

Variation in Reproductive
Parameters of Three Neotropical
Snakes, *Coniophanes fissidens*,
Dipsas catesbyi, and
Imantodes cenchoa

GEORGE R. ZUG, S. BLAIR HEDGES,
and SARA SUNKEL

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ABSTRACT

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Variation in Reproductive Parameters of Three Neotropical Snakes, *Coniophanes fissidens*, *Dipsas catesbyi*, and *Imantodes cenchoa*

George R. Zug, S. Blair Hedges,
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Introduction

Snakes are likely as reproductively diverse as their sister lineage, the lizards. Owing to the higher population densities and the more tractable nature of lizards, however, our knowledge of reproduction is many times greater for lizards than for snakes. Presumably snakes will share many of the reproductive patterns with lizards, and some of the generalizations being developed and refined for lizards will be applicable to all squamates.

Like lizards, snake reproductive patterns will commonly prove to be adapted to local climatic and biotic regimes. Such local adaptation will be superimposed on the species specific patterns of reproduction and limited by them. Fitch's review (1970) provides a compendium to the species specific patterns of reproduction and drew our attention to the numerous unknowns of snake reproduction, particularly those concerned with intraspecific variation and tropical species. Thus, we

were encouraged to examine reproductive parameters in several species of Neotropical snakes.

Clutch size has been demonstrated to possess intraspecific variation in lizards (Tinkle, Wilbur, and Tilley, 1970) and turtles (Christiansen and Moll, 1973); therefore, we selected it as our primary measure of the variability of reproductive patterns in Neotropical snakes. Periodicity of egg deposition is examined to test the assumption of continuous or aseasonal reproduction in tropical reptiles. These and other life history parameters of three Neotropical snakes are examined in this article.

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W. R. Heyer, C. J. McCoy, C. W. Myers, and R. Shine read the manuscript in an earlier, rudimentary state. Its present improved state is due greatly

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to their careful evaluation. We remain, of course, responsible for the errors of omission and interpretation.

Materials and Methods

The three species of snakes that were examined were selected because each is oviparous; each derives from a different habitat and possesses a different body form; each has a large geographic range and is well represented in museum collections. The latter criterion is critical in studying reproductive biology of snakes. Large samples are needed because of the usual preponderance of males in collections (Shine and Bull, 1977). Samples must be obtained throughout the year in order to detect seasonal phenomena. Furthermore, samples should be derived from restricted geographic areas to avoid compounding variability by the potential of different reproductive patterns in adjacent populations, e.g., Vanzolini and Reboucas-Spieker (1976). As will become evident in the following analyses, the samples used

here, although large, are still insufficient to unquestionably define the reproductive biology of these three snake species.

Data obtained from each specimen included the following: *snout-vent length*, the distance from the anterior tip of the snout to the posterior edge of the anal scale; *tail length*, the distance from the vent (posterior edge of anal scale) to the tip of the tail (incomplete or broken tails were noted); *gonad placement*, distance from posterior edge of left gonad to the vent; the posterior edge of the ovary was delimited by the last follicle in the ovary; *gonad or sex cell size*, maximum lengths of the left and right testes and maximum width of largest testis; maximum length of every visible follicle and ovum; *sex*, determined by dissection and examination of the gonads; *date of capture and/or preservation*. Snout-vent and tail length were measured to the nearest millimeter on a meter stick. All gonadal measurements were taken with dial calipers to the nearest tenth of a millimeter. The condition of the fat bodies and genital ducts were recorded by using predetermined classes.

The reproductive state of the males was evaluated by the proportion of testis length to snout-vent length. This value is largely ineffectual in distinguishing the various phases of testicular activity due to the poor state of preservation in many specimens. Weight or volume may have been more indicative.

The reproductive state of the females was evaluated by dividing the various phases of follicle or ovum growth into classes (Table 1) and then scoring each female's follicles in these classes. We recognize

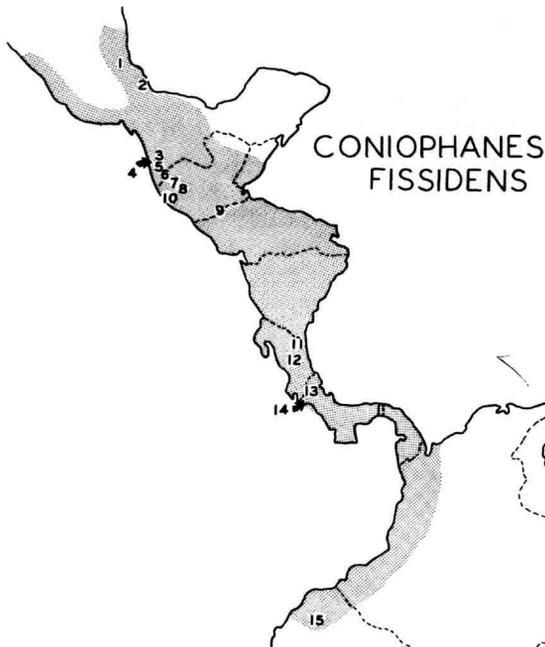


FIGURE 1.—Presumed range and sample localities for *Coniophanes fissidens*. (Numbers = localities listed in Appendix.)

