation of bird predation by *E. striatus*. Here, as part of a continuing study of the trophic ecology of West Indian snakes, we present the results of examination of 214 Hispaniolan *Epicrates* (133 *E. striatus*, 48 *E. fordi*, 33 *E. gracilis*).

Materials and Methods

The snakes examined were in the herpetological collections of the American Museum of Natural History (AMNH), the Albert Schwartz Field Series (in Miami, ASFS), the Museum of Comparative Zoology (MCZ), the Milwaukee Public Museum (MPM), and the Florida State Museum (UF-FSM). They were collected at various localities under dry and wet season conditions over a span of about 80 years. Methods used for taking morphological measurements and determining the size (volume) of individual prey items have been described in detail elsewhere (Henderson, 1982, 1984). These results were compared with those for Hispaniolan colubrid snakes (six genera, eight species) based on examination of 1874 specimens which yielded 326 prey items identified to species and for which volume was determined (Henderson, 1984 and unpubl.). Data were analyzed using one-way analysis of variance (ANOVA), and regression. Differences among group means were determined with Student-Newman-Keuls (SNK) test. Prey species volume data were logarithmically transformed prior to analysis to normalize their distribution. All analyses were performed using the Statistical Analysis Systems (SAS) package.

Results

Examination of *Epicrates striatus* yielded 28 prey items, and these are summarized in Table 1. This large snake exhibits a sharp ontogenetic shift in diet: snakes < 60 cm SVL ate predominantly *Anolis* lizards; snakes 60-80 cm SVL took anoles and small rodents; and snakes > 80 cm SVL ate birds and rats (*Rattus rattus*). Lizards were not

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Table 1. Summary of the diet of Hispaniolan *Epicrates striatus*. Means are followed by ± standard error.

Prey Group	Percent volume of prey group	mean vol. (cm^3)	Mean SVL of snakes preying on group (cm)
Lizards	2.1	4.6 ± 0.7	57.2 ± 39.1
Anolis coelestinus			
Anolis cybotes			
Anolis sp.			
Birds	5.2	50.0 ± 11.0	82.2 ± 17.8
Dulus dominicus			
Quiscalus niger			
Coereba flaveola (?)			
Mammals	92.7	100.4 ± 13.5	116.6 ± 73.0
Mus musculus			
Rattus rattus			

consumed once snakes reached 80 cm SVL, and *R. rattus* comprised the sole prey species of snakes > 105 cm SVL (Fig. 1). *Epicrates striatus* that preyed on rats were significantly longer than those that ate birds, which in turn were larger than those eating anoles (ANOVA, F = 36.48, $P < .0001$). Although rodents comprise a large percentage of the total prey volume eaten by *E. striatus, Anolis* is obviously an important food source for small boas: 8 of 12 (75%) prey items taken by snakes < 80 cm SVL were anoles. Mean size of prey eaten by *E. striatus* was 66.7 cm^3 (n = 26).

Our prey sample sizes for *Epicrates fordi* (n = 6) and *E. gracilis* (n = 6) are inadequate for detailed analysis. *Epicrates fordi* exploited lizards (*Anolis cybotes* and *Anolis* sp.; n = 4) and small rodents (*Mus*; n = 2). The very slender *E. gracilis* had fed only on anoles (*A. cybotes* and *A. distichus*). Mean size of prey taken by *E. fordi* was 6.8 cm^3 (n = 2), and 2.4 cm^3 (n = 5) for *E. gracilis*.

Discussion

All three species of Hispaniolan *Epicrates* are nocturnal. *Epicrates fordi* is largely ground-dwelling, *E. gracilis* is exclusively arboreal, and *E. striatus* is largely arboreal. Adults of the two smaller species have been observed crawling slowly through above-ground vegetation at night, presumably foraging actively for sleeping anoles. Small *E. striatus* have been encountered in similar situations, and adults have been observed sprawled out in the branches of low trees at night, and one was captured crawling on the ground with a freshly eaten rat in its stomach. During the day, *E. striatus* will coil in limestone crevices, in bird nests, in tree hollows, in clumps of vegetation growing on broad horizontal branches, or coil in the shade on the upper surfaces of broad horizontal branches, frequently at considerable heights above the ground (5-20 m; RWH, pers. observ. and pers. commun. with native collectors). It is possible that foraging mode

