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## THE DIETS OF HISPANIOLAN COLUBRID SNAKES II. PREY SPECIES, PREY SIZE, AND PHYLOGENY

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**ABSTRACT:** Eight species of xenodontine colubrid snakes ( $n = 1874$  specimens) from Hispaniola were examined for prey remains and yielded 557 prey items of which 63.1% were lizards of the iguanid genus *Anolis*. With the exception of *Darlingtonia haetiana*, an *Eleutherodactylus* frog specialist, all of the species in our sample preyed heavily upon anoles. In general, Hispaniolan colubrids were opportunistic predators, but the widespread exploitation of a single prey genus (*Anolis*) may be unique to the West Indies. Frequently exploited prey species were geographically widespread and generally found at high densities (*Osteopilus dominicensis*, *Anolis coelestinus*, *A. cybotes*, *Ameiva chrysolema*). Active foraging snakes (*Alsophis*, *Antillophis*) were more euryphagic, while sit-and-wait strategists (*Hypsirhynchus*, *Uromacer oxyrhynchus*) were trophically specialized. All of the species in our sample tended to eat relatively small prey items, even though larger individuals of a given prey species were available. The historical (phylogenetic) component of trophic ecology of these snakes is discussed.

**Key words:** *Anolis*; *Eleutherodactylus*; Phylogeny; Hispaniola; Snake diets

DESPITE its richness and geographical uniqueness, the Antillean snake fauna has, until recently, been ignored ecologically. Investigation of the diets of West Indian boid, tropidophiid, colubrid, and viperid snakes has revealed a spectacular (although not altogether surprising) trophic relationship between the snakes and the iguanid lizard genus *Anolis*. Nearly 57% of all prey items ( $n = 707$ ) and 75.8% of all lizards recovered from the digestive tracts of West Indian colubrid snakes were anoles (Henderson and Crother, 1988). In

addition, anoles are uniformly exploited as food by colubrid snakes on all major islands and island groups in the Antilles (50-60% of all prey items; Henderson and Crother, 1988). Hispaniola has the richest snake fauna and one of the largest anole faunas (second only to Cuba) of any West Indian island, and it has been singled out for detailed studies of its boid (Henderson et al., 1987b) and colubrid (e.g., Henderson, 1984a; Henderson et al., 1987a,c) snakes. Besides a rich anole fauna, Hispaniola harbors the richest frog and lizard faunas in

TABLE 1.—Some ecological characteristics of four species of Hispaniolan, and one species of Cuban, colubrid snakes. All of the snakes are diurnal.

Variable	<i>Alsophis cantherigerus</i>	<i>Antillophis parvifrons</i>	<i>Darlingtonia haettiana</i>	<i>Hypsigirhynchus ferox</i>	<i>Ialtris dorsalis</i>
Head and body morphology	long, racer type body ( $\bar{x}$ SVL = $62.9 \pm 2.9$ cm) with blunt head	small ( $\bar{x}$ SVL = $38.4 \pm 0.7$ cm), stocky body with blunt head	short ( $\bar{x}$ SVL = $21.4 \pm 1.2$ cm) slender body with small blunt head	medium ( $\bar{x}$ SVL = $46.7 \pm 1.8$ cm) size, stocky body, attenuated head	long, stocky body ( $\bar{x}$ SVL = $62.6 \pm 5.3$ cm) with long blunt head
Adaptive zone	primarily ground-dweller; may ascend into bushes	ground-dweller	secretive ground-dweller	ground-dweller	ground-dweller
Foraging mode	active	active	active	sit-and-wait	active?
Diet	very catholic; primarily lizards but also frogs, snakes, birds, mammals	catholic; primarily lizards but also frogs and mammals	almost exclusively <i>Eleutherodactylus</i> frogs (eggs and adults)	exclusively lizards (primarily <i>Anolis</i> , <i>Leiocephalus</i> , and <i>Ametoa</i> )	catholic?
Mean prey size (cm <sup>3</sup> )	$6.5 \pm 1.5$	$2.5 \pm 0.3$	$1.2 \pm 0.3$	$8.2 \pm 1.6$	$10.7 \pm 4.7$
Distribution	widespread in Cuba	islandwide	mountains on "south" island	widespread on "south" island	islandwide
Source	Henderson and Schwartz, unpubl.	Henderson et al., 1987a	Henderson and Schwartz, 1986	Henderson, 1984b	Henderson, 1984a

the West Indies: i.e., a vertebrate fauna very rich in potential prey items for colubrid snakes.

In this paper, a continuation of Henderson (1984a), we describe the prey species exploited by the xenodontine colubrid snakes of Hispaniola, the West Indian island with the richest colubrid fauna. Specifically, we address not only questions originally posed by Henderson (1984a) but also ask: (1) What prey species make the greatest contributions (frequency and volume) to the diets of Hispaniolan colubrids? (2) What characteristics (if any) are shared by frequently eaten prey species? (3) Do Hispaniolan colubrids, despite having potential access to rich frog and lizard (other than *Anolis*) prey faunas, still predominantly exploit anoles as their primary food source? (4) Is there an historical (phylogenetic) component to trophic ecology of these snakes?

#### MATERIALS AND METHODS

A sample of 1874 colubrid snakes (representing six genera and eight species) was examined for prey items. All were from Hispaniola except for *Alsophis cantherigerus*, which is native to Cuba and the Cayman Islands. Hispaniola harbors two endemic species of *Alsophis*, but because of their rarity in museum collections, we chose the closely related *A. cantherigerus* to represent the genus. It is common in museum collections and is intermediate in size between the two Hispaniolan *Alsophis* (*A. anomalus* and *A. melanichnus*). Tables 1 and 2 provide brief summaries of the natural history of Hispaniolan colubrids and *A. cantherigerus*.

Techniques of dissection, determination of prey volumes, and recording morphological measurements were explained in detail in Henderson (1984a). Many prey items were not identifiable to species, and we generally did not determine volumes for such items. There is probably some bias in our prey identifications. Some common, frequently exploited species (e.g., *Anolis cybotes*) were easily identified, even from largely digested remains. Other less common and infrequently consumed species

TABLE 2.—Comparison of different aspects of the biology of three species of *Uromacer*. All are arboreal and diurnal.