TABLE 1.—Size classes of ovarian follicles and shelled ovidual eggs in *C. fissidens*, *D. catesbyi*, and *I. cenchoa* (measurements in mm, choice of size classes explained in text)

Classes	<i>C. fissidens</i>	<i>D. catesbyi</i>	<i>I. cenchoa</i>
Follicles			
I	< 1.0	< 1.0	< 1.0
II	1.1- 3.0	1.1- 3.0	1.1- 3.0
III	3.1- 6.0	3.1- 7.0	3.1- 7.0
IV	6.1-11.0	7.1-17.3	7.1-23.5
V	> 11.1	> 17.4	> 23.6
Eggs	> 14.8	> 21.5	> 27.8

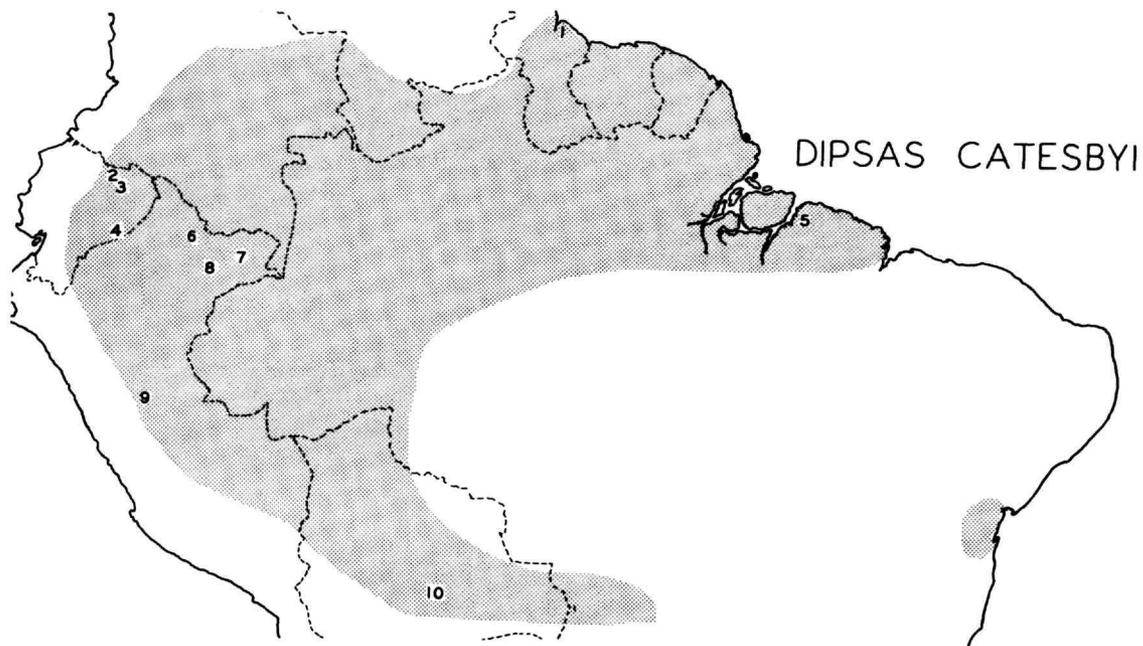


FIGURE 2.—Presumed range and sample localities for *Dipsas catesbyi*. (Numbers = localities listed in Appendix.)

six phases in sex cell maturation; I, oogenesis; II, early growth; III, hydration and initial vitellogenesis; IV, active vitellogenesis; V, maturation, immediately preceding ovulation; oviducal, presence in the oviduct and shell formation. The definition of these phases is based on the observed oogenetic phases of temperate-zone squamates and an examination of our data on sex cell size to determine the existence of similar phases and their usual size ranges.

Betz (1963) recognized four nonoverlapping follicle classes in *Nerodia rhombifera*; these classes correspond to our Classes I, III, IV, and V. Betz observed that a follicle required approximately 2.5 years for maturation. Oogenesis occurred in the early fall. The follicle grew slowly, reaching early vitellogenesis the succeeding fall and late vitellogenesis the next fall. Maturation occurred during the second winter so that the ovum would be ovulated and fertilized in the spring. This gradualness conflicts somewhat with the findings of Dessauer and Fox (1959, *Thamnophis sauritus*), Clark, (1970, *Carphophis vermis*), and Jones (1975, *Anolis carolinensis*). Dessauer and Fox observed slow follicle growth to a maximum diameter of 2.0 mm, then a

faster growth through hydration. When the follicle reached a diameter of 7.0 mm, active vitellogenesis began. The actual time span between phases was not given. Jones noted that a growth spurt (active vitellogenesis) began at a follicle diameter of 2.6 mm and that approximately 30 days were required for maturation. Clark reported follicles growing from 6.5 mm in mid-March to maturation at 26.0 mm in late May, about 75 days. Based on these observations, we have placed follicles less than 1.0 mm in Class I, 1.1 to 3.0 mm follicles in Class II, and 3.1 to 6.0 or 7.0 mm follicles in Class III. The size ranges of the remaining classes depend upon the sizes of the oviducal ova. The maximum size of Class IV and the minimum size of Class V were established by subtracting the standard deviation of the mean oviducal egg length from the minimum oviducal egg length. We assumed that this value would account for both the difference between the length of a shelled egg and the length of a follicular ovum immediately prior to ovulation and the variation in preovulatory ova lengths. The smallest oviducal egg represents the base for the oviducal class, excluding eggs less than two-thirds the mean egg

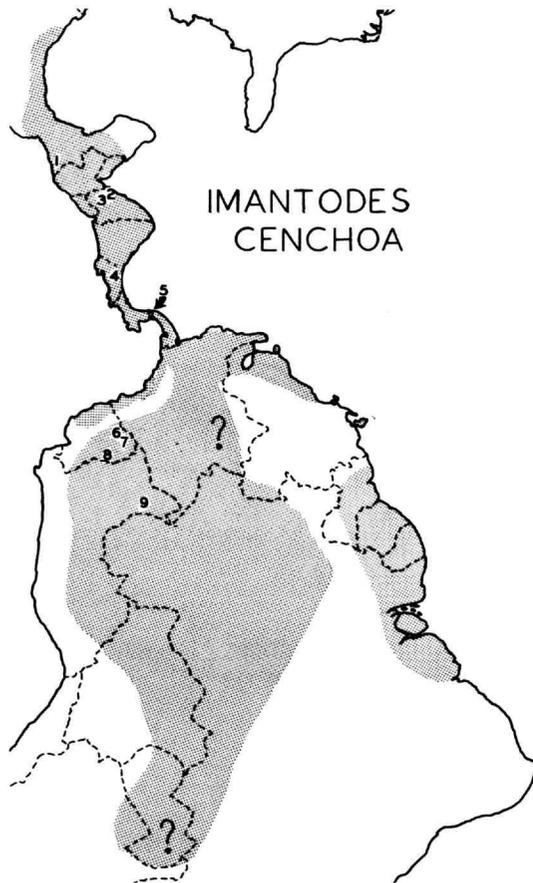


FIGURE 3.—Presumed range and sample localities for *Imantodes cenchoa*. (Numbers = localities listed in Appendix.)

