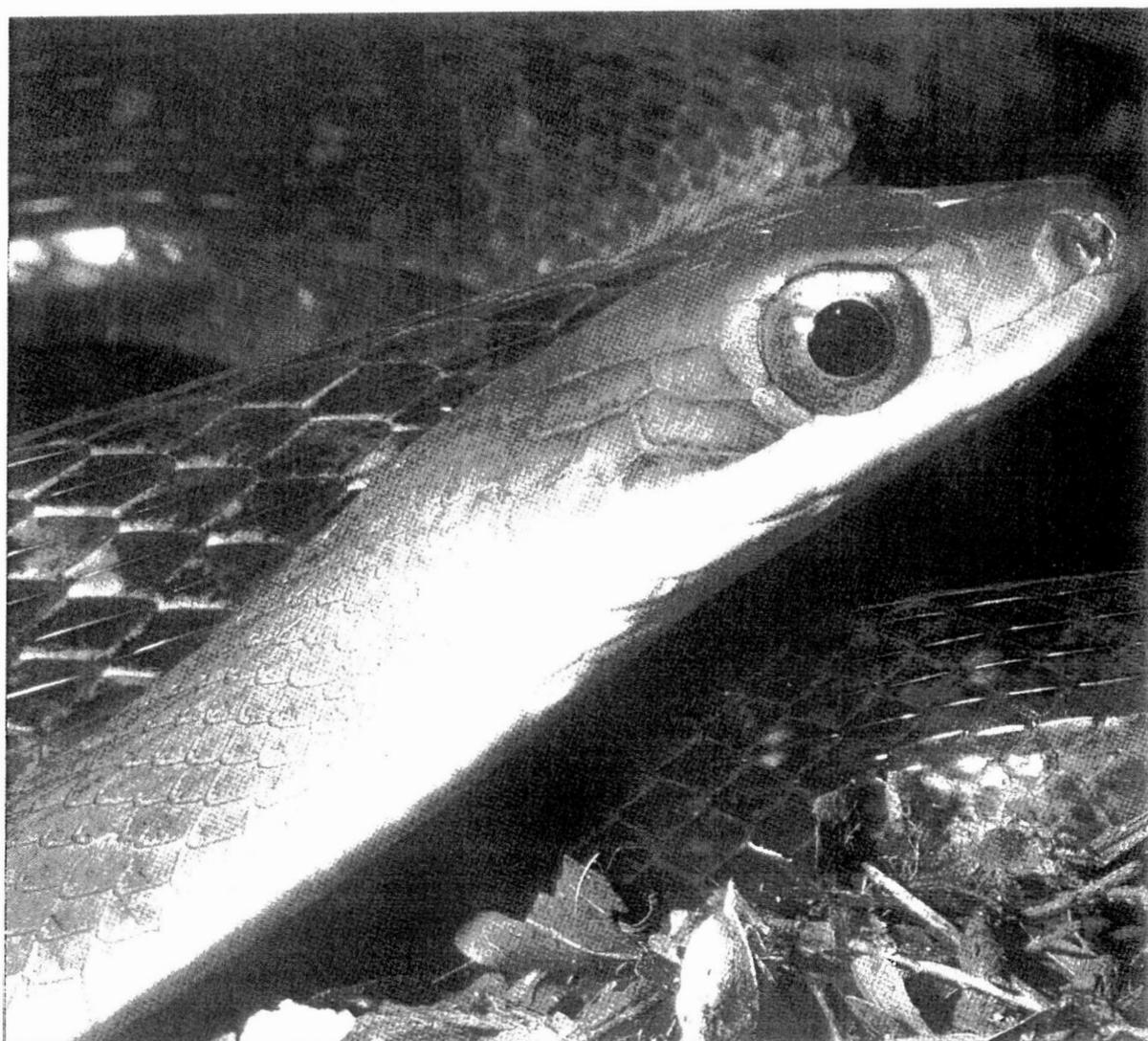


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TROPHIC ECOLOGY AND REPRODUCTION IN THREE SPECIES OF NEOTROPICAL FOREST RACER (*DENDROPHIDION*; COLUBRIDAE)

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Aspects of ecology are described and compared for three species of the Neotropical colubrid genus *Dendrophidion*: *D. nuchale*, *D. percarinatum* and *D. vinitor*. These slender, racer-like snakes of Central American rainforests have overlapping distributions and similar, relatively specialized diets. Within each species, over 50% of prey items recovered from museum specimens were leptodactylid frogs. *Dendrophidion vinitor* is a small species that feeds almost entirely on these anurans (>90% by frequency), whereas *D. nuchale* and *D. percarinatum* are larger forms that in addition to frogs also eat lizards, mostly anoles (Polychrotidae). Sample numbers were limited and the dietary data insufficient for conclusive analysis, but niche separation based on this taxonomic difference in food habits – and also prey size (larger mean prey volume in *D. nuchale*) – may be important for these snakes in areas of co-occurrence. Reproductive data for *D. percarinatum* and *D. vinitor* in lower Central America suggest an extended or possibly continuous cycle and the production in individual females of more than one clutch per year. The intensity of reproduction in all three species, however, is likely to fluctuate with annual variation in rainfall and prey availability. *Dendrophidion percarinatum* shows a much higher frequency of tail breakage than *D. nuchale* or *D. vinitor*, suggesting that predation pressure in this species is relatively more intense.

Se describen aspectos de la ecología de tres especies de culebras neotropicales pertenecientes al género *Dendrophidion*: *D. nuchale*, *D. percarinatum* y *D. vinitor*. Estas delgadas y rápidas culebras de los bosques tropicales de América Central, tienen una distribución solapada y dietas similares y relativamente especializadas. Para cada especie, más de un 50% de las presas recuperadas de especímenes de museos fueron ranas leptodactílicas. *Dendrophidion vinitor* es una culebra pequeña, que se alimenta casi exclusivamente de estos anuros (>90% en frecuencia), mientras que *D. nuchale* y *D. percarinatum* son especies de mayor tamaño, que a parte de ranas, también se alimentan de lagartijas, principalmente de anoles (Polychrotidae). Se contó con un número limitado de ejemplares, por lo que los datos sobre la dieta fueron insuficientes para un análisis concluyente, sin embargo, la separación de sus nichos basada en las diferencias de alimentación y tamaño de las presas (un mayor volumen de la presa en promedio en *D. nuchale*), pueden ser importantes para estas culebras en áreas donde co-ocurren. Datos reproductivos de *D. percarinatum* y *D. vinitor* en la parte sur de América Central sugieren un ciclo extenso o posiblemente continuo y en el caso de algunas hembras, más de una puesta por año. Sin embargo, la intensidad reproductora de las tres especies, posiblemente varíe con la precipitación anual y la disponibilidad de presas. *Dendrophidion percarinatum* muestra rotura de cola con una mayor frecuencia que *D. nuchale* o *D. vinitor*, lo que sugiere que esta especie sufre una más intensa presión por parte de sus predadores.