Variable	<i>U. catesbyi</i>	<i>U. frenatus</i>	<i>U. oxyrhynchus</i>	Source
Head and body morphology	blunt snout; heavy body; wide head	attenuated snout; slender body; narrow head	attenuated snout; slender body; narrow head	Henderson et al., 1981
Skull morphology	least specialized	highly specialized	highly specialized	Henderson et al., 1987c
Internal topography	anterior organ position (= primitive)	intermediate organ position, but closer to <i>oxyrhynchus</i>	posterior organ position	Maglio, 1970
Foraging mode	active and sit-and-wait	sit-and-wait	sit-and-wait	Martinez et al., 1985
Binocular field of vision	presumably the narrowest of genus	presumably wide	very wide	Henderson 1982
Striking distance and accuracy	strikes from closer distance; misses more frequently; chases prey	strikes from greatest distance and rarely misses	intermediate between <i>catesbyi</i> and <i>frenatus</i>	Henderson et al., 1987c
Diet	tree frogs; trunk and ground	terrestrial <i>Ametiba</i> ; grass, trunk, and ground	primarily trunk and ground	Ulrich and Ford, 1985
Mean prey size (cm <sup>3</sup> )	<i>Anolis</i> 4.0 ± 1.0	<i>Anolis</i> 2.8 ± 0.3	<i>Anolis</i> , some grass 2.2 ± 0.3	Henderson et al., 1987c
Movement ecology	moves long distances on ground; uses heavy branches	probably intermediate between <i>catesbyi</i> and <i>oxyrhynchus</i>	rarely travels on ground; uses slender branches	Henderson et al., 1981, 1982
Distribution	islandwide	"south" island	"north" island with invasion of "south"	Horn, 1979; Schwartz, 1980

were difficult to identify from body fragments.

Index of relative importance (IRI) was used to evaluate the relative importance of food items in snake diets (Pinkas et al., 1971). IRI was calculated by summing the numerical and volumetric percentage values of a food item (= prey species) and multiplying by percentage of occurrence

$$(N + V)F = \text{IRI}$$

where N = numerical percentage, V = volumetric percentage, F = frequency of occurrence percentage, and IRI = index of relative importance.

Prey species diversity (H') for each snake species was calculated with the Shannon-Weiner information theoretic measure:

$$H' = - \sum_{i=1}^s p_i \log_e p_i$$

where S is the number of prey categories (= species) and  $p_i$  is the proportion of the total number of prey consisting in the  $i$ th category.

Data were analyzed using one-way analysis of variance (ANOVA), Spearman rank correlation (one-tailed), regression, and chi-square. Differences among group means were determined with Student-Newman-Keuls test (SNK). Principal component analysis (PCA) with promax rotation examined the relationship among snake morphological variables; estimated factor scores of prey genera were calculated along each principal component axis. Data for prey volume were logarithmically transformed prior to analysis to normalize their distribution. All analyses were performed using the Statistical Analysis System package (SAS, 1985), with  $\alpha = 0.05$ .

Specimens from the following collections were examined for prey remains: American Museum of Natural History (AMNH), Albert Schwartz Field Series (ASFS), Florida State Museum at the University of Florida (UF-FSM), Museum of Comparative Zoology at Harvard University (MCZ), Milwaukee Public Museum (MPM), the Richard Thomas (RT) collection, and the National Museum of Natural

History (USNM). The snakes were collected at many localities throughout Hispaniola over a span of about 80 yr. Some comparisons were made with diets of Hispaniolan boids (*Epicrates*) of which 214 were examined (Henderson et al., 1987b).

Species of snakes were categorized by foraging mode on the basis of quantitative (Henderson et al., 1982) and qualitative observations in the field by the authors (Henderson and Schwartz) and by colleagues. We have designated each snake species as either a sit-and-wait (ambush) or active forager. We are aware that there exists a continuum of modes between these two extremes, but our data preclude making fine distinctions.

Abbreviations used for morphometric variables are: SVL = snout-vent length; HL = head length; MBC = mid-body circumference; SAW = snout anterior width; SBW = snout base width; SL = snout length; HW = head width.

Sample sizes for each species are (number of snake specimens examined/number of prey items): *Alsophis cantherigerus* (169/40); *Antillophis parvifrons* (649/199); *Darlingtonia haetiana* (131/46); *Hypsirhynchus ferox* (201/49); *Ialtris dorsalis* (37/9); *Uromacer catesbyi* (258/62); *U. frenatus* (257/108); *U. oxyrhynchus* (172/44). Because of the small sample size for *I. dorsalis*, we excluded it from some of our analyses.

Detailed analyses of diets for individual species or genera have appeared elsewhere (Henderson, 1984b; Henderson and Schwartz, 1986; Henderson et al., 1987a, c). Morphometric data appear in Henderson (1984a:Table 1).

## RESULTS

### Prey Species

Examination of preserved snakes yielded 557 prey items: 17.7% frogs, 79.6% lizards, 0.4% snakes, 0.2% birds, and 2.1% mammals. Most prey items were identified to genus, but only 326 were identified to species; we were able to calculate volume for 260 of those identified to species.

Twenty-three (44.2%) of the minimally 52 prey species in our sample are repre-

TABLE 3.—Some ecological characteristics of prey species frequently eaten by Hispaniolan colubrid snakes. Means are followed by  $\pm 1$  SE,  $n$  is in parentheses.

Species	$\bar{x}$ size (vol.) consumed	Distribution	Adaptive zone	When active
<i>Eleutherodactylus abbotti</i>	0.9 $\pm$ 0.0 (7)	nearly islandwide	ground-dweller to low vegetation	nocturnal
<i>Osteopilus dominicensis</i>	4.4 $\pm$ 1.5 (27)	islandwide	primarily arboreal, occasionally on ground	nocturnal
<i>Anolis coelestinus</i>	3.1 $\pm$ 0.4 (22)	widespread on "south" island	scansorial; leaf surfaces, occasionally on ground	diurnal
<i>Anolis cybotes</i>	3.6 $\pm$ 0.3 (56)	islandwide	scansorial; ground, tree trunks	diurnal
<i>Anolis distichus</i>	1.3 $\pm$ 0.1 (20)	islandwide	scansorial; tree trunks	diurnal
<i>Anolis olssoni</i>	1.0 $\pm$ 0.1 (24)	widespread on "north" island; enters "south" island	scansorial; grass, low shrubs	diurnal
<i>Anolis semilineatus</i>	0.9 $\pm$ 0.1 (9)	islandwide	scansorial; grass, low shrubs	diurnal
<i>Leiocephalus melanochlorus</i>	7.0 $\pm$ 1.6 (6)	widespread on southwest peninsula	ground-dweller	diurnal
<i>Leiocephalus personatus</i>	5.2 $\pm$ 1.2 (6)	widespread on "north" island	ground-dweller	diurnal
<i>Ameiva chrysoleama</i>	8.3 $\pm$ 1.6 (31)	islandwide at low elevations	ground-dweller	diurnal

sented by a single record, and 38 species (73.1%) are represented by fewer than five records. Because we are here concerned primarily with trends and patterns in prey exploitation and consequences of foraging strategies (of predators and prey), our analyses will concentrate on those prey species that were most frequently eaten.