length (of the species), since we assume that such an egg would not develop normally.

Coniophanes fissidens

NATURAL HISTORY

Coniophanes fissidens is a small (snout-vent length to 550 mm, but adults usually less than 400 mm), predominantly diurnal snake of the forest floor. It is most common in the leaf litter of well-drained mesic forest below 1000 m (Myers, 1969), although it has been found up to 1600 m (Landy, et al., 1966) and in secondary growth forests (Duellman, 1963; Minton and Smith, 1960). Hidden beneath

the leaf litter with only its head and neck exposed and elevated, the snake surveys the surrounding area for prey or prowls and searches for prey (Myers, 1969). Small, terrestrial amphibians and reptiles appear to be the major prey, e.g., *Leptodactylus* (Landy, et al., 1966; Minton and Smith, 1960), *Colostethus*, and *Lepidoblepharis* (Myers, 1969).

BODY SIZE

HATCHLINGS.—The largest snake with a yolk-sac scar had a snout-vent length of 123 mm. Our total *Coniophanes* sample contained 10 individuals this length or less, three (114, 120, and 123 mm long) of which had yolk-sac scars. The mean snout-vent length of hatchlings is 117.7 mm (standard deviation, ± 3.6 mm; range, 111–123 mm). Perhaps owing to the small sample size, the hatchlings from southern Mexico ($N = 7$) average somewhat larger (118.6 mm) than those from Costa Rica and Panama (115.7 mm; $N = 3$); however, geographic variation in hatchling size is a possibility.

GROWTH AND SEXUAL MATURITY.—In the absence of long-term mark and recapture data on individual snakes, it is impossible to provide precise information on growth and sexual maturity. Nonetheless, we believe that we can provide estimates of these two life history parameters. Females with class V follicles or oviducal ova are considered sexually mature. Such females are assumed to be, at most, a month or two away from egg deposition.

Combining the sexually mature females ($N = 27$) from all localities yields an average snout-vent length of $298.8 \pm$ a standard deviation of 51.5 mm and a range of 230–425 mm. The mean snout-vent length of females (13) with only oviducal eggs is slightly higher, 307.8 ± 44.9 mm (244–425 mm). The sexually mature females from Chiapas (10) have a mean length of 306.6 ± 28.8 mm (276–374 mm), from Guatemala (13) 267.6 ± 30.1 mm (230–330), from Costa Rica (3) 361.0 ± 55.6 mm (325–425), and from Panama (1) 439.0. Thus, we estimate that, on the average, most females with a snout-vent length greater than 250 mm are sexually mature even if they do not possess mature follicles or oviducal eggs. Our data do not permit us to estimate the size at which males reach sexual maturity; however, based on results of most snake species studied (Shine, 1978), we speculate that it is reached at a smaller size.

Hatchling size and the size at sexual maturity provide the two end points for the period of fastest and greatest postembryonic growth. They further provide a means of estimating the history of growth in terms of months and years when the distribution of body size classes is analyzed in a size-month matrix (Figure 4).

Although the adequacy of our sample sizes has forced the combination of sample localities, thereby possibly obscuring discrete size classes or age cohorts, a general trend is indicated in the body size/month matrix (Figure 4). Using this matrix, we speculate that most hatchlings appear in June to September. By nine months, the juveniles have grown to approximately 150–180 mm and to 170–210 mm by first year. At the end of their second year, they range in size between 210–250 mm. A few larger ones have attained a body length indicating sexual maturity; however, the entire cohort probably does not reach sexual maturity until the end of three years of growth. These speculative data suggest an approximate growth rate of 1 mm/week for the first two years. Neither the rate of growth nor the timing of sexual maturity is greatly different from the small

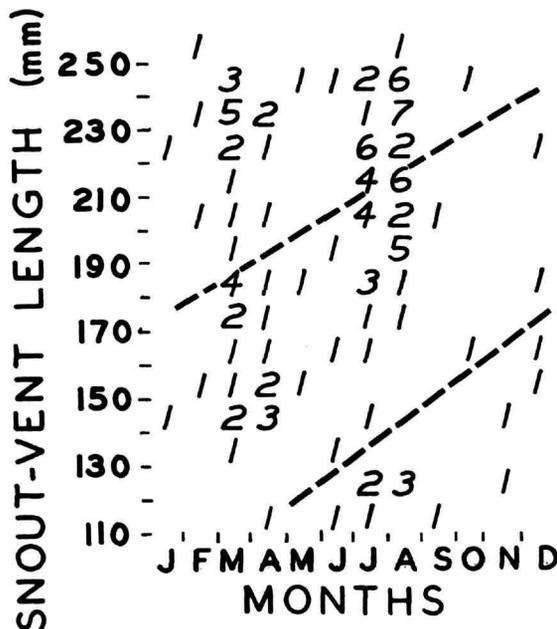


FIGURE 4.—Body size-month matrix for all immature *Coniophanes fissidens*. (Numbers = individuals of a given body length class found in a specific month.)

terrestrial snake *Carphophis vermis* (Figure 5). *Carphophis vermis* is, however, a temperate-zone species and has little or no growth during the winter months, yet it still averages a growth rate of about 1.2 mm/week for the first two years of life (Clark, 1970). There is no reason to assume that growth rate is continuous in tropical snakes, for most live in seasonal environments where parameters other than temperature, e.g., rainfall and prey abundance, fluctuate throughout the year.