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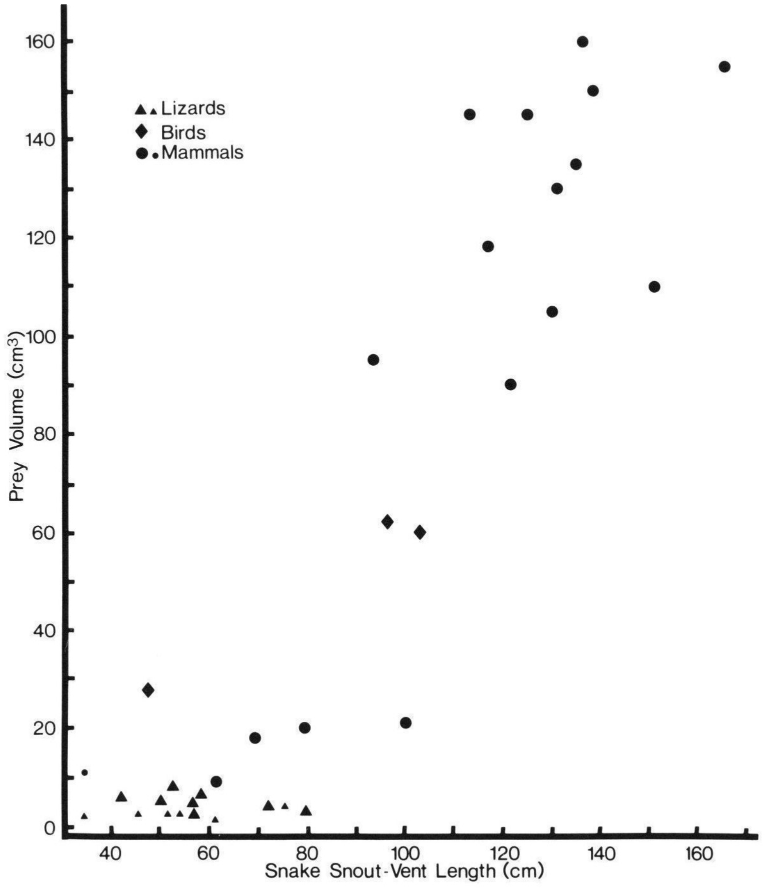

Fig. 1. Relationship between snake size (snout-vent length) and prey size (volume). Large symbols (triangles, diamonds, and dots) are for *Epicrates striatus*. Small symbols (triangles and dots) are for *E. fordi* and *E. gracilis*.

shifts with age and increasing size. Small *E. striatus* that eat sleeping anoles at night must be actively foraging, but those eating rodents may be employing a sit-and-wait strategy. It is likely that a combination of tactics may be used, as has been suggested for *Boa constrictor* (Greene, 1983a).

Epicrates gracilis is the most morphologically (Sheplan and Schwartz, 1974) and trophically specialized of the trio. Prey size between these three species is dependent on head width and MBC, with the very slender *E. gracilis* taking the smallest food items and the large, heavy-bodied *E. striatus* taking, by far, the largest.

Although the opportunistic predation on bats by some species of *Epicrates* has received attention (Hardy, 1957b; Rodriguez and Reagan, 1984), bats were not among the

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prey items in our sample. This does not mean that bats are not included in the diet of *E. striatus*, but only that bat predation is geographically very localized. Where concentrations of bats are large enough to make foraging for them energetically rewarding, *E. striatus* undoubtedly exploits them. In a similar situation, Hardy (1957a) found the active foraging Cuban colubrid *Alsophis cantherigerus* collected near the mouth of a cave to have eaten bats. However, examination of the stomachs of 466 West Indian *Alsophis* (including 173 *A. cantherigerus*) by one of us (RWH) has yielded the remains of only a single bat. The implication is that, under certain conditions, exploitation of bats as food may be occasionally advantageous, but that it is probably not a widespread occurrence.

Similarly, one of us (Ottenwalder, 1980 and unpublished) has documented heavy predation by *Epicrates striatus* on birds living in a huge free-flight aviary at the National Zoo in Santo Domingo, Dominican Republic. Free-living snakes had easy access to the large aviary and between 12 February and 23 October 1980, at least ten birds were killed by individuals of *E. striatus*. It is highly likely that some snakes repeatedly returned to roost and nest sites to eat adult and fledging birds, and also eggs. Genera of birds just killed, or killed and eaten, include *Amazona* and *Aratinga* (Psittacidae), *Columba* and *Zenaida* (Columbidae), *Chrysolophus* and *Phasianus* (Phasianidae), and *Ortalis* (Cracidae). The species of psittacines and pigeons involved are gregarious and native to Hispaniola. Although birds are certainly taken as food by *E. striatus* living off the grounds of the Santo Domingo Zoo, we interpret this as another example of opportunistic predation by Hispaniolan boas; i.e., exploiting a convenient and abundant food supply under semi-natural conditions. Snakes in general are opportunistic predators, and our data on Hispaniolan colubrids supports this (Henderson, 1984; Henderson and Schwartz, 1986; Henderson et al., 1987a, 1987b, MS): they eat those vertebrate prey species that are the most ubiquitous geographically and ecologically, which occur in the highest relative densities and which provide the proper energetic rewards. This apparently applies to *Epicrates* also.