Table 3 summarizes some ecological characteristics of 10 prey species that were frequently exploited. Most have wide distributions on Hispaniola, and except for the frogs *Eleutherodactylus abbotti* and *Osteopilus dominicensis* all of the species are diurnal. The *Anolis* lizards are all scansorial, but some are more arboreal than others; *A. cybotes* is the single most ubiquitous species in terms of geographical distribution and in vertical distribution within a given habitat. In terms of mean size (volume), the diurnal arboreal prey species tend to be smaller than the diurnal terrestrial prey species ( $P < 0.0001$ ,  $F = 73.1$ , ANOVA).

Figure 1 compares the frequency with which 10 species occur in our overall sample compared to the volume of food contributed by each. Some species that were frequently eaten (e.g., *Anolis distichus* and

*A. olssoni*) did not contribute proportionately in volume. Other species contributed a disproportionate volume compared to their frequency of exploitation (e.g., *Ameiva chrysoleama* and *Mus musculus*). *Anolis cybotes* was consumed frequently and contributed a high proportion of prey volume.

Principal component analysis of snake morphometric data revealed two axes explaining 95% of the variation in the data. Measurements of snake body width (MBC, HW, SAW, SBW) had high loadings on the first axis, and measures of elongation (SVL, SL, HL) had high loadings on the second axis (Table 4). The analysis further revealed that the prey genera *Eleutherodactylus* and *Sphaerodactylus* (i.e., small prey species) are taken by those snakes that are the shortest and most slender (e.g., *Antillophis*, *Darlingtonia*) (Fig. 2). The most frequently consumed prey genera fall into the center of Fig. 2, implying that they are most often eaten by those species that are not at morphometric extremes. The largest prey items (rodents, birds) were taken by those species that were longest and had the widest heads and bodies (e.g., *Alsophis*, *Ialtris*).

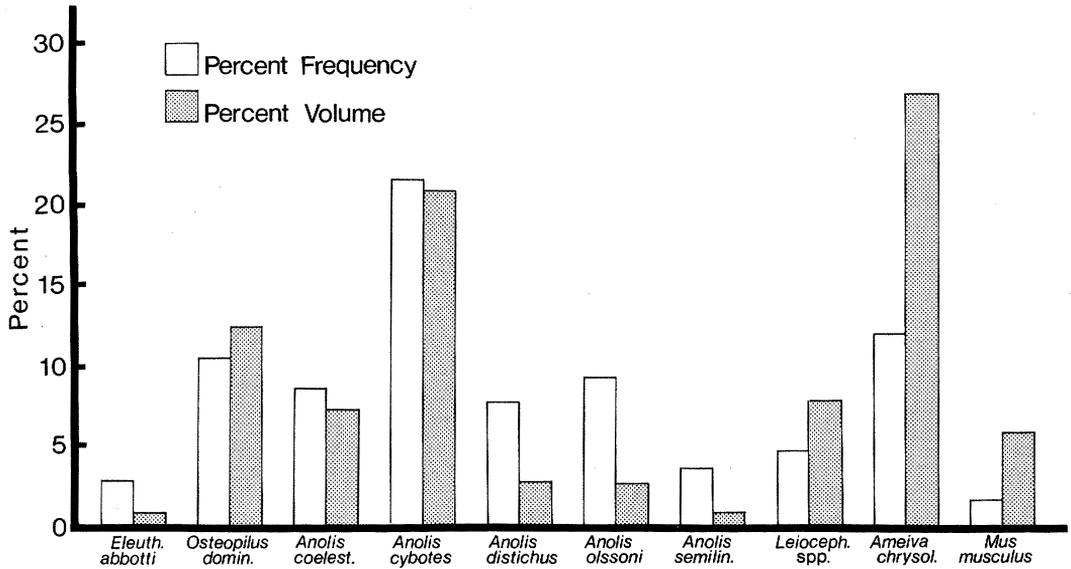


FIG. 1.—Percent (by frequency and volume) contribution of 10 species of prey commonly eaten by Hispaniolan colubrid snakes. Abbreviations are: *Eleuth.* = *Eleutherodactylus*; *domin.* = *dominicensis*; *coelest.* = *coelestinus*; *semilin.* = *semilineatus*; *Leioceph.* = *Leiocephalus*; *chrysol.* = *chrysolaelma*.

### Trophic Niche Breadth

Shannon-Weiner values ( $H'$ ) for prey species diversity for each snake species in order from broadest to narrowest trophic niche breadth are *Antillophis parvifrons* = 2.304, *Alsophis cantherigerus* = 2.233, *Uromacer frenatus* = 1.970, *Darlingtonia haetiana* = 1.861, *Uromacer oxyrhynchus* = 1.767, *Uromacer catesbyi* = 1.373, *Hypsirhynchus ferox* = 1.189. Three of the four snakes with the highest  $H'$  values are active foragers, and the three snakes with the lowest  $H'$  value are exclusively (*U. oxyrhynchus*, *H. ferox*) ambush foragers or, at least, a part-time ambush forager (*U. catesbyi*). Spearman rank correlation procedure indicated no significant correlations ( $P > 0.05$ ) between  $H'$  and sample size,  $H'$  for prey species diversity, and  $H'$  for prey genera diversity for each snake species (Henderson, 1984a) or for  $H'$  and any of several morphological variables (SVL, MBC, HW, SA).

### Index of Relative Importance

IRI values for selected prey genera and species are tabulated in Tables 5 and 6. With the exception of the two long-snout-

ed species of *Uromacer* and *Antillophis parvifrons*, each species of snake has its highest IRI value for a different genus of prey. *Alsophis cantherigerus* and *A. parvifrons* exploit the most prey genera while *Darlingtonia haetiana* and *U. oxyrhynchus* record the highest IRI values for single prey genera (respectively, *Eleutherodactylus* and *Anolis*).

IRI values for prey species suggest that single prey species are sometimes very important in diets of snakes. *Uromacer catesbyi* feeds largely on *Osteopilus dominicensis*, *Hypsirhynchus ferox* on *Ameiva chrysolaelma* and *A. parvifrons*, and *U. oxyrhynchus* on *Anolis cybotes*. *Uromacer*

TABLE 4.—Correlations of snake morphological variables with the first and second principal component axes.