SEXUAL DIMORPHISM

BODY AND TAIL LENGTH.—Myers (1969) noted that the ranges in relative tail lengths of females (26–38 percent of total length) and males (33–41 percent) were not greatly different in Panamanian *C. fissidens*. Our samples also demonstrate little difference in male and female tail lengths (Figure 6). However, most overlaps in tail length occur in the immature individuals, i.e., those less than 250 mm snout-vent length. Thus, in *C. fissidens* sexually mature males average longer tails than females, but only slightly longer.

GONAD POSITION.—Since the difference in tail length of males and females has been hypothesized as caudad displacement of the cloaca-vent region in females or the craniad displacement in males, the position of the gonads relative to the vent might also be sexually dimorphic. The relative position of the posterior edge of the left gonad was determined by dividing gonad displacement by snout-vent length. Sexual dimorphism of this displacement

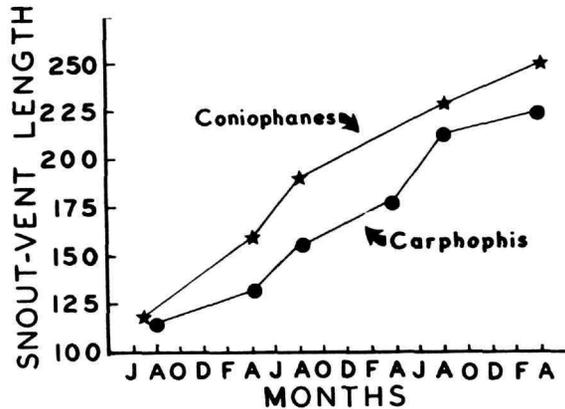


FIGURE 5.—Comparison of growth in *Carphophis vermis* (data from Clark, 1970) and *Coniophanes fissidens*.

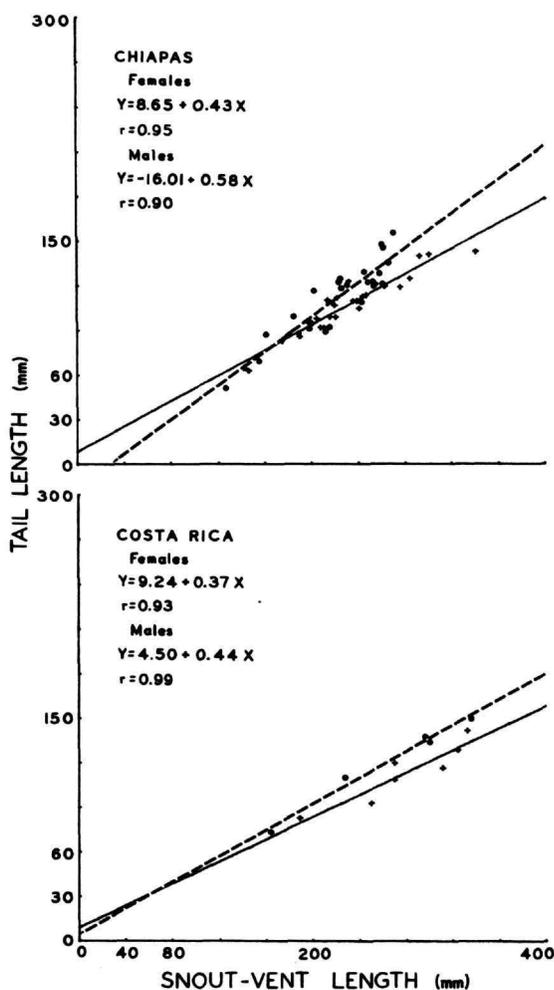


FIGURE 6.—Relationship of tail length to snout-vent length of *Coniophanes* in Chiapas and Costa Rica. (Crosses and solid lines = females; circles and broken lines = males.)

does not exist in any regional samples, e.g., Chiapas sample $F = 0.1$, $df 1/54$. The mean displacement falls between 0.15 and 0.16 for adults of both sexes in the entire *Coniophanes* sample.

TAIL BREAKAGE.—*Coniophanes fissidens* shows a high frequency of broken tails (approximately 30 percent of our sample). The frequency of broken or regenerated tails has been used in lizards to indicate the intensity of predation (Vitt and Ohmart, 1977). It is an oft-stated assumption that female snakes are more secretive than males and are presumably exposed less to predation. The frequency of broken

tails is a potential indicator of differential predation.

Considering snakes of all sizes, only three localities show a Chi-square probability of less than 25 percent, which suggests a differential predation on the sexes. In the Guatemalan Olas de Moca sample, females have more broken tails (8 broken: 11 entire, females; 1:8, males; $\chi^2 = 2.69$). The Guatemalan Porvenir sample also suggests higher predation on females, whereas the adjacent Costa Rican Río Frío samples suggests higher predation on males; however, their sample sizes (8 and 11, respectively) are too small to be more than indicative. At all other localities, males and females share the same proportion of broken and entire tails and presumably the same level of predation.

Considering only the sexually mature snakes (viz., snout-vent length greater than 250 mm), the trends are the same as observed above. The local samples were combined into regional samples (Figure 7) to the Chiapas and Guatemalan samples show no differential predation ($\chi^2 = 0.001$ and 0.341, respectively), whereas the Costa Rican sample indicates a higher frequency of predation on males ($\chi^2 = 2.778$).