It is of interest to compare aspects of the diet of the primitive boids with that of the advanced colubrids. The boids are nocturnal, largely arboreal and kill prey by constriction. The colubrids are diurnal, ground-dwelling or arboreal, and subdue prey with a weak venom or else swallow it alive. The mean size (= volume) for 260 prey items eaten by eight species of Hispaniolan colubrid snakes was 3.60 $\pm$ 0.3 cm^3; for individual species, means ranged from 1.21 $\pm$ 0.29 cm^3 for *Darlingtonia haetiana* to 10.7 $\pm$ 4.67 cm^3 for *Ialtris dorsalis*. In comparison, the mean prey size for the three species of *Epicrates* combined was 53.3 $\pm$ 10.5 cm^3, ranging from 2.4 $\pm$ 0.5 cm^3 for *E. gracilis* to 66.7 $\pm$ 12.0 cm^3 for *E. striatus*.

Diet overlap between the two families occurs for *Anolis* lizards. Mean anole size taken by all colubrids (n = 175) was 2.3 $\pm$ 0.1 cm^3; for individual species, means range from 2.1 $\pm$ 0.3 cm^3 for *Uromacer catesbyi* to 4.0 $\pm$ 0.8 cm^3 for *Hypsirhynchus ferox*. Mean size of anoles taken by all *Epicrates* was 3.6 $\pm$ 0.5 cm^3, with a range of 2.5-4.6 cm^3. The boas combined took *Anolis* of a significantly larger mean size than the col-

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ubrids (ANOVA, $F = 7.91$, $P < .006$). *Epicrates striatus* took larger anoles than any other species of boid or colubrid, followed by *Hypsirhynchus ferox* (SNK, $P < .05$). It is noteworthy that the anoles exploited by boas are not larger species, but, rather, larger individuals of the same species most commonly eaten by colubrids.

Epicrates striatus is significantly larger than the other boids and colubrids examined for each of eight morphological characters. The smaller boid species, *Epicrates fordi* and *E. gracilis*, exhibit no morphological extremes in any of seven morphological characters (SVL, mid-body circumference, head width and length, snout length, snout base width and anterior snout width) when compared to the colubrids, but show more similarities to members of the tree snake genus *Uromacer* than to any other Hispaniolan taxa. *Epicrates fordi* and *E. gracilis* take prey items of a size comparable to the colubrids as do small *E. striatus*. A noteworthy difference between *E. striatus* and the colubrids, aside from sheer body size and size of prey, is that, while large colubrids take small and large prey items (as opposed to just small prey items by small colubrids), large *E. striatus* take only large prey items (Fig. 1). This has implications in energetics and, probably, the mechanics of subduing prey. Hispaniolan boids and colubrids show similarities in trophic ecology in that members of both families take those prey species that are geographically and ecologically widespread and abundant.

Finally, we here discuss the historical dietary transition by *Epicrates striatus* from native mammals to introduced rodents. *Ratus rattus* was probably introduced onto Hispaniola soon after the arrival of the first Europeans, and at least by the 1570's it was already considered a pest (Lopez de Velasco, reported in Rodriguez, 1942). Although *Mus* and *Rattus* now constitute an important portion of the diet of *Epicrates striatus*, Hispaniolan boas were obviously exploiting native mammals before the arrival of Europeans in the late 15th century. Prior to the introduction of exotics, *E. striatus* was most likely eating small to medium sized rodents (*Brotomys, Isolobodon* and *Plagiodontia*) and shrew-like insectivores (three species of *Nesophontes*). *Brotomys* was about the size of *R. rattus*, while the *Nesopontes* exhibited sizes ranging from that of *Mus* to that of *Rattus*. *Isolobodon* was about the size of *Plagiodontia aedium* (head and body length 350 mm). The remains of these now-extinct mammals are abundant in cave and Indian midden deposits, and widely distributed throughout Hispaniola. Evidence suggests that these species survived up until the early decades of the 20th century, and simultaneously with *Mus* and *Rattus* (Allen, 1942; Miller, 1929, 1930). Available evidence also suggests that Barn Owls (*Tyto alba*) were still eating *Brotomys, Isolobodon* and *Nesophontes* as late as 1930, but that a dietary shift to *Mus* and *Rattus* had been initiated. This shift would have increased gradually until the extirpation of endemic species was complete, or at least until it became energetically disadvantageous to continue foraging for them. Since *Tyto* and *Epicrates* are both nocturnal foragers and have similar diets (Wetmore and Swales, 1931; Ottenwalder, unpubl.), a similar timetable could be postulated for *Epicrates striatus*.

Only two non-volant native mammals now survive on Hispaniola: a rodent (*Plagiodontia aedium*) and an insectivore (*Solenodon paradoxus*); adults of each are about three

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times heavier than an adult *Rattus rattus*. Both species utilize rock crevices, and *Plagiodontia*, which is capable of arboreal activity, will often use hollow tree trunks. Both species are rare, occur at very low densities, and have restricted distributions (Ottenwalder, 1985). It is likely that both species still occasionally fall prey to *Epicrates striatus*, particularly during subadult dispersal; in fact, in 1974 an extremely large *E. striatus* (248.9 cm total length) was found that contained remains of a *Plagiodontia* in its digestive tract (C.A. Woods, reported in Ottenwalder, 1985).

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