Variable	Factor 1	Factor 2
MBC	0.999	-0.046
HW	0.875	0.163
SAW	0.755	0.019
SBW	0.649	0.318
SVL	-0.057	0.990
SL	0.077	0.990
HL	0.377	0.689

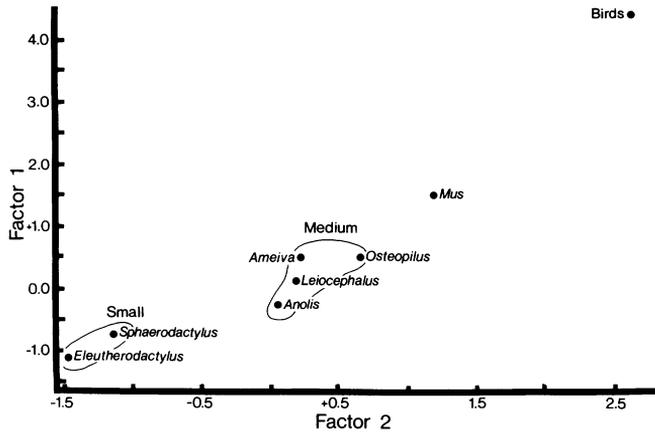


FIG. 2.—Plot of mean scores for seven genera of prey and birds on the first two principal component axes. Factor 1 represents snake head and body width, Factor 2 represents snout, head, and body length.

*frenatus* recorded high IRI values for *Anolis olssoni* and *A. chrysolae*, but it also had relatively high values for a number of other lizard species.

*Prey Size*

Hispaniolan colubrids took a wide range of prey sizes (0.1–40.0 cm<sup>3</sup>), but most prey items consumed were <3.0 cm<sup>3</sup>. Among the three most commonly exploited anoles (*A. coelestinus*, *A. cybotes*, and *A. distichus*), 60.6% were <3.0 cm<sup>3</sup> and 19.1% were >5.0 cm<sup>3</sup>. Conversely, in a sample (*n* = 74) of the same three species collected by local residents from a single locality, 79.7% were >3.0 cm<sup>3</sup> (Fig. 3). The stomach content sample of *Ameiva chrysolae* had 67.9% <10.0 cm<sup>3</sup>, but the collected sample (*n* = 25) had 92% >10.0 cm<sup>3</sup> (Fig. 3).

Within major prey groups (frogs, liz-

ards, mammals), 67.2% of all frogs eaten were <2.0 cm<sup>3</sup>, and all of the mammals (*n* = 10) were >12.0 cm<sup>3</sup>. Lizards occurred in every size class, but the vast majority (64.0%) were <3.0 cm<sup>3</sup>.

Figure 4 illustrates the contribution of four lizard genera to snake diets by prey size class. All *Sphaerodactylus* were <1.0 cm<sup>3</sup> and so were many *Anolis*, but most of the anoles eaten were 1–5.9 cm<sup>3</sup>. Anoles were less common in larger classes of prey size, and as their number decreased, *Leiocephalus* and *Ameiva* became more important; *Ameiva* was the only lizard genus represented in the prey size class >14.9 cm<sup>3</sup>.

Prey size is a function of snake head width (*P* < 0.0001, *F* = 71.7, regression). Figure 5 illustrates the percent contribution of prey size classes to the diets of snakes of various head widths. The snakes with

TABLE 5.—Index of Relative Importance values for eight genera of prey exploited by six species of colubrid snakes.

Genus	Alsop.	Antil.	Darling.	Hypstr.	<i>Uromacer catesbyi</i>	<i>Uromacer frenatus</i>	<i>Uromacer oxyrhyn.</i>
<i>Eleutherodactylus</i>	89.8	576.3	17,955.1	—	—	—	—
<i>Osteopilus</i>	177.4	4.9	—	—	6016.2	—	—
<i>Sphaerodactylus</i>	21.7	72.7	—	—	—	2.1	—
<i>Anolis</i>	1545.5	7564.7	55.1	1806.6	2601.9	7619.0	14,406.3
<i>Leiocephalus</i>	24.5	30.2	—	445.8	73.8	338.6	27.5
<i>Ameiva</i>	—	31.9	—	4963.1	—	1109.6	255.3
<i>Celestus</i>	—	—	—	74.5	—	—	—
<i>Mus</i>	2245.0	28.0	—	—	—	—	—

TABLE 6.—Index of Relative Importance values for frequently eaten species of prey by five species of Hispaniolan colubrid snakes. *Alsophis cantherigerus* was excluded, because it does not share prey species with the Hispaniolan snakes.

Species	Antil.	Darling.	Hypstr.	<i>Uromacer catesbyi</i>	<i>Uromacer frenatus</i>	<i>Uromacer oxyrhyn.</i>
<i>Eleutherodactylus abbotti</i>	43.5	740.8	—	—	—	—
<i>Osteopilus dominicensis</i>	8.7	—	—	6016.2	—	—
<i>Anolis armouri</i>	15.7	91.2	—	—	—	—
<i>Anolis caudalis</i>	3.1	—	14.7	—	12.6	—
<i>Anolis chlorocyanus</i>	3.5	—	—	—	18.4	21.6
<i>Anolis coelestinus</i>	538.4	—	—	190.2	216.1	—
<i>Anolis cybotes</i>	3433.9	—	1025.0	247.1	213.7	2541.7
<i>Anolis distichus</i>	2.4	—	—	402.6	25.1	1811.6
<i>Anolis olssoni</i>	—	—	—	—	1323.1	16.6
<i>Anolis semilineatus</i>	9.9	—	—	9.4	10.2	272.8
<i>Leiocephalus melanochlorus</i>	—	—	—	73.8	120.6	—
<i>Leiocephalus personatus</i>	2.7	—	354.6	—	6.2	—
<i>Leiocephalus vinculum</i>	—	—	—	—	43.0	—
<i>Ameiva chrysoleama</i>	26.6	—	6135.4	—	1189.4	—
<i>Ameiva taeniura</i>	—	—	—	—	4.0	96.6

the narrowest heads took prey only from the smallest size classes, but snakes with broader heads took a wide range of prey sizes, although the smallest prey items were not exploited by the snakes with the broadest heads.