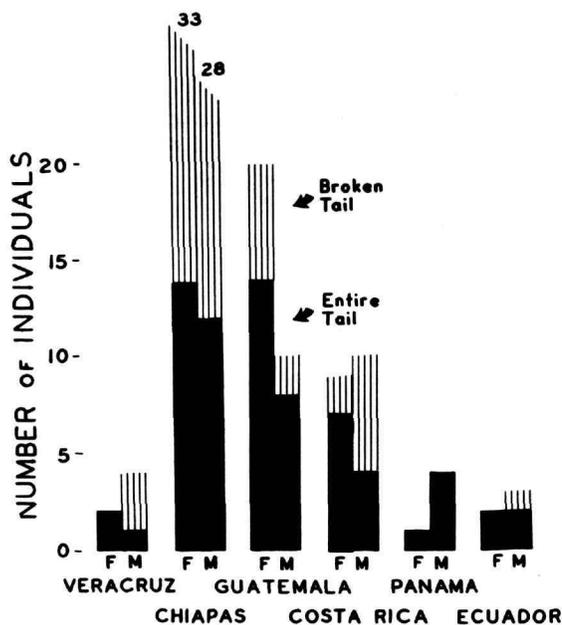


FIGURE 7.—Histogram of the number of broken and entire tails in regional samples of *Coniophanes fissidens*.

In respect to all the samples, it appears that females and males are usually subjected to equal predation pressure.

SEX RATIO

Males did not strongly outnumber females even in the smaller samples. A 1:1 ratio or close approximation thereof (Chi-square less than 0.800) occurs in 11 of the 13 local samples when considering only sexually mature snakes—in contrast to five local samples when snakes of all sizes are included. The majority (5) of the remaining eight samples show a preponderance of males, with females strongly dominant in only the Escuintla and Olan de Moca samples. The regional samples (Figure 7) show the mixed pattern of the local samples, whereas the combination of all the samples clearly demonstrates a 1:1 ratio ($\chi^2 = 0.021$, all sizes; 0.256, mature). In spite of our small sample size and the nonrandomness of museum specimen samples, the evidence suggests an equality of sexes in *Coniophanes fissidens*.

REPRODUCTION

CLUTCH SIZE.—The modal clutch size for oviducal eggs in *C. fissidens* is three. Classes IV and V folli-

cles show the same modal clutch size (Table 2). The range in the entire *Coniophanes* sample is one to seven. The seven eggs occurred in the largest gravid female (snout-vent length 425 mm; Costa Rica) and suggest a correlation between body size and clutch size. A positive correlation does exist (Figure 8), although a larger sample size is required to confirm this correlation. Factors other than body size also appear to affect clutch size, since four females between 275–330 mm snout-vent length possess only one or two eggs. Furthermore the largest female (439 mm) has only a single class V follicle, but five class IV follicles. Presumably these numbers reflect the next two clutches; however, a single clutch of six eggs might occur next.

We assume that each follicle class represents a discrete clutch. The ranges and modes of follicle classes IV and V (Table 2) support this assumption. The number of class III follicles usually equals those of the older follicle classes. A few females do have more III follicles than those of either IV or V so retrogression of III follicles may occur. Retrogression or atrophy of a portion of the class II follicles seems certain, because the number of II follicles is seldom less than double the number of the follicles in classes IV or V and often more. The number of class I follicles usually does not exceed four, prob-

TABLE 2.—Summary of clutch size in local samples of *Coniophanes fissidens* for Classes IV and V follicles and oviducal eggs (N = sample size, R = range, \bar{X} = mean, SD = standard deviation, M = mode)

Locality	Class IV Follicles					Class V Follicles					Oviducal Eggs				
	N	R	\bar{X}	SD	M	N	R	\bar{X}	SD	M	N	R	\bar{X}	SD	M
Mexico, Veracruz															
Catemaco	1		2		2	0					0				
Mexico, Chiapas															
Muste	0					0					2	3-4	3.5	0.71	-
Escuintla	1		3		3	2		3		3	5	1-4	2.4	1.14	2
San Jerónimo	1		1		1	1		5		5	5	1-4	2.4	1.14	2
Total	2	1-3	2.0		-	3	3-5	3.7		3	7	1-4	2.7	1.11	-
Guatemala															
Finca La Paz	1		3		3	3	1-4	3.0	1.73	4	1		3		3
Olan de Moca	6	1-3	2.3	0.82	3	7	1-3	1.7	0.76	-	2	2-3	2.5	0.71	-
Porvenir	1		4		4	0					0				
Total	8	1-4	2.6	0.92	3	10	1-4	2.1	1.20	1	3	2-3	2.7	0.58	3
Costa Rica															
Rio Frio	0					0					2		4		4
Turrialba	3	1-3	2.3	1.15	3	0					1		7		7
Total	3	1-3	2.3	1.15	3	0					3	4-7	5.0	1.73	4
Panama															
Boquete	1		5		5	1		1		1	0				
Ecuador															
Santo Domingo	2	1-3	2.0	1.41	-	0					0				
Grand Total	17	1-5	2.5	1.12	3	14	1-5	2.4	1.34	1	13	1-7	3.2	1.48	3

ably owing to our failure to see and record the tiny follicles.

Livezey and Peckham (1953) reported a female (240 mm snout-vent length) from San Marcos, Guatemala, with two oviducal eggs in May. This body length suggests that this was her first clutch. The eggs were 25.1 and 33.2 mm long. Our sample of oviducal eggs ranged from 14.8 to 31.0 mm long with a mean of 22.4 and standard deviation of 3.66.