Key words: Central America, Colubridae, *Dendrophidion*, diet, ecology, reproduction, sympatry

INTRODUCTION

Snakes of the genus *Dendrophidion* are a distinctive group of Neotropical colubrids noted for their attenuate body-shape, large eyes, and great speed of movement. Eight species are currently recognized, with a combined geographic range extending from southern Mexico (*D. vinitor*) to the Guianas, northern Brazil and east-central Peru (*D. dendrophis*); a complex of populations in the southern Amazon basin of Bolivia and vicinity appears

to represent a ninth, undescribed species (Lieb, 1988). Commonly known as 'forest racers', they are diurnal and mostly terrestrial inhabitants of low-moderate elevation rainforests, although several also occur in upland areas, and for *D. bivittatum* in the northern Andes there are admissible records from above 2300 m (Dunn, 1944).

Previous studies on *Dendrophidion* have clarified the taxonomic status, overall relationships, and distributions of species (Lieb, 1988), and summarized available data on the four known Central American forms (Lieb, 1991a,b,c, 1996). Our basic knowledge of these snakes, however, is marked by an otherwise distinct lack of in-

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formation, particularly with respect to their diet and life history patterns. In this paper I present a general account of morphology, food habits and reproduction in three *Dendrophidion* species from Central America and north-western South America – *D. nuchale* (W. Peters), *D. percarinatum* (Cope), and *D. vinitor* H. M. Smith – based on examinations of preserved museum specimens and records of field observations. The information enables some preliminary comparisons between the ecologies of these taxa, which occur widely in the region over similar elevational ranges, and in various combinations are not infrequently ‘sympatric’.

Dendrophidion nuchale, *percarinatum* and *vinitor* are similar in overall morphology but attain different body sizes and are distinct also in features of colour pattern (for colour illustrations see Renjifo & Lundberg, 1999; Stafford & Meyer, 2000; Köhler, 2001; Savage, 2002). The largest is *D. nuchale*, adults of which may attain total lengths in excess of 1.5 m. *Dendrophidion nuchale* also has the most extensive distribution, ranging from east-central Guatemala and Belize, south through Honduras, Nicaragua, Costa Rica, and Panama, to northern Venezuela and the Pacific versants of Colombia and Ecuador (75–1585 m). *Dendrophidion percarinatum* is a moderately-sized species (<1.3 m) known mostly from lower Central America (Honduras to Colombia and western Ecuador, 4–1200 m), while *D. vinitor*, a smaller form (<1.1 m), occurs from southern Veracruz to Panama and the adjacent Chocó area (15–1528 m). Data presented by Lieb (1988) suggest that *D. nuchale* and *D. vinitor* are closely related forms allied to the nominate South American *D. dendrophis*. As a group, these species are segregated from *percarinatum* and the remaining members of the genus by the more extensive development of dorsal scale keeling, differences in posterior dorsocaudal scale row reductions, and features of hemipenal morphology.

MATERIALS AND METHODS

In total, 41 *D. nuchale*, 58 *D. percarinatum* and 55 *D. vinitor* were examined. These included individuals from throughout the range of each species, but most originated from lower Central America, particularly north-eastern Costa Rica. All snakes were first sexed by inspection of the gonads through a mid-ventral incision (or in some males by the presence of everted hemipenes) and their date of collection, provenance, snout-vent length (SVL) and tail length (TL) recorded. In order to quantify any differences between the species in head and body proportions, and to determine whether there was a relationship between morphology and diet, the following additional measurements were also taken; mid-body circumference (MB-C, determined by wrapping a piece of tape around the snake’s mid-body and measuring the length used), head length (HL, measured along the upper jaw to its point of articulation), head width (HW, measured at the angle of the jaw), head depth (HD, measured from a point directly above the eye), snout length (SL, measured from the anterior border of the eye to the front face of the rostral), and diameter of the eye (ED).

Approximately one half of the specimens within each species sample were then dissected to obtain diet and reproductive data; a small number of these were selected by palpating the abdomen for the presence of food, but the remainder (>95%) were selected on a wholly random basis. Prey items recovered from stomachs were counted, identified, and whenever possible their length (SVL), volume (determined by fluid displacement), mass, and orientation were also recorded. The sizes of more fully digested prey items were estimated by comparison with similar-sized intact specimens in the collection of the Natural History Museum (BMNH), and to reduce error in determining prey mass all spirit-preserved material was thoroughly drained before

TABLE 1. Comparisons of relative head and body measurements in *Dendrophidion nuchale*, *D. percarinatum* and *D. vinitor*, based on the ten largest individuals examined (5 male and 5 female). Data are mean, SE and range (first three rows) and test results of Mann-Whitney *U* comparisons (NS, $P>0.05$; * $P<0.05$; ** $P<0.01$). See text for abbreviations.

Species	SVL/MBC	SVL/HL	HL/HW	HL/HD	HL/SL	HL/ED
<i>D. nuchale</i>	14.02±0.48 (11.98-16.14)	25.39±0.43 (23.0-27.04)	2.27±0.06 (2.01-2.57)	2.84±0.04 (2.63-3.08)	3.42±0.06 (3.21-3.82)	4.73±0.02 (4.58-4.81)
<i>D. percarinatum</i>	14.01±0.21 (12.91-15.08)	26.12±0.33 (24.51-27.41)	2.17±0.02 (2.06-2.28)	2.84±0.06 (2.60-3.17)	3.62±0.06 (3.40-3.92)	4.8±0.05 (4.64-5.09)
<i>D. vinitor</i>	14.69±0.42 (11.86-16.32)	26.81±0.27 (25.35-27.90)	2.23±0.05 (2.04-2.48)	2.67±0.04 (2.50-2.84)	3.76±0.05 (3.54-4.00)	4.48±0.08 (3.93-4.92)
<i>D. nuchale</i> × <i>D. percarinatum</i>	$z=0.03$ NS	$z=1.21$ NS	$z=1.21$ NS	$z=0$ NS	$z=2.31^*$	$z=1.74$ NS
<i>D. nuchale</i> × <i>D. vinitor</i>	$z=0.9$ NS	$z=2.41^*$	$z=0.45$ NS	$z=2.35^*$	$z=3.06^{**}$	$z=2.57^{**}$
<i>D. percarinatum</i> × <i>D. vinitor</i>	$z=1.59$ NS	$z=1.59$ NS	$z=1.02$ NS	$z=2.24^{**}$	$z=1.66$ NS	$z=2.95^{**}$

TABLE 2. Body sizes and sexual dimorphism in *Dendrophidion nuchale*, *D. percarinatum* and *D. vinitor*. *Includes selected data from Smith (1941) and Lieb (1988). TL, total length; Tail L, tail length.

	<i>D. nuchale</i>		<i>D. percarinatum</i>		<i>D. vinitor</i>	
	male (n=25)	female (n=17)	male (n=28)	female (n=27)	male (n=31)	female (n=25)
Maximum SVL (cm)*	96.8	94.8	71.2	75.6	66.4	64.5
Mean adult SVL ±SE (cm)	78.7±3.44	74.8±3.73	64.4±1.31	67.4±1.35	60.0±1.20	57.8±1.10
Ratio mean adult SVL m/f (±SE)	1.05 (±0.03)		0.96 (±5.0×10 ⁻³)		1.04 (±4.7×10 ⁻³)	
Ratio TL/Tail L (range)	0.350-0.408	0.350-0.405	0.365-0.450	0.367-0.417	0.339-0.381	0.313-0.366
Ventrals*	153-175	156-174	149-169	152-169	149-168	155-167
Subcaudals*	138-163	132-157	141-163	143-151	111-127	110-126

weighing. Reproductive maturity was determined in females by the presence of ovarian follicles >5 mm diameter or oviducal eggs. Males were considered mature if the testes were enlarged and the vasa deferentia distinctly thickened. Finally, the numbers and dimensions of enlarged ovarian follicles and oviducal eggs were recorded in reproductive females. All measurements of less than 5 cm were made using digital calipers accurate to 0.1 mm.