*Alsophis cantherigerus* and *Uromacer catesbyi* took the widest range of prey sizes (Fig. 6). The *Anolis* specialist *U. oxyrhynchus* took the highest percentage (71%) of prey from a single size class (1–2.9 cm<sup>3</sup>). *Alsophis* and *Hypsirhynchus ferox*, both relatively heavy bodied, took more prey from the larger size classes than did the other species. Although there were significant differences ( $P < 0.001$ ,  $F = 8.8$ , ANOVA) in mean prey size taken by each snake species, there was considerable overlap.

Two species, *Antillophis parvifrons* and *Uromacer frenatus*, showed geographic differences in size of prey items consumed, and, concomitantly, in SVL ( $P < 0.01$ , ANOVA). Figure 7 presents a frequency distribution of SVL's for the two species on one or two satellite islands and at various other localities. The largest specimens of *A. parvifrons* came from Ile de la Gonâve and Ile-à-Vache, Haiti. Both of these species had exploited larger prey (*Leiocephalus*, *Ameiva*, *Mus*) on the satellite islands than they did elsewhere, and these dietary differences have been described in

detail elsewhere (Henderson et al., 1987a, c), but see "Discussion" below.

#### Summary

To gain a clearer picture of levels of trophic specialization, we ranked each species of snake in our sample (except *Ialtris dorsalis*) by each of the variables that we used to quantify trophic ecology (IRI for prey genera/species; H'; prey size) and added another simple ranking based on the number of taxonomic classes and orders of prey that each species ate. Snakes were scored two points for each prey class (Amphibia, Reptilia, etc.) and one point for each prey order or suborder (Anura, Squamata–Sauria, Squamata–Serpentes, Rodentia, etc.) eaten. Thus, each species of snake (except for *Alsophis cantherigerus* which did not have an IRI for the species of prey calculated) had a total of five numbers summed to get the final value; the less specialized, the higher the total score. For those Hispaniolan species that are members of Maglio's (1970) *cantherigerus* species assemblage, their scores were: *Uromacer catesbyi*, 20; *Uromacer frenatus*, 19; *Hypsirhynchus ferox*, 17; *Uromacer oxyrhynchus*, 13. The two species outside the assemblage had the following scores: *Antillophis parvifrons*, 24; *Darlingtonia haetiana*, 19. By contrast, although having one less value to be summed, *Alsophis*

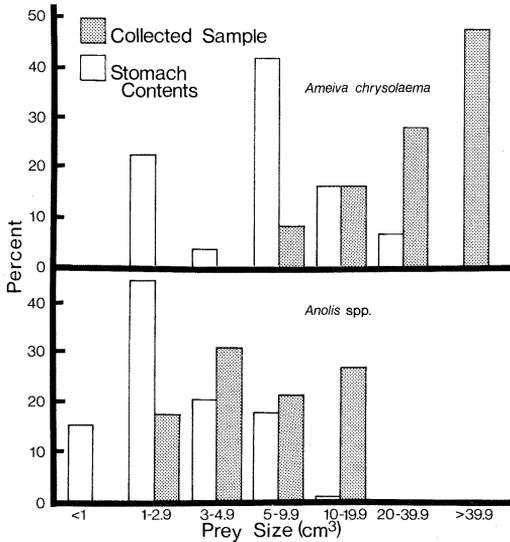


FIG. 3.—Percent of prey size classes found in stomach content samples collected by us and in samples collected by natives. The collected sample of *Ameiva chrysoleama* was taken at 3 km NW Oviedo, Pedernales Prov., Dominican Republic; the *Anolis* sample (*coelestinus*, *cybotes*, *distichus*) was taken at 15 km NW Cabral, Barahona Prov., Dominican Republic.

*cantherigerus* had the highest total score (33) indicating trophic generalization.

DISCUSSION

Prey Species

Although at least 52 species of prey were exploited by the snakes in our sample, only about 20% of those species were eaten frequently. The total number of prey species in our sample would certainly have in-

creased if we had examined larger samples, but we doubt if any trophically “important” species are absent from our sample. It is possible that we have underestimated the importance of some geographically restricted prey species, but in gaining a broad view of trophic ecology, it is unlikely that increasing sample sizes would modify our results or interpretations.

All of the dominant prey species (Table 3), whether frogs or lizards, diurnal or nocturnal, are geographically widespread on the Hispaniolan main island, and most of them occur on one or more satellite islands (Henderson and Schwartz, 1984), and frequently in high relative densities (R. W. Henderson, A. Schwartz, personal observations). Most of the smaller prey species are scansorial, whereas the larger lizards (*Leiocephalus*, *Ameiva*) are ground-dwelling. The primary lizard species are diurnal, and the frogs are all nocturnal.

*Anolis* lizards were eaten more frequently (63.1%) than any other type of prey, although most do not make a proportionate contribution to prey volume consumed (Fig. 1). Other, less frequently eaten species contributed proportionately more food volume (e.g., *O. dominicensis*, *A. chrysoleama*, *M. musculus*).

The IRI values (Tables 5, 6) indicate that all of the snake species exploit *Anolis* at least occasionally, and some species (*A. parvifrons*, *U. frenatus*, *U. oxyrhynchus*) rely heavily upon anoles as a food source. Certain species of *Anolis* (e.g., *coelestinus*, *cybotes*, *distichus*, *olssoni*) make large fre-

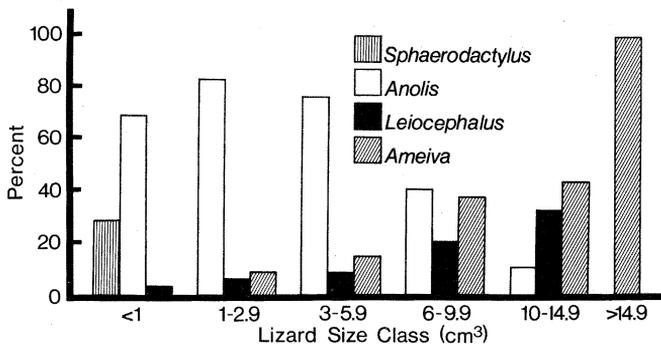


FIG. 4.—Percent of exploitation by Hispaniolan colubrids on four genera of lizards in six size classes.