REPRODUCTIVE CYCLE.—Our data (Table 3) are too sparse to provide an unequivocal answer to the existence of cyclic or acyclic reproduction in *C. fissidens* populations. All large monthly samples contain both gravid and nongravid individuals, but no locality has adequate representation for all months. Thus, our data can be used to argue for either a cyclic or acyclic pattern. We interpret the data (Table 3) to suggest that Chiapas snakes have an extended reproductive period from May through September (because of hatchlings present in July and gravid females in August); Guatemalan snakes, March through June; and Costa Rican snakes, April through July. Panamanian snakes may lay their eggs at the beginning of the dry season, December through February.

Dipsas catesbyi

NATURAL HISTORY

Dipsas catesbyi is a small (snout-vent length to 590 mm, most adults less than 500 mm), thin-bodied nocturnal snake. It is predominantly a denizen of shrubs and low trees in primary and secondary forests below 1000 m but may descend to the ground occasionally in search of prey. Snails are the major prey, although soft-bodied insects are also eaten (Beebe, 1946).

BODY SIZE

HATCHLINGS.—Only one snake (148 mm snout-vent length) possessed a yolk-sac scar. Peters (1956) found 39 such specimens but did not report their sizes; we were unable to find his original data. Our total *Dipsas* sample contained four individuals 148 mm or smaller. The mean snout-vent length of these four hatchlings is 141.0 mm (standard deviation, ± 10.5 mm; range, 123–148 mm).

GROWTH AND SEXUAL MATURITY.—The smallest female with oviducal eggs is 338 mm snout-vent

TABLE 3.—Monthly distribution of nongravid-mature and gravid females and hatchling *Coniophanes fissidens* by locality (number without suffix = nongravid-mature females; V = Class V follicles of gravid females; 0 = oviducal eggs of gravid females; H = hatchling, individuals less than 123 mm snout-vent length with or without yolk-sac scars; N = sample size)

Locality	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	N
Veracruz	1						1	1			1-H		3
Chiapas				2	1		16 2-V 3-0 2-H	22 4-0 2-H			1		51
Guatemala	1-V		10 8-V 1-0		1 2-V 1-0								24
Costa Rica	1	1	1 2-0			2 1-H	1-0	1				1	10
Panama		1		1 1-H									
Ecuador								1		1			

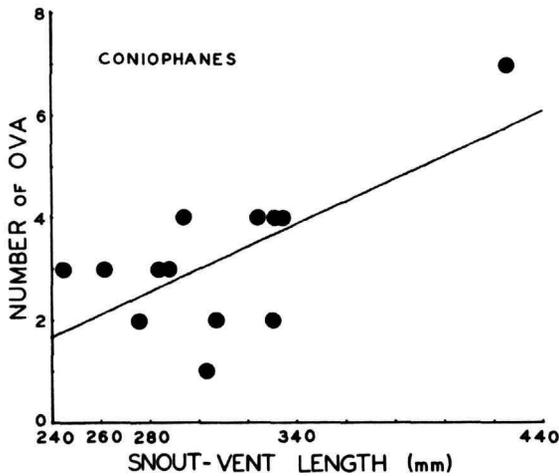


FIGURE 8.—Relationship of clutch size (oviducal eggs) to body size in *Coniophanes fissidens*. ($Y = 3.64 + 0.20X$, $r = 0.66$.)

length, with class V follicles 356 mm. Thus, we assume that most females greater than 335 mm snout-vent length are sexually mature. Presumably males of this length are also sexually mature, for Peters (1956) could not discern any difference in growth rate between the two sexes.

The average snout-vent length of sexually mature females ($N = 51$) is 402.1 ± 48.6 with a range of 338–542 mm. The mean snout-vent length of females (8) with oviducal eggs and class V follicles is slightly smaller, 399.1 ± 47.8 mm (338–492 mm). The sexually mature females from Ecuador (13) have a mean snout-vent length of 401.9 ± 55.8 mm (338–502 mm), from Bolivia (9) 384.4 ± 44.0 mm (340–455), from Iquitos, Peru (19) 414.1 ± 53.0 mm (340–542), and all Peru localities (29) 407.6 ± 46.9 mm (340–542). In spite of the disparity in sample sizes, the mean length of mature females at each locality is approximately 400 mm. Without an unequivocal identifier for the attainment of sexual maturity in males, we hesitate to document mean length of mature males.

Various body size-month matrices were constructed in order to estimate growth rate from hatching to sexual maturity. None showed sufficient segregation of size classes to provide a reasonably accurate estimate. At best, we can guess that sexual maturity is attained in not less than two years. Peters (1956, fig. 16) estimates the age of size classes of *D. catesbyi* from Iquitos, Peru. From these esti-

mates, the snakes do not reach sexual maturity until three and a half years—roughly 1 mm/week.

SEXUAL DIMORPHISM

BODY AND TAIL LENGTH.—Peters (1956) notes that the tail length of females (32–41 percent of body length) was less than that of males (35–43 percent). He further observes that tail length is proportionately greater in larger, hence older, individuals of both sexes. Three of our samples, Pastaza, Bolivia (Figure 9), and Tingo Maria show the