RESULTS

MORPHOLOGY

Dendrophidion nuchale, *D. percarinatum* and *D. vinitor* are slender, attenuate-bodied snakes with rela-

tively long tails, short snouts, and large eyes. As a proportion of head length, the eye in *D. vinitor* is especially large, and *D. vinitor* also has a shorter snout, deeper head, and shorter tail compared with *nuchale* and *percarinatum* (Tables 1 and 2, Fig. 1). In other features of morphology the three species are relatively similar. Interspecific differences in body size (SVL), however, are marked (Table 2). *Dendrophidion nuchale* is much the largest, and for any given SVL in the sample studied, *D. nuchale* also had a significantly larger head. This difference is greatest with regard to *D. vinitor*, but was evident in comparisons between all three species (single-factor ANCOVA based on head length with SVL as the covariate, $F_{2,122} = 41.07, P < 0.0005$) and remains proportionally consistent with increasing SVL (Fig. 2).

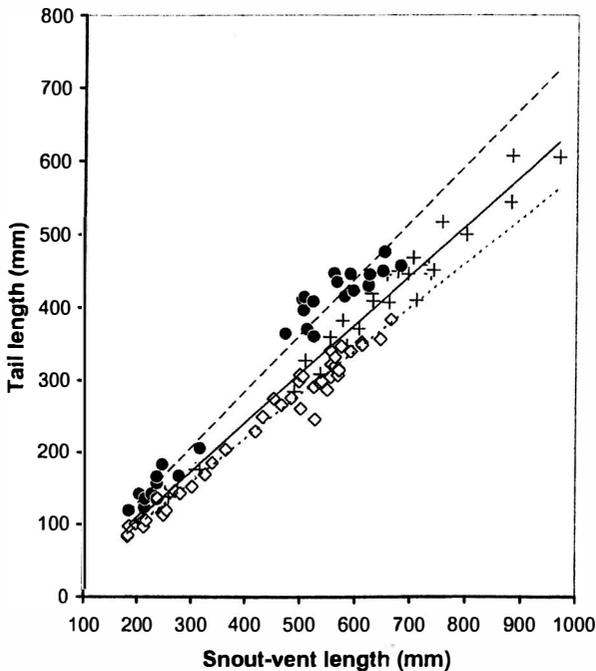


FIG. 1. Regressions of tail length on SVL in *D. nuchale* (crosses and continuous line; $y = 0.6764x - 29.391, R^2 = 0.9815$), *D. percarinatum* (circles and dashed line; $y = 0.7726x - 23.183, R^2 = 0.9698$), and *D. vinitor* (squares and dotted line; $y = 0.6064x - 22.836, R^2 = 0.9776$). Note proportionally longer tail of *D. percarinatum*.

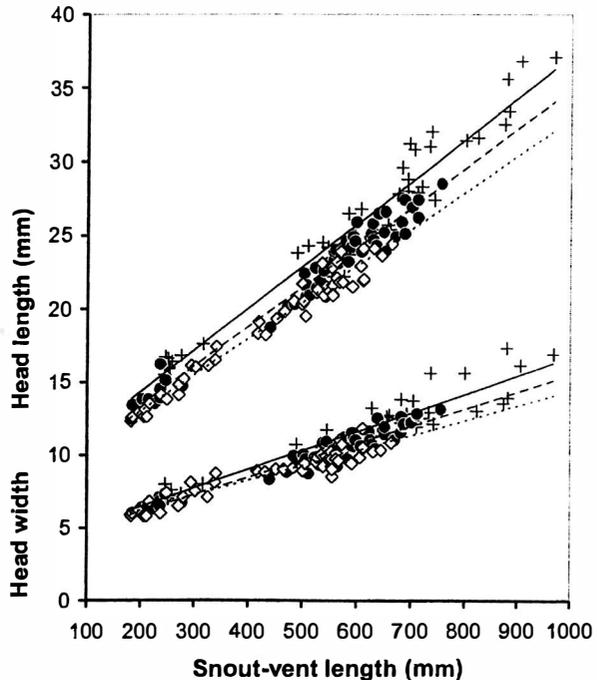


FIG. 2. Relationship of head length and width to SVL in *D. nuchale* (crosses and continuous line), *D. percarinatum* (circles and dashed line) and *D. vinitor* (squares and dotted line). Note larger head of *D. nuchale*. The regression equations are, head length: $y = 0.0286x + 8.6251, R^2 = 0.9408$ (*nuchale*); $y = 0.0269x + 8.0226, R^2 = 0.9635$ (*percarinatum*); and $y = 0.0249x + 8.0073, R^2 = 0.9633$ (*vinitor*); head width $y = 0.0128x + 3.8975, R^2 = 0.8855$ (*nuchale*); $y = 0.0117x + 3.763, R^2 = 0.9174$ (*percarinatum*) and $y = 0.0102x + 4.1712, R^2 = 0.8977$ (*vinitor*).

TABLE 3. Prey types identified from stomachs of *Dendrophidion nuchale*, *D. percarinatum* and *D. vinitor*. Data are number of prey items, % total number of prey items (for that species) and frequency (number of snakes with that category of prey). n =proportion of specimens with food / total number of specimens examined for dietary data.

Prey category	<i>D. nuchale</i> (n=8/27)	<i>D. percarinatum</i> (n=12/23)	<i>D. vinitor</i> (n=13/25)
Frogs – unidentified spp.		3 / 15.8 / 3	
<i>Hyla</i> spp.			1 / 4.2 / 1
<i>Colostethus</i> sp?			1 / 4.2 / 1
<i>Eleutherodactylus</i> spp.	7 / 63.6 / 5	8 / 42.1 / 5	19 / 79.2 / 9
Unidentified leptodactylids	2 / 18.2 / 2	2 / 10.5 / 2	3 / 12.5 / 3
Lizards – unidentified spp.		1 / 5.3 / 1	
<i>Norops</i> spp.	2 / 18.2 / 2	4 / 21.1 / 4	
<i>Cnemidophorus</i> sp.		1 / 5.3 / 1	
Totals	11 / 100 / 9	19 / 100.1 / 16	24 / 100.1 / 14

Dendrophidion percarinatum is conspicuous in having an exceptionally long tail, accounting in males for up to 45% of the total adult length (Table 2, Fig. 1). Based on the total number of specimens examined, *D. percarinatum* also showed a much higher incidence of broken tails than *D. nuchale* and *D. vinitor* (47% compared with 23% and 19% respectively). Frequency of tail breakage may be a useful indicator of predation pressure in snakes and also a potential indicator of differential predation (Zug *et al.*, 1979; Henderson *et al.*, 1981). Only the Costa Rican sample of *D. percarinatum* and *D. vinitor* contained sufficient numbers of individuals to draw comparisons between species in an area of sympatry, but the results were significant, indicating an appreciably greater level of predation in *D. percarinatum* (17/32 [53.2%] versus 6/29 [20.7%] in *D. vinitor*; $\chi^2=7.28$, $df=1$, $P=0.007$).