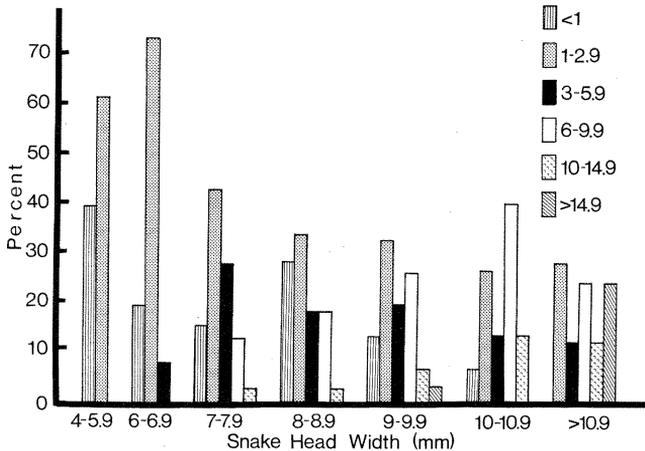


FIG. 5.—Percent of exploitation of prey size classes by snakes with different head widths.

quency and/or volume contributions to the diet of some snakes; *A. cybotes* contributed over 40% of the total volume of prey to the diet of *Antillophis parvifrons* and about 50% of the total volume of prey for *Uromacer oxyrhynchus*. Conversely, the slender grass anole *Anolis olssoni* contributed over 30% of the prey items taken by *U. frenatus*, but only about 10% of the prey volume.

*Ameiva chrysolaeama* contributed more to the total prey volume of all snake species combined, but it was only important in the diet of *Hypsirhynchus ferox* and, to a lesser extent, *Uromacer frenatus* (but primarily on Ile de la Gonâve: Henderson et

al., 1987c). Similarly, *Osteopilus dominicensis* was a major contributor to prey volume, but only *U. catesbyi* benefitted. It was the anoles that uniformly fell prey most frequently to all Hispaniolan colubrids in our sample (*Darlingtonia haetiana* the exception).

Hispaniola has a rich anole fauna (Williams, 1983) with species occurring from sea level to >2400 m. They occur in most habitats from ground level to the crowns of tall trees, in sunlight, shade, and sunshade mosaics. Many species are tolerant of disturbance and can be found on and in human habitations; not surprisingly, some of the most widespread species are

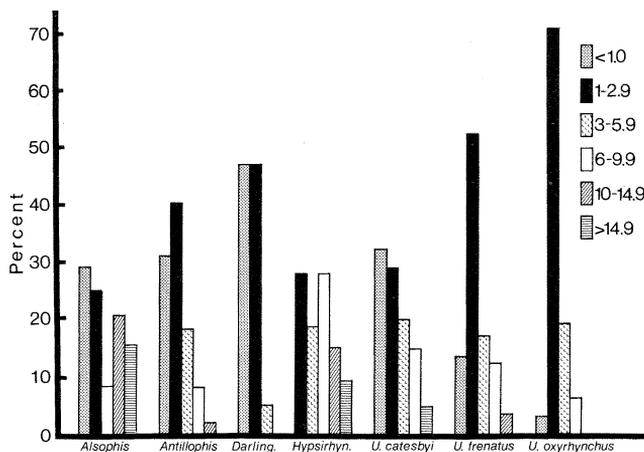


FIG. 6.—Percent exploitation of prey size classes by seven species of snakes.

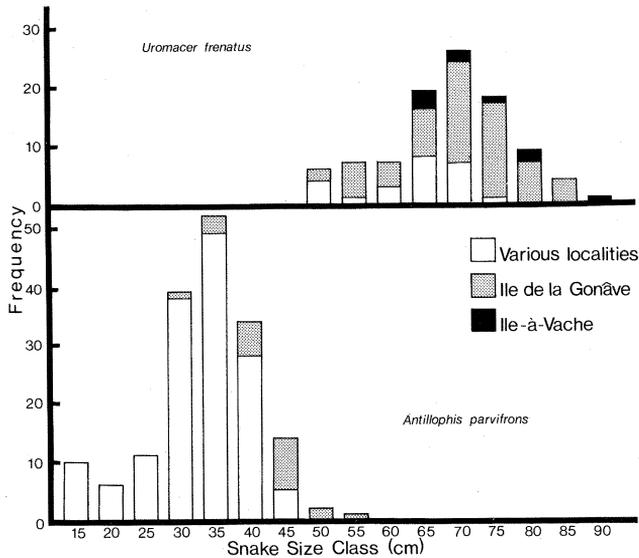


FIG. 7.—Frequency distribution of size classes (SVL) for *Uromacer frenatus* and *Antillophis parvifrons* at satellite (Ile de la Gonâve, Ile-à-Vache) and other localities.

those that are most tolerant of habitat disturbance. Although species densities are not known for any Hispaniolan anoles, elsewhere West Indian species are known to reach very high densities (Gorman and Harwood, 1977; Ruibal and Philibosian, 1974; Schoener and Schoener, 1980). *Anolis cybotes* is the single most frequently exploited prey species by Hispaniolan boid and colubrid snakes. It is a geographically widespread species, occurs in a variety of habitats, and has a wide vertical distribution (ground to crown) in many habitats. It is occasionally found under rocks (Schwartz and Henderson, 1982), and juveniles and females are frequently found on the ground. *Anolis* lizards in general are the most conspicuous vertebrates on Hispaniola, ranging throughout the main island, most satellite islands, in most habitats, and frequently at high densities. Diurnal colubrid snakes, regardless of foraging mode, must encounter them frequently and, obviously, eat them routinely.

What Hispaniolan colubrids do eat has now been well defined. What they do not eat is worthy of discussion. We have not recorded a single invertebrate in the diet of any Hispaniolan colubrid, and in a sam-

ple of 778 prey items from West Indian boid, trophidophiid, colubrid, and viperid snakes ( $n =$  approximately 2700 specimens), only 0.3% were invertebrates (and all from Lesser Antillean *Liophis*; Henderson and Crother, 1988). That invertebrates may occasionally fall prey to Hispaniolan snakes would not be surprising, but possibly the ubiquitous distribution of anoles in a wide array of sizes precludes the necessity of predation on invertebrate size prey. It is also noteworthy that invertebrate predation by snakes may be relatively rare except in North America (Shine, 1977), although it is the rule in snakes of the families Typhlopidae and Leptotyphlopidae.

*Eleutherodactylus* is the most speciose vertebrate genus on Hispaniola; species occur from sea level to >2400 m and in a variety of habitats. The frogs are ground-dwelling and scansorial, occur in a wide range of sizes, and can reach high densities (Stewart and Pough, 1982). With the exception of *Darlingtonia* and *Antillophis*, Hispaniolan snakes rarely eat them (Fig. 1). The snakes that do eat *Eleutherodactylus* are all active foragers: the diet of *Antillophis* is comprised of about 12% *Eleutherodactylus* by frequency and about

17% by volume (Henderson et al., 1987a); the diet of *Alsophis* is about 6% by frequency *Eleutherodactylus*; the diet of *Darlingtonia* is virtually 100% by frequency and volume *Eleutherodactylus*; *Ialtris dorsalis* exploits *Eleutherodactylus*, but we have not examined sufficient stomachs to gain an accurate view of the importance of these frogs in its diet.