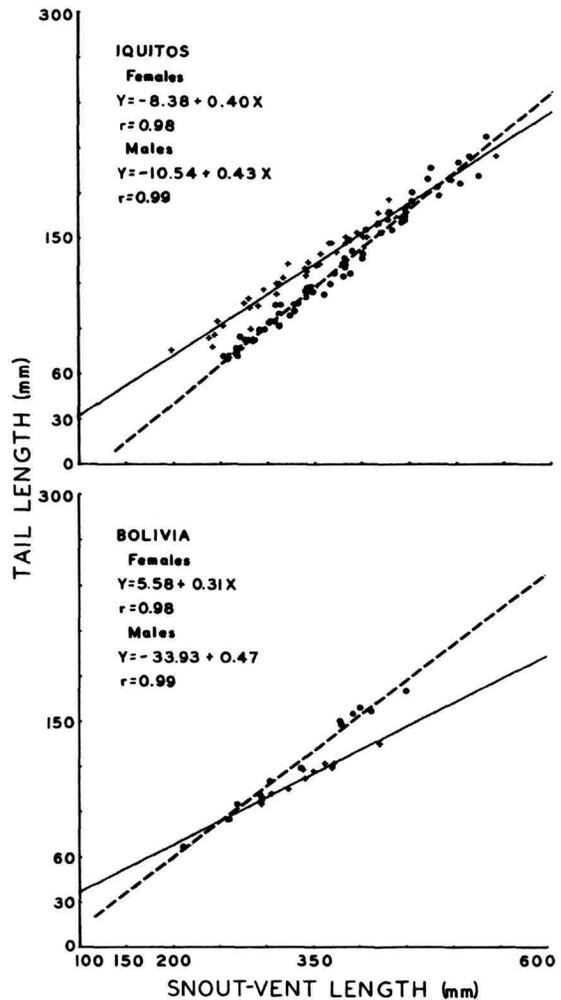


FIGURE 9.—Relationship of tail length to snout-vent length of *Dipsas catesbyi* in Iquitos (Peru) and Bolivia. (Females and males same as in Figure 6.)

tendency for adult males to have longer tails than females. The Napo and Iquitos (Figure 9) samples, however, show a strikingly different trend. Juvenile and most adult males have shorter tails than females and only at body lengths greater than 400 mm do tail lengths of females and males overlap.

GONAD POSITION.—The relative position of the gonads is identical in both sexes. Comparison of the sexes by a one-way analysis of variance yields non-significant F values, e.g., 6.79, df 1/101 for Peruvian sample to 0.21 df 1/12 for Napo sample. The posterior edge of the left gonad lies 14 to 16 percent of snout-vent length from the vent.

TAIL BREAKAGE.—The frequency of broken tails is low (ca. 1 percent) in the entire *Dipsas catesbyi* sample. Most samples have no snakes with broken tails. Only the Bolivian sample differs strikingly with a 10 percent incidence of broken tails, which was evenly distributed between the sexes ($\chi^2=0.006$).

SEX RATIO

Combining all samples, the 1:1 ratio is a perfect fit (150 females: 150 males), but including only sexually mature snakes (83:109; $\chi^2=1.51$), males dominate. At a local level, the Guyana (all sizes and mature), Santa Cecilia (all sizes), Río Bobonaza (all sizes), and Iquitos (all sizes) samples deviate significantly ($\chi^2 \geq 1.32$) from a 1:1 ratio and all except Iquitos with males most numerous. Thus, the majority of the samples indicates an equality of sexes in *Dipsas catesbyi*.

REPRODUCTION

CLUTCH SIZE.—The modal clutch size for oviducal eggs in *D. catesbyi* is two. Classes IV and V follicles show a modal clutch of three (Table 4). The range for the entire *Dipsas* sample is one to four eggs. Clutches of four occur only in the Tingo Maria and Alto Río samples and only as class IV follicles. The potential for a clutch of four eggs may exist only in these populations or may indicate atrophy of follicles continuing into class V follicle development. Within classes II and III follicles, potential clutch size ranges from 2–23 with 7–9 follicles dominating in class II and 4–6 follicles dominating in class III. As an aside, the difference in number of gravid females in our examination of the Bassler

Iquitos collection and that of Fitch (1970) results from his inclusion of any enlarged yolk follicles (Fitch, pers. comm.), some of which fall in our classes III and IV groupings.

With such small clutch size and our limited samples, regional differences in clutch size are not apparent. In spite of the positive regression of clutch size on body size (Figure 10), we doubt that an actual correlation exists, for the slope of the line is nearly zero. The production of a clutch of one, two, or three eggs may be more dependent upon a female's physical well-being than on her actual body size.

Dixon and Soini (1977) reported the capture of three females, each with two oviducal eggs, from Iquitos, Peru. Oviducal egg size in our sample ranges from 21.5 to 34.1 mm long with a mean of 27.7 ± 4.1 mm.

REPRODUCTIVE CYCLE.—The *Dipsas* data, like that for *Coniophanes*, is inadequate to draw definite conclusions on the cyclic-acyclic nature of reproduction. Our data (Table 5) does show that the Ecuadorian population lays eggs from April to June and the Peruvian population in June. February reproduction is implied for the Bolivian population, since hatchlings appear in May. Reproduction may occur at other times but cannot be discerned from our data. The addition of Dixon and Soini's (1977) observations of females with oviducal eggs in February, September, and December to our April and June records strongly indicates that the Iquitos population reproduces continually.

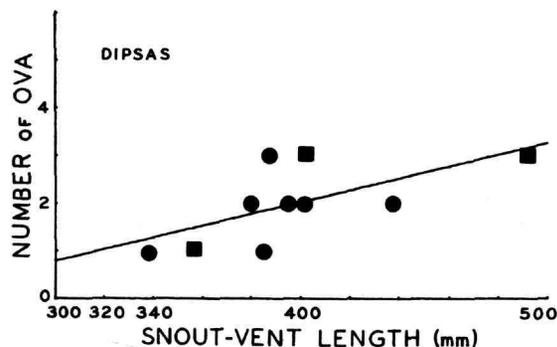


FIGURE 10.—Relationship of clutch size to body size in *Dipsas catesbyi*. (Circles = oviducal eggs; squares = class V follicles; $Y = -2.18 + 0.01X$, $r = 0.44$, for only oviducal eggs.)