Sexual size differences (SVL) within the species were minimal, males averaging slightly larger than females in *D. nuchale* and *D. vinitor*, but smaller in *D. percarinatum* (Table 2). Differences between the sexes in tail length and abdominal scale counts were also relatively minor.

DIETS

Fifty-four identifiable food items were recovered from the stomachs of 8 *D. nuchale*, 12 *D. percarinatum* and 13 *D. vinitor* (Table 3). The most common prey in all three species were small frogs, predominantly of the genus *Eleutherodactylus* (Telmatobiinae; Leptodactylidae). These anurans comprised at least 63% and probably >75% (since most unidentified frogs had one or more characteristics associated with this group) of the total number of feeding records, and with the exception of a single hylid and *Colostethus* were the only prey type recorded for *D. vinitor*, whereas the stomachs of *D. nuchale* and *D. percarinatum* also contained lizards, mostly anoles (Polychrotidae). This taxonomic difference between species in composition of the diet was statistically significant (Fisher's exact tests=6.151, $P=0.025$ and 10.431, $P=0.002$ for each respective com-

parison), but sample numbers were small and the data too limited for definitive interpretation. In the relative proportions of frogs and lizards eaten by *D. nuchale* and *D. percarinatum* there was no apparent difference (Fisher's exact test=0.971, $P=0.841$). *Dendrophidion nuchale* and *D. percarinatum* of all size classes contained frogs, but the individuals that contained lizards were all mature adults over 480 mm SVL. This may again simply reflect a bias due to the small sample sizes, but it may also indicate an ontogenetic broadening of prey spectrum in these species. Various other items were found in the stomachs of *D. percarinatum* and *D. vinitor*, including a number of lizard eggs, a spider, and unidentified arthropods, but these were invariably associated with frog or lizard remains and hence were probably ingested secondarily. Lizard eggs, however, may occasionally be eaten by these snakes. A 512 mm SVL *Dendrophidion bivittatum* examined from SW Colombia (BMNH 1909.4.30.66) contained two fully shelled lizard eggs in its stomach but no other remains of prey, and predation on lizard eggs is not uncommon among other colubrids that feed on lizards, e.g. *Drymobius margaritiferus* (Sieb, 1984), *Drymoluber dichrous* (Martins & Oliveira, 1998).

Most prey items for which identification to species level (or species group) was possible were terrestrial or leaf-litter forms. Common prey species recorded for *D. percarinatum* included *Eleutherodactylus bransfordii*, *E. fitzingerii*, and the anoline lizard *Norops limifrons*. Several *D. vinitor* from Costa Rica had eaten *E. bransfordii* and members of the *E. gollmeri* group, and others from Mexico contained *E. cf. lineatus*, while specific prey records for *D. nuchale* included *Eleutherodactylus laticeps* (Belize), *E. cf. conspicillatus* (Ecuador) and *Norops rodriguezii* (Belize). Only two of the frogs recovered were arboreal, an eleutherodactylid with prominently expanded toe pads (species unknown) that had been eaten by a *D. nuchale*, and a transforming metamorph of *Hyla ebraccata* contained by a *D. vinitor* (C. Guyer, pers. data). The number of prey items in stomachs ranged from 1-4, with 38% of

the specimens (all three species combined) containing >1. Most of the lizards for which direction of ingestion could be determined had been swallowed head-first, but a significant proportion of the frogs had been consumed instead by the 'tail' (48%). There was also an apparent relationship between direction of ingestion and the number of frogs eaten; in snakes that contained only a single frog, almost all (94%) had been ingested head-first, whereas regardless of size, 70% of frogs eaten by snakes that contained two or more items had been ingested tail-first.

The size range of prey was greatest in *D. nuchale*, a probable correlate of the larger head and body size attained by this species; mean prey size (vol.) in *D. nuchale* was 2.71 cm³ (± 1.48 , range 0.4-11.5, $n=7$), compared to 1.33 (± 0.25 , range 0.3-3.5, $n=14$) in *D. percarinatum* and 0.49 (± 0.15 , range 0.15-1.30, $n=9$) in *D. vinitor*. Notwithstanding the limited sample numbers, *D. nuchale* also contained food less frequently than did *D. percarinatum* and *D. vinitor* (Table 3; $\chi^2=8.90$, $df=1$, $P<0.005$ and $\chi^2=4.13$, $df=1$, $P<0.05$ for each respective comparison). All three species had fed mostly on relatively small prey and only an occasional larger item was found in their stomachs. For example, a 36.5 gm (498 mm SVL) *D. vinitor* contained three juvenile *Eleutherodactylus* sp., of which the largest had a mass of less than 1.2 gm (MR <3.3%). An 89.3 gm (639 mm SVL) *D. percarinatum* had eaten two *Eleutherodactylus fitzingeri* that were 1.73 (MR 1.9%) and 1.44 gms (MR 1.6%). The largest single prey item relative to snake body length was a 34.8 mm SVL *Eleutherodactylus* sp. found in a 308 mm SVL *D. nuchale*, for which a prey/predator mass ratio of 24.2% was calculated.

Feeding activity occurs throughout the year, but primarily during the wet season (May-December over most of the species' combined Central American range). Within each species, several females that contained food also contained ovulatory-sized follicles or shelled eggs, indicating that females do not habitually abstain from feeding when gravid; among snakes in general, a reduction or complete cessation of feeding activity in gravid females is more typical (Shine, 1979).

REPRODUCTION

Clutch sizes within the three species relative to female body length (SVL) were small, averaging 6.3 (± 0.75 , range 5-8, $n=4$) in *D. nuchale*, 4.9 (± 0.16 , range 4-6, $n=14$) in *D. percarinatum* and 4.2 (± 0.25 , range 3-5, $n=10$) in *D. vinitor*. In the two species for which sufficient data were available (*percarinatum* and *vinitor*), there was a positive correlation between clutch size and SVL (Fig. 3), but in *vinitor* the strength of this relationship is not great, and within both species the presence of small clutches in relatively large individuals suggests that factors other than body size (e.g. feeding success, overall health) may have a significant controlling influence on fecundity. Mean lengths of the largest shelled oviducal eggs ranged from 29.8 mm in *D.*

nuchale (range 28.4-31.2, $n=5$) to 25.1 (range 22.3-29.8, $n=6$) in *D. percarinatum* and 18.2 (range 17.1-19.4, $n=10$) in *D. vinitor*.