Before the arrival of Europeans in the late 15th century, the only *Mus*-sized mammal on Hispaniola was the insectivore *Nesophontes zamicus* (Miller, 1929). It was widespread on the island (J. A. Ottenwalder, personal communication) and likely fell prey to boid and colubrid snakes, but most Hispaniolan mammals attained adult sizes too large for colubrids to swallow. Only large examples of the boid *Epicrates striatus* feed routinely on mammals on Hispaniola (Henderson et al., 1987b).

According to Henderson and Crother (1988), xenodontine colubrids "may have been the optimum 'type' of snake for radiating in the West Indies . . ." They are adapted morphologically, ecologically, and behaviorally to trophically exploit the kinds of vertebrate prey that occur with the greatest diversity and at the highest population densities in the West Indies (i.e., lizards and frogs). Nussbaum (1984) similarly suggested that snakes that eat lizards and birds are more common on oceanic islands because lizards and birds are more common on oceanic islands.

#### *Trophic Niche Breadth*

The Shannon-Weiner values ( $H'$ ) for each species of snake produced expected as well as unexpected results, and certainly results different from earlier calculations done for the same prey items identified only to genus (Henderson, 1984a). That the active foragers *Antillophis parvifrons* and *Alsophis cantherigerus* have the highest  $H'$  values was expected. At first glance, *Uromacer catesbyi* and *Hypsirhynchus ferox* do not seem trophically specialized, but examination of ontogenetic changes in their diets indicates that they both become quite restricted. Small *U. catesbyi* feed

predominantly on anoles, but with increasing size comes increasing diet specialization on the common, widespread hylid frog *Osteopilus dominicensis*. Adult *U. catesbyi* prey on large adult *Osteopilus* and the ephemerally abundant, recently metamorphosed young (and usually in multiples) (Henderson et al., 1987c). Similarly, young *H. ferox* prey predominantly on anoles, but large adults feed almost exclusively on the teiid lizard *Ameiva chrysolema* (Henderson, 1984b). *Uromacer frenatus* and *U. oxyrhynchus* feed predominantly on anoles, although on Ile de la Gonâve, *U. frenatus* prey heavily on *A. chrysolema*. Perhaps most misleading is the  $H'$  value determined for *Darlingtonia haetiana*. This small species feeds almost exclusively on *Eleutherodactylus* and its egg clutches; it will feed occasionally on anoles. It is the most trophically unique of the Hispaniolan colubrids but, because it feeds on a wide variety of *Eleutherodactylus* species (Henderson and Schwartz, 1986), it scored a fairly high  $H'$  value. Although we advocate identifying prey items to the highest possible taxonomic level, we suggest that, just as prey identifications at broad taxonomic levels may be misleading (Greene and Jaksic, 1983), so too can identifications at narrow levels.

#### *Prey Size*

Hispaniolan colubrids, although eating a wide array of prey sizes, fed primarily on small prey items. Although it was expected that small snakes would consume small prey items, large snakes routinely ate small prey items in addition to "large" ones (Fig. 5). Even if our native-collected sample is biased towards larger individuals, it still indicates that larger prey items were available.

*Antillophis parvifrons* and *Uromacer frenatus* attain larger SVL's on Ile de la Gonâve, Haiti than elsewhere in their ranges (Fig. 7), and this is reflected in their diets (Henderson et al., 1987a,c); both species eat a greater proportion of *Ameiva chrysolema* on Gonâve than elsewhere, and it is the only place that *Antillophis* exploited rodents. We have the impression

from fieldwork on Gonâve that populations of *Ameiva* (and *Leiocephalus*) reach greater densities there than most other areas in which we have collected. It is possible that increased body size may be a response to the presence of an abundant, "large" prey species. Similar patterns of insular trends in body size related to type (size) and abundance of prey have been noted in viperid (Case, 1978) and elapid (Schwaner, 1985) snakes.

### Trophic Ecology and Phylogeny

Ecological and behavioral characteristics within monophyletic lineages can be shown to be under phylogenetic constraints (thus have an historical explanation) or be the result of recent, independent selective forces, through their fit on cladistic estimations of relationship (Coddington, 1985; Dobson, 1985; Greene, in press; Wanntorp, 1983). "Fit" refers to the ratio of the number of steps required for the evolution of a character on the cladogram to the minimum number of possible steps.

Maglio (1970) completed the only phylogenetic study encompassing all the West Indian xenodontines. He concluded that four unique lineages are present, three of which occur on Hispaniola. *Alsophis*, *Hypsirhynchus*, and *Uromacer* belong to the "cantherigerus" assemblage, with only *Alsophis* found elsewhere. *Antillophis parvifrons* is part of the "andreae" assemblage, with its only other member on Cuba, and *Darlingtonia* belongs to the "funerous" assemblage whose supposed relations are with *Arrhyton*, which is restricted to Puerto Rico, Cuba, and Jamaica. Trophic ecologies were only known for the Hispaniola taxa, thus they were examined in terms of interspecific relationships within Hispaniola.

Within the "cantherigerus" assemblage, Maglio (1970) concluded that *Alsophis* is the sister taxon to a *Hypsirhynchus-Uromacer* clade (Fig. 8a). *Alsophis* actively forages and is a generalist in diet, whereas *Hypsirhynchus* and *Uromacer* are clearly more specialized in diet and forage in a sit-and-wait fashion. Two hypotheses

of polarity (or evolution of the traits) are possible. The first (Fig. 8b) suggests that the generalized diet and active foraging mode are primitive, with the specialized diet and sit-and-wait foraging mode derived. The alternative (Fig. 8c) suggests that the generalized diet and active foraging mode are derived for *Alsophis*, whereas the specialized diet and sit-and-wait foraging mode are primitive. The presence of these two equally parsimonious hypotheses requires a decision based on additional information.

Thomas (1976), in his work on the snake genus *Philodryas*, suggested that *Alsophis* was a close relative to the former, and was perhaps derived from that stock. By using *Philodryas* as an outgroup, it was possible to choose between the competing hypotheses. *Philodryas* is an active foraging opportunist, as is *Alsophis*. Consequently, we feel this supports hypothesis 8b (Fig. 8), because hypothesis 8c requires reversals to explain the character state distributions.