TABLE 4.—Summary of clutch size in local samples of *Dipsas catesbyi* (abbreviations explained in Table 2)

Locality	Class IV Follicles					Class V Follicles					Oviducal Eggs				
	N	R	\bar{X}	SD	M	N	R	\bar{X}	SD	M	N	R	\bar{X}	SD	M
Ecuador															
Santa Cecilia	1		2		2	0					2	1			1
Limoncocha	1		2		2	0					0				0
Alto Río	1		4		4	0					0				0
Total	3		2.7	1.15	2	0					2	1			1
Bolivia															
Buena Vista	5	2-4	2.8	0.84	-	0					0				0
Peru															
Iquitos	6	1-3	2.2	0.75	3	3	1-3	2.3	1.15	3	4	2-3	2.2	0.50	2
Pebas	1		3		3	0					1	2			2
Tingo María	4	3-4	3.5	0.58	-	0					0				0
Total	11	1-4	2.7	0.90	3	3	1-3	2.3	1.15	3	5	2-3	2.2	0.45	2
Grand Total	19	1-4	2.7	0.87	-	3	1-3	2.3	1.15	3	7	1-3	1.9	0.69	2

TABLE 5.—Monthly distribution of nongravid-mature and gravid females and hatchling *Dipsas catesbyi* (abbreviations same as Table 3 except hatchling is 148 mm snout-vent length with yolk-sac scar)

Locality	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	N
Ecuador				6 1-0		1 1-0	1	1					11
Bolivia	2		1	1	1 1-H	1						1	7
Peru			1			1-0	1	3		2	1		9

Imantodes cenchoa

NATURAL HISTORY

Imantodes cenchoa is a slender, elongate (snout-vent length to 901 mm but adults usually less than 800 mm), arboreal snake. It occurs in primary and secondary forests mainly below 1500 m but up to 2000 m. Frequenting low vegetation, it is commonly found in bromeliads (Stuart, 1948; Taylor, 1951) and coffee trees (Slevin, 1939; Landy, et al., 1966) during the day. In a simulated natural environment, captive specimens spent 90 percent of daylight hours coiled in bromeliads (Henderson and Nickerson, 1976). One adaption for arboreal living, an enlarged middorsal scale row, provides rigidity while spanning gaps between branches (Schmidt and Inger, 1957) as much as one-half its body length

(Gans, 1974). It forages for food at night, often feeding on sleeping anoles (Henderson and Nickerson, 1976). Small arboreal lizards (mainly *Anolis* sp.) appear to be the principal prey (Henderson and Nickerson, 1976; Landy, et al., 1966; Stuart, 1948, 1958; Wehekind, 1955), although reptile eggs have also been reported as stomach contents (Landy, et al., 1966). Beebe (1946) reported an individual pursuing a tree frog (*Oloolygon rubra*). In captivity, frogs (*Colostethus* and *Eleutherodactylus*) are accepted as food (Test, et al., 1966).

BODY SIZE

HATCHLINGS.—The largest snake with a yolk-sac scar was 327 mm (snout-vent length). Out of 17 individuals of this length or less, five (232, 255, 259,

272, and 327 mm long) possessed yolk-sac scars. The average snout-vent length of hatchlings is 279.7 ± 27.2 mm; range 232–327.

GROWTH AND SEXUAL MATURITY.—Sexually mature females of *Imantodes* (all localities) had a mean snout-vent length of 715.9 ± 67.7 mm and a range of 621–901 mm ($N = 33$). Females (5) with oviducal ova and class V follicles have an average snout-vent length of 789.4 ± 96.7 mm (637–901). The sexually mature females from Chiapas (2) have a mean length of 708.5 (693–724), from Honduras (3) 640.7 ± 21.7 mm (621–664), from Costa Rica (1) 639.0 mm, from Panama (7) 734.3 ± 83.4 mm (662–901), from Ecuador (15) 742.5 ± 59.6 mm (641–818), and from Peru (5) 674.0 ± 47.6 mm (628–732). From these data, we infer that female *Imantodes* reach sexual maturity at about 620 mm. Again, as in both *Coniophanes* and *Dipsas*, we can only speculate that males mature at about the same size or less.

A size-month matrix for *Imantodes* (Figure 11) exhibits weak segregation of size classes. We propose that most hatchlings appear from March through August. After one year, they have grown to an average of 450 mm, and after two years of growth, their average body length approaches 640 mm. This suggests that most of the snakes have attained sexual maturity by the end of two years. From these speculations, an approximate growth rate of 3.5 mm/week (first two years) can be estimated.

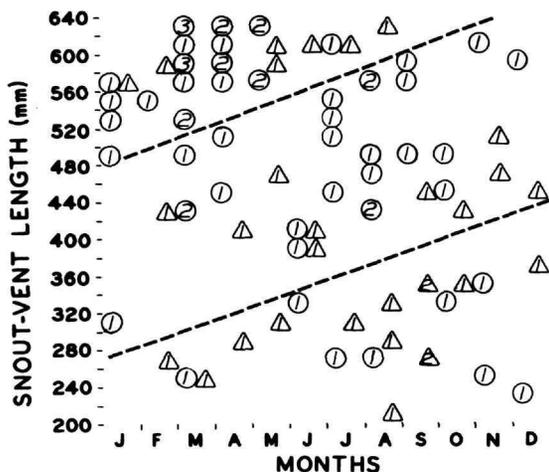


FIGURE 11.—Body size-month matrix for immature *Imantodes cenchoa*. (Circles = specimens from Mexico to Panama; triangles = specimens from Ecuador and Peru.)

SEXUAL DIMORPHISM

BODY AND TAIL LENGTH.—In the more northern samples (Chiapas; Yoro, Honduras; Costa Rica) adult males on the average have longer tails than equal-sized females (Figure 12) but only slightly so. Snakes from southern localities (Panama, Ecuador, and Peru) do not show sexual dimorphism in tail length (Figure 12). The Ulúa River, Honduras, sample ($N = 20$) females possess longer tails.