For most localities the reproductive data were insufficient to draw conclusions on the frequency or timing of reproduction. Females with developing follicles or oviducal eggs were present in samples from throughout the range of each species, but no individual locality had adequate representation of specimens for all months of the year. Combining localities in Costa Rica for *D. percarinatum* and *D. vinitor*, however, permits at least some measure of insight into the reproductive phenology of snakes in this area. Within *D. percarinatum*, enlarged follicles (>5 mm) were recorded for specimens collected between January and November, while females with oviducal eggs were found in May, July and

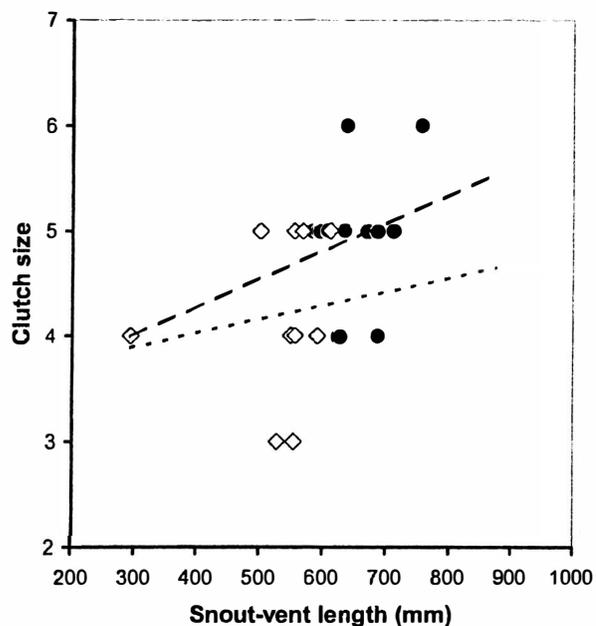


FIG. 3. Relationship of clutch size to female SVL in *D. percarinatum* (circles and dashed line; $y = 0.0027x + 3.2098$, $R^2 = 0.0526$) and *D. vinitor* (rhomboids and dotted line; $y = 0.0013x + 3.5016$, $R^2 = 0.0218$).

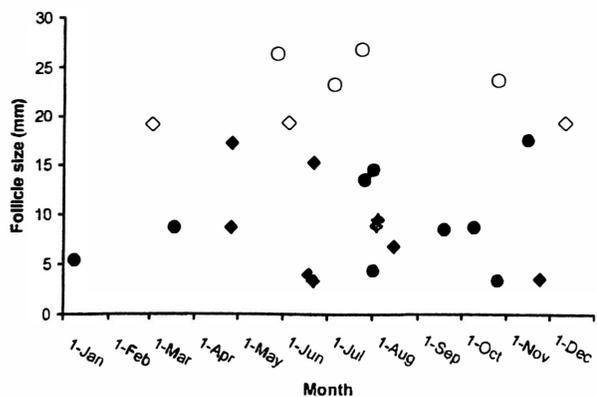


FIG. 4. Monthly variation in size of the largest ovarian follicle in female *D. percarinatum* (circles) and *D. vinitor* (rhomboids) from Costa Rica. Hollow symbols indicate oviducal eggs.

October (Fig. 4). Ovaries of *D. vinitor* contained enlarged follicles over a shorter period (April–August), but eggs were present in specimens with collection dates ranging from early March to mid-December. Hatchlings of *D. percarinatum* were collected in August and December, and others of *D. vinitor* in January, June and July. The irregular nature of this pattern suggests an extended or possibly continuous reproductive cycle in Costa Rican *D. percarinatum* and *D. vinitor*. Oviposition and hatching appear to be coincident mostly with the wet season, but are not restricted to this time. The overall length of the breeding cycle and lack of a well-defined single period of vitellogenesis further implies the production in some females of more than one clutch per year. Another possible explanation is that vitellogenesis is protracted over several months and reproduction occurs in alternate years, as suspected for Yucatán populations of the morphologically similar *Dryadophis melanolomus* (Censky & McCoy, 1988). However, the relatively large proportion of females in the sample that were reproductive (i.e. gravid, with enlarged follicles or oviducal eggs: 85% [11/13] in *percarinatum* and 82% [9/11] in *vinitor*) is more suggestive of ‘multiple’ annual cycles, and this is further supported by the presence in some individuals of follicles at different stages of enlargement. One 554 mm SVL *D. vinitor* collected in mid-April contained follicles of three size classes (15.4–17.2 mm, $n=3$; 8.6–8.7 mm, $n=3$; and 4.3–4.5 mm, $n=11$), each presumably representing a discrete and separate clutch. In addition, clutch size in all three species is relatively small, this being consistent with other data (Zug *et al.*, 1979), indicating that selective pressure may exist among tropical snakes for fewer or larger eggs per clutch and more clutches per year.

Body length (SVL) measurements of the smallest individuals examined provide an indication of size at hatching; for *D. nuchale* this measurement was 245 mm, for *D. percarinatum* 185 mm, and for *D. vinitor* 182 mm. Smaller body sizes may have been recorded had sample numbers been larger, but the presence of yolk sac scars on the smallest individuals of *percarinatum* and *vinitor*, combined with differences between the species in relative egg size, suggest that the figures are a close if not precise estimate of actual size at hatching. The smallest females exhibiting reproductive activity had SVL measurements of 536 mm (*nuchale*), 441 mm (*percarinatum*), and 294 mm (*vinitor*). Males reach sexual maturity at similar or larger sizes, with lengths of 556 (*nuchale*), 473 (*percarinatum*), and 364 mm (*vinitor*) recorded for the smallest individuals with enlarged testes and thickened sperm ducts.

DISCUSSION

Dendrophidion nuchale, *percarinatum* and *vinitor* are diurnal, essentially terrestrial snakes apparently adapted for rapid movement and visually-orientated predation. The large eye is a particularly distinctive feature

and probably evolved as a specific adaptation for searching out and following prey that moves quickly and erratically; this has been suggested previously by Dixon *et al.* (1993) for species of the derived genus *Chironius*, many of which occur in similar habitats and also feed chiefly on *Eleutherodactylus*. Large eye size in *Dendrophidion* may be further related to the difficulties of visual hunting at ground level in closed-canopy forests (i.e., low angle of view, reduced light), and this may also explain why the HL/ED ratio in these snakes is greater than that in many arboreal colubrids, including certain nocturnal forms (for comparisons see Henderson & Binder, 1980).

Body sizes (SVL) differ considerably among the three species, but not between sexes within species. In *D. nuchale* and *D. vinitor* adult males were generally larger than females, whereas in *D. percarinatum* the largest individuals examined were females. Statistical comparisons of these relative size differences were not significant (Mann-Whitney *U*-tests, $P>0.30$). Information on maximum body size in the sexes of other species of *Dendrophidion* is meagre; for *D. dendrophis*, however, males are reported to attain total lengths of 1142 mm (Gasc & Rodrigues, 1980), while females reach 1183 mm (tail 44.9–52.2% of total length) (Martins & Oliveira, 1998). The approximate equivalence of males and females in body size is a frequent correlate of male combat in snakes (Shine, 1978, 1994) and offers incidental evidence for the occurrence of such behaviour in *Dendrophidion*. There are no published reports of physical combat between males of the three species discussed here or others within the genus, but this may simply reflect the lack of behavioural observations on these snakes. Males of some related taxa do show combat (e.g., *Chironius bicarinatus*, Almeida-Santos & Marques, 2002; *C. carinatus*, see Starace, 1998).