The genus *Uromacer* shows a similar pattern. According to Horn (1969) and Maglio (1970), *U. catesbyi* is the sister taxon to a *U. frenatus-U. oxyrhynchus* clade. Within this genus, foraging mode and diet preferences reflect phylogeny (*Alsophis* was the outgroup). From the above analysis, active foraging habits are primitive and sit-and-wait foraging habits are derived from *Uromacer*. *Uromacer catesbyi*, however, retains the active mode as well. Thus, two hypotheses of the evolution of foraging habits within *Uromacer* are possible. One suggests that *U. catesbyi* retained the primitive state (active foraging) in combination with the derived state (sit-and-wait foraging) and that the primitive state was lost in *U. frenatus* and *U. oxyrhynchus* (Fig. 8d). The alternative suggests that the *U. catesbyi* condition is not the retention of the primitive trait, but is a reversal or convergency (Fig. 8e). It seems unlikely that the presence of the active foraging mode in *U. catesbyi* is due to an independent evolutionary event. The former (Fig. 8d) is a more tenable hypothesis. The diet preference character for *Uromacer* also reflects phylogeny. Specialized

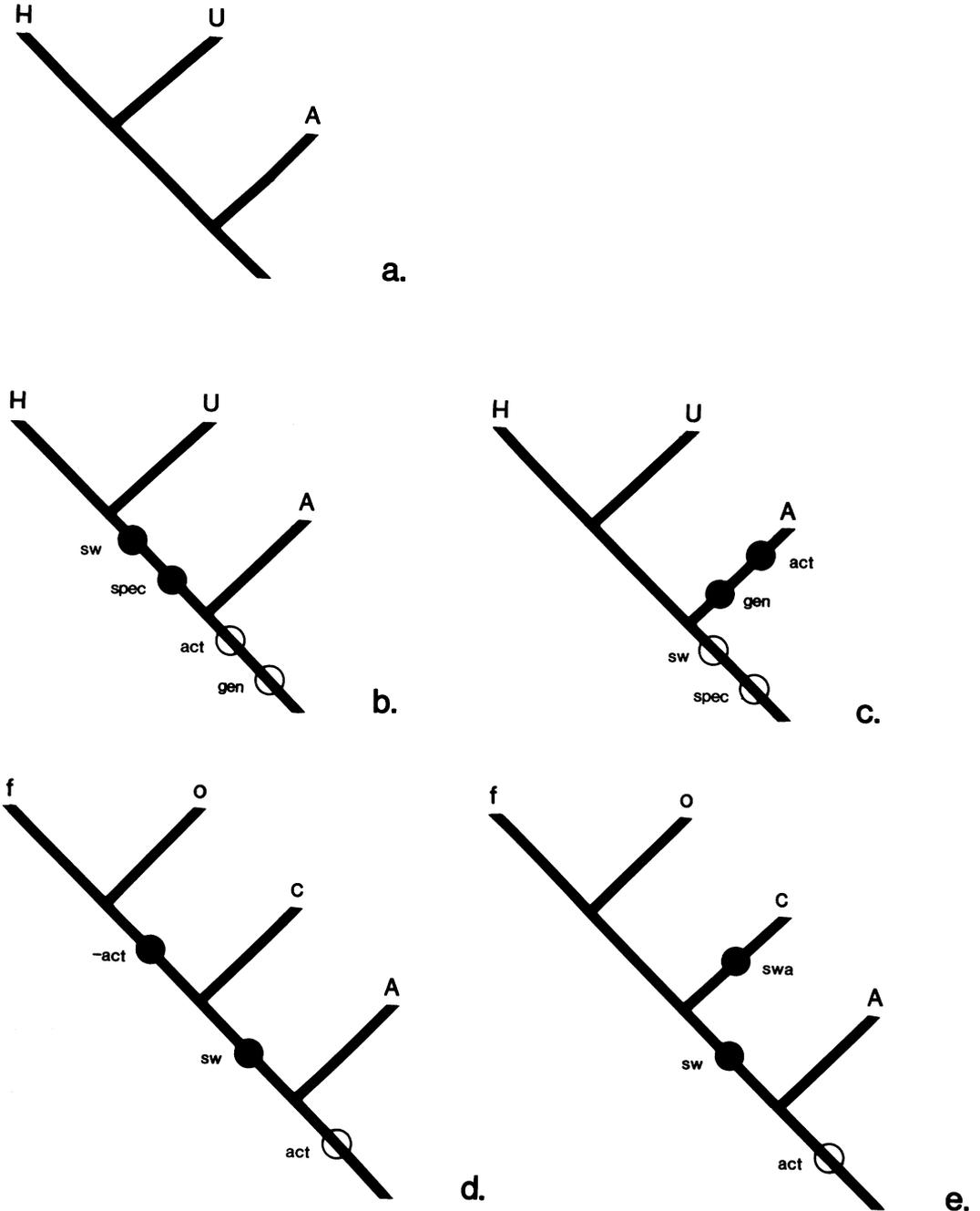


FIG. 8.—Hypotheses of ecological character evolution as plotted on phylogenetic estimates of relationship for the Hispaniolan colubrids: (a–c) the *cantherigerus* assemblage; (d, e) *Uromacer* with foraging mode. Abbreviations: H = *Hypsirhynchus*, U = *Uromacer*, A = *Alsophis*, f = *frenatus*, o = *oxyrhynchus*, c = *catesbyi*, sw = sit-and-wait, act = active forager, spec = specialist, gen = generalist, swa = sit-and-wait and active.

diet evolved from a generalized diet and became further differentiated within *Uromacer*. *Uromacer catesbyi* exploits *Osteopilus*, whereas *U. frentus* and *U. oxyrhynchus* exploit lizards.

The trophic characteristics of the relatives of the three remaining taxa, *Darlingtonia*, *Ialtris*, and *Antillophis*, are not known. This prevents analysis of the evolution of their foraging habits or diet preferences. *Antillophis parvifrons* and *Ialtris dorsalis* are active foraging generalists, so they possess the primitive condition. *Darlingtonia* is an active forager and is specialized in diet, feeding almost exclusively on the frogs of the genus *Eleutherodactylus*. This unique diet may reflect the unique lineage, but without additional information other explanations are plausible.

Hypothesized patterns of polarity were derived without convergences. This suggests that the ecological and behavioral characteristics of the Hispaniolan xenodontines are best explained in historical terms, and not with independent adaptive or selective explanations.

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