PREDATION INTENSITY

Differences between the three species in the number of individuals with damaged tails suggest that predation pressure in *D. percarinatum* is relatively more intense. More than half of the *D. percarinatum* examined showed evidence of tail injury, compared with less than 25% in *D. nuchale* and *D. vinitor*. A possible explanation for this difference is that *D. percarinatum* may forage in a wider range of habitats than *D. nuchale* or *D. vinitor*, including less densely forested environments with a more open canopy (see discussion of foraging ecology). The tail in this species may also be more fragile and easily broken (or more liberally discarded). In the absence of any quantitative observations, however, a direct explanation of this phenomenon must await further study. An interesting feature of the tail in *D. nuchale* is its distinct reddish colour, often more vivid in adults (disruptive/aposematic?).

High predation pressure in *Dendrophidion* may explain why these and many other diurnal snakes sleep in vegetation at night (Martins, 1993; Martins & Oliveira, 1998). At La Selva in Costa Rica, many more *D.*

percarinatum and *D. vinitor* can be observed at night than during the day, sleeping in shrubs and bushes approximately 2 metres from the ground (C. Lieb, pers. comm.).

DIETS AND FORAGING ECOLOGY

The presence of a small and taxonomically limited range of organisms in the diets of *D. nuchale*, *D. percarinatum* and *D. vinitor* suggests that the species are relatively specialized in their feeding habits. Over 75% of prey items were small frogs of the family Leptodactylidae (>80% of these in one genus, *Eleutherodactylus*) and *D. vinitor* appears to feed almost exclusively on these anurans. Although dietary overlap was substantial in terms of the main prey type consumed, however, differences between the species in composition are seemingly apparent, with *D. nuchale* and *D. percarinatum* feeding also on lizards. This feature of the diet is not in itself unique or especially remarkable but may explain the coexistence in some areas of *D. vinitor* with *D. nuchale* and *D. percarinatum*, particularly in the absence of any clear differences among the species in habitat occupancy, foraging mode, or the times of day/year when foraging occurs. Division of prey on the basis of size may also be important for these snakes, as indicated by the larger body size, head size, and overall mean prey size in *D. nuchale*. Possible competition between syntopic *Dendrophidion*, however, as well as between these snakes and other species with similar habits, may presumably be expected only if resource availability was limiting.

That no *Anolis* or other non-anuran prey items were recovered from *D. vinitor* is strong evidence of anurophagy but does not necessarily imply active selection of frogs by this species. As noted for some elapids (Shine, 1977), species that feed on frogs but which live in habitats where lizards are also found often eat both prey types, possibly because the nutritional benefits of eating all potential prey items whenever they are encountered far outweigh the operative 'costs' of capturing and handling them. The fact that anoles are ubiquitous throughout much of Central America and often abundant in the same microhabitats as *Eleutherodactylus*, however, contends that if indeed *D. vinitor* does eat lizards, this prey type should appear frequently in its diet. Why this is not reflected by the data, albeit limited due to the small sample numbers, may therefore be significant. Specialist frog predators that forage in habitats where lizards also occur are not uncommon among Neotropical colubrids (e.g. members of the Xenodontini), and this trait may be ultimately due to phylogenetic constraints. Lee (2000) referred to a *D. vinitor* that ate lizards (*Norops* sp.) in captivity.

Accounts of food habits published previously for *D. nuchale*, *D. percarinatum* and *D. vinitor* are generally consistent with the results of this study, although no evidence was found of toads in the diet of *nuchale*, as indicated by Roze (1952), or rodents and other small mammals (Lancini & Kornacker, 1989; Pérez-Santos &

Moreno, 1988, 1991). Test *et al.* (1966) reported on a captive *D. nuchale* from Venezuela (as *percarinatum*) that ate *Prostherapis* (= *Mannophryne*) *trinitatis*, *M. neblina*, and *Eleutherodactylus cornutus maussi*, noting that the same snake refused a toad (*Bufo granulosus*) and gecko (*Gonatodes taniae*). For *D. percarinatum* in Panama specific prey items have included *Eleutherodactylus diastema*, frogs of the genus *Leptodactylus*, and other (unidentified) frogs (Sexton & Heatwole, 1965). All three species are characterized by Savage (2002) as frog-eating forms. Information available for *D. dendrophis* (Cunha & Nascimento, 1978; Dixon and Soini, 1986; Duellman, 1978; Nascimento *et al.*, 1987; Vanzolini, 1986) suggests that frogs are an important component in the diet of this South American species as well, a variety of different taxa having been recorded (*Adenomera*, *Eleutherodactylus*, *Colostethus*, *Hyla* and *Scinax*). Cunha & Nascimento (1978) stated that in addition to frogs *dendrophis* feeds on insect larvae, and – according to Abuys (1982) and Starace (1998) – this species will also eat lizards and birds, an observation disputed by Martins (2000).

Predator-prey size relationships inferred for the three species are comparable with those demonstrated by Martins & Oliveira (1998) for *D. dendrophis* in Central Amazonia. Individuals of this species, with total lengths ranging from 946-1128 mm (17-62.5 g) were found to have also fed predominantly on small frogs, usually less than 10% of their mass (range <3-18%). Similar ratios were recorded by Sieb (1984) for two other Neotropical racers that feed on frogs and lizards, *Drymobius chloroticus* and *D. margaritiferus*. Mean prey/predator mass ratios for these species were 4.1% and 5.3% respectively, and the largest prey item, contained by a *D. margaritiferus*, was 28.6% the mass of the adult snake.

The stomach content data are to some extent informative also about foraging habits in *D. nuchale*, *percarinatum* and *vinitor*. Of the 35+ prey organisms identified to species level (or morphotypic group in the case of some unidentified leptodactylids), only two were arboreal, confirming the predominantly terrestrial habits of these snakes; Savage (2002), however, indicates that *D. vinitor* will readily climb into bushes or trees when foraging or to escape predation, and all three species may be commonly observed sleeping above ground at night. The preponderance of *Eleutherodactylus* further indicates that prey-searching activities are restricted mostly to areas where there is extensive canopy cover (e.g. see Guyer, 1990 and individual species accounts in Lynch and Myers, 1983; Savage, 1987, 2002). Some foraging by *D. percarinatum*, however, may occur in more open environments, as suggested by the presence in its diet of *Leptodactylus* frogs and lizards of the genus *Cnemidophorus*. Often, species in these genera are found in habitats that are relatively exposed and devoid of significant tree cover (see Lee, 1996; Wright, 1993). *Dendrophidion* are diurnal snakes and the two genera of lizards identified from stomachs are also strictly diurnal. In contrast, the frogs are active mostly at night. The

greater part of the diet would thus appear to consist of prey that are effectively inactive and possibly also hidden from the snakes when they are foraging, many *Eleutherodactylus* being procryptic and emerging from shelter only at night or, if by day, during/following rain (Duellman, 1978; Toft & Duellman, 1979). Detection and capture of these frogs may be further complicated by their erratic leaping behaviour and the habit in some species when attempting to evade predators of adopting a motionless, low crouching posture (e.g. *E. bransfordii*; C. Lieb, pers. comm.).

Field observations indicate that prey is located by active searching. An adult *D. nuchale* and a juvenile *D. vinitor* observed moving slowly across leaf litter in dense forest (Belize and Costa Rica) would pause at intervals to push their snouts into the substrate, and Test *et al.* (1966) similarly described individuals of *D. nuchale* from Venezuela (as *percarinatum*) moving through leaf litter 'in a manner suggestive of foraging'. The head is often held well above the ground, probably to aid detection of prey and/or maintain visual contact with flushed and escaping prey.

REPRODUCTION

Reproductive data for *D. percarinatum* and *D. vinitor* from Costa Rica suggest a nearly continuous cycle with the production in individual females of more than one clutch per year. Most adult-sized females from localities in this area contained enlarged vitellogenic follicles or oviducal eggs, and a small number contained both. Because the majority of gravid females were collected during the wettest period of the year (May-December) however, the possibility of a more seasonally-orientated cycle cannot be ruled out, particularly in view of the fact that samples consisted of individuals collected over many years (50+), thus obscuring annual variation in season length. It is perhaps significant, however, that the dry season in north-eastern Costa Rica is not severe (Hammel, 1990), and a common prey species of *Dendrophidion* in this area, *Eleutherodactylus bransfordii*, also appears to reproduce nearly year-round (Donnelly, 1999). Food availability has been implicated as a major determinant of reproductive frequency in snakes (Vitt, 1983; Seigel & Ford, 1987) and in certain species the intensity of reproduction from year to year has been shown to fluctuate widely as a direct result of annual variation in prey abundance (e.g. Andr n & Nilson, 1983). Given the clear importance of frogs in the diets of *D. nuchale*, *D. percarinatum* and *D. vinitor*, and the often high correlation in tropical regions between anuran activity and rainfall (see Neill, 1962; Henderson & Hoevers, 1977; and individual species accounts in Lee, 1996; Savage, 2002), it is thus likely that reproduction during prolonged dry periods is less frequent.

Data from other localities within lower Central America (Nicaragua, Panama, Chococoan Colombia) collectively showed a similar trend towards more or less

continuous reproduction in *D. percarinatum* and *D. vinitor*. Egg-laying by individuals of *D. nuchale* during the non-rainy season in Venezuela suggests that reproductive activity in snakes from this area may follow a similar pattern (Test *et al.*, 1966). An interpretation of the reproductive cycles in other populations of these three snakes, however, is not possible without the benefit of additional data. The potential of a species for modifying its pattern at different localities has been indicated in a number of tropical colubrids (e.g. Zug *et al.*, 1979), and owing to the pronounced seasonality of rainfall in certain areas, particularly northern Central America, a seasonal cycle may well be found in some populations. In keeping with this is the observation that all three hatchlings of *D. vinitor* from Mexico were collected between August and October, corresponding to the middle part of the wet season in this area, as were the only two hatchlings of *D. nuchale* (from Belize and Guatemala).

Clutch sizes in *Dendrophidion nuchale*, *percarinatum* and *vinitor* are generally consistent with other fecundity data published for the snakes of this genus. For a 633 mm SVL *D. brunneum*, Kuch & Freire (1993) reported a clutch size of six, and another examined by myself with an SVL of 668 mm contained four. Mean egg length (unshelled) in the latter clutch was 25.6 mm (x 8.7 wide). A 512 mm SVL *D. bivittatum* in the collection of the BMNH (1909.4.30.66; Colombia) also contains four eggs (shelled), the average length of which is 33.4 mm (x 10.5). For *D. dendrophis* in Surinam, Abuys (1982) reported a clutch size range of 12-15. Limited data available for this species in other parts of its range, however, would seem to contradict this observation; Duellman (1978) refers to an individual from Ecuador that contained six eggs (30.2 mm in length), and for two others in Central Amazonia Martins & Oliveira (1998) recorded clutch sizes of four and six, the latter from a female having an SVL of 571 mm.

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Museum). George Zug and Ronald Crombie confirmed SVL measurements and provided other data for a number of *D. vinitor* paratypes in the collection of the U.S. National Museum, and Richard Lehtinen provided similar information for a paratype at the University of Michigan's Museum of Zoology. Measurements for a number of Nicaraguan specimens were contributed by Gunther Köhler (Forschungsinstitut und Naturmuseum Senckenberg). Craig Guyer (Auburn University) and Carl Lieb (University of Texas at El Paso) gave freely of their observational data on *Dendrophidion* in the field, and for help regarding access to a number of Costa Rican specimens I am indebted also to Jay Savage. Robert Henderson (Milwaukee Public Museum), Marcio Martins (Instituto de Biociências, Universidad de São Paulo) and Wolfgang Wüster (University of Wales) provided helpful comments on the original draft version of this manuscript, and the Spanish summarization was kindly prepared by Mamen Peña.

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APPENDIX I

SPECIMENS EXAMINED

Dendrophidion nuchale

BELIZE – *Cayo District*: 1.6 km W Baldy Sibun (LSUMZ 8901); Dos (Las) Cuevas, 500 m (LSUMZ 8902); Sibun Hill (LSUMZ 8903); Cuxta Bani, upper Raspaculo River, 425 m (PJS field nos. 9703, 9704). *Stann Creek District*: Middlesex, 125 m (UCM 25708, 25794, 25805, 25806, 25846, 25847, 25874). GUATEMALA – *Alta Verapaz*: btw Coban and Lanquin (BMNH 64.1.26.4-5). *Izabal*: Sierra de Las Minas, Los Amateas, Aldea Vista Hermosa, 1000 m (KU 190916). HONDURAS – *Atlántida*: Quebrada de Oro (ROM 19970). NICARAGUA – no specific locality (USNM 14220). COSTA RICA – *Puntarenas*: Finca Helechales, 1050 m (LSUMZ 11636); 4-6 km S San Vito de Jaba, Finca Las Cruces, 1200 m (LACM 148556); 6.4 km S San Vito de Java, Finca Las Cruces, 1219 m (LACM 148553). PANAMÁ – *Bocas Del Toro*: Bocas Del Toro Boquete trail (MCZ 22210). *Darien*: Laguna, 820 m (KU 75681). COLOMBIA – *Caldas*: Pueblo Rico, Santa Cecilia, Pacific side, 800 m (FMNH 54939). *Chocó*: Cãno Decordo, btw Cucurupí and Noanomá, on Río San Juan, ca. 100 m (CAS 119591, 119604); Pueblo Rico, slopes of San Juan River, SW Colombia, 5200 ft (BMNH 1910.7.11.24). *Valle de Cauca*: Cisneros, 1100 m (FMNH 43738, 43741). ECUADOR – *Paramba*, 3500 ft (BMNH 98.4.28.59); St. Javier (BMNH 1901.3.29.28). *Carchi*: Maldonado, 1410 m (KU 179499). *NW Ecuador*: Bulim, 160 ft (BMNH 1901.8.3.4); Río Sapayo, 450 ft (BMNH 1902.7.29.17). PERU – *Cuzco*: Tono (FMNH 229571). VENEZUELA

– *Aragua*: Rancho Grande (UMMZ 142678); Rancho Grande, nr biological station (UMMZ 122355); Rancho Grande Biological Station, Portachelo Pass (CAS 139477); Rancho Grande, Telegraph Trial nr Portachelo Pass (UMMZ 142679). *Guarico*: 5 km NE La Colonia guard station, Parque Guatopo, 3250 ft (TCWC 59025). *Miranda*: 37.4 km N Altigracia, 1400 ft (TCWC 59020); 26.2 km N Altigracia (TCWC 59020); 27 km N Altigracia, 2200 ft (TCWC 59024); 2 km E Hwy 12, 26 km N Altigracia, 3000 ft (TCWC 59026).

Dendrophidion percarinatum

No data (FMNH 154510, 154516). HONDURAS – *Ailántida*: Lancetilla (MCZ 29677). NICARAGUA – Comoapa (MCZ 9550); Río Mico, 10 mi above Recero (UMMZ 79764). *Santo Domingo*: Chontales Mines, 2000 ft (BMNH 94.10.1.18). *Zelaya*: 7 mi above Rama, Río Siquia (UMMZ 79767). COSTA RICA – no specific locality (LACM 148579, 148584). *Alajuela*: Venado, 9 km N Arenal, 252 m (LACM 148580). *Cartago*: Bataan (KU 30998); Turrialba, 605 m (LACM 148577). *Heredia*: Finca La Selva, 40 m (LACM 148585); Finca La Selva, 60 m (LACM 148586); Finca La Selva, 2.4 km SE Puerto Viejo, 60 m (LACM 148558, 148560). *Limón*: Barra del Colorado, 4 m (LACM 148587); vic Cahuita, ca 4 m (LACM 148582); Los Diamantes (KU 30997); Pandora, 17 m (LACM 148581); Sixaola, Talamanca, 800 ft? (BMNH 1956.1.6.48). *Puntarenas*: Cajón (BMNH 1978.767); Finca Las Cruces, nr San Vito de Jaba on road to Villa Neily, 4 km, 1200 m (LACM 148566); 0.4 km W of Motel Bella Vista, Golfito, 15 m (LACM 148564); Golfito, 12 m (LACM 148568); 6.3 km S of Pan Am Hwy on Golfito road, 7 m (LACM 148567); Gromaco, between Río Coton and Río Coto Brus at juncture, 480 m (LACM 148569); La Lola, 39 m (LACM 148578); Palmar (KU 31948); vic Río Disciplina, 1680 ft? (LACM 148588); 2 km S entrada Palmar Sur, 15 m (LACM 148592); Rincón de Osa, 5 m (KU 102506); 3.5 km WSW Rincón de Osa, 40 m (LACM 148562); vic Rincón de Osa, 20 m (LACM 148563); 3 km WSW Rincón de Osa, 0.5-1 km S Osa Field Station, 4060 ft (LACM 148571); 4 km SW Rincón de Osa, Holdridge Trail, 60 m (LACM 148575); 5 km SW Rincón de Osa, 10 m (LACM 148570); 7.5 km SW Rincón de Osa, Quebrada Rayo, 20 m (LACM 148576); San Luis River at footbridge, ca. 740 m (LACM 148559). PANAMÁ – *Canal Zone*: Barro Colorado Island (KU 80589); Barro Colorado Island, Wheeler Trail (UMMZ 63762); Fort Clayton (KU 107649); Fort Randolph (MCZ 20552); Gatun (FMNH 16760); Hydrographic Station, Salamanca (MCZ 39978); Juan Mina (MCZ 26646). *Chirikui* (BMNH 94.5.17.8-9). *Darien*: Cana, 500 m (KU 107651); Ortiga site (FMNH 170152); Río Tiura at Río Mono, 130 m (KU 107653, 107655); Tacarcuna, 550 m (KU 75677). *Veraguas*: Isla Gobernadora (KU 107648). COLOMBIA – *Antioquia*: Uraba, Río Currulao (FMNH 63761, 63773); Villa Arteaga (FMNH

78118). *Chocó*: Piña Lisa, Condoto, 300 ft (BMNH 1913.11.12.40).

Dendrophidion vinitor

MÉXICO – no specific locality (BMNH 60.6.17.13); Forest at Cascapel, upper Uzpanapa River, Isthmus of Tehuantepec (BMNH 1936.6.6.8). *Oaxaca*: no specific locality (UCM 39911-39912); Donaji, Mije District (UCM 44481); La Gloria (FMNH 126555); La Gloria, 1500 ft (FMNH 126554); Río Negro (Grijua), Juchitrán (UCM 41162). *Veracruz*: 60 km SW Jesus Carranza (KU 23965); nr Coyame, 1400 ft (UMMZ 111450); Volcán San Martin, nr base (UMMZ 122767); SE slope Volcán San Martin, ca. 2600 ft (UMMZ 121145). GUATEMALA – *Alta Verapaz*: btw Coban and Lanquin (BMNH 64.1.26.21). NICARAGUA – Matagalpa (MCZ 9561). *Atlántico Sur*: Cara de Mono, 50 m (KU 112974). *Santo Domingo*: Chontales Mines, 2000 ft (BMNH 94.10.1.19-20). COSTA RICA – *Alajuela*: Poco Sol de La Tigre, 540 m (LACM 148601). *Cartago*: 2.5 km N Pavones, nr Río Revantazon, 700 m (LACM 148594); Pavones, ca. Turrialba (KU 140055). *Guanacaste*: Cacao Biological Station, 729-1528 m (LACM 148589); Volcán Orosí, trail from Maritza Biological Station to Cerro Cacao, 750 m (PJS field no. 9618). *Heredia*: Finca de Selva, 60 m (LACM 148616); Finca La Selva, 2.4 km S Puerto Viejo, 60 m (LACM 148605, 148619); Finca La Selva, 2.4 km SE Puerto Viejo, 60 m (LACM 148591, 148609); Finca La Selva, research trail at forest plot, 40 m (LACM 148593); Finca La Selva, river road, 40 m (LACM 148595, 148597, 148611); Finca La Selva, river road at cacao plot, 40 m (LACM 148598); Finca La Selva, cacao plot nr. Quebrada Experimental (LACM 148603); Finca La Selva, Quebrada Esquina at SE boundary, 100 m (LACM 148604); Finca La Selva, south loop trail (LACM 148621). *Limon*: Pandora, 50 m (LACM 148618); Puerto Viejo (KU 35639). *Puntarenas*: 4 km S San Vito de Jaba, 1200-1300 m (LACM 148614); 6.4 km S San Vito de Jaba, Finca Las Cruces, 1219 m (LACM 148596); Finca Las Cruces, nr San Vito de Jaba on road to villa, 4 km S San Vito, 1200 m (LACM 148599, 148613, 148617); Las Cruces field station at San Vito de Java, 1100 m (LACM 148606); Las Cruces, San Vito (LACM 148608); Las Cruces, down toward Río Jaba, 1100 m (LACM 148615); Finca Loma Linda, 2 km SSW Canas Gordas, 1170 m (LACM 148590, 148620). PANAMÁ – Pequeni-Esperanza ridge, nr head R Pequina, 2 mi E of Panama R (MCZ 42782); Pequeni-Esperanza ridge, 2 mi E of Panama R (MCZ 42783). *Bocas Del Toro*: Almirante (KU 80223); 11 km NW Almirante, 600 ft (FMNH 153653, 154038-154039). *Darien*: Laguna, 820 m (KU 75680); San Blas Territory; border of Darien, Summit site (FMNH 170138). COLOMBIA – *Chocó*: Quebrado, Bochorama, Loma de Encarnacion on Right bank (LACM 45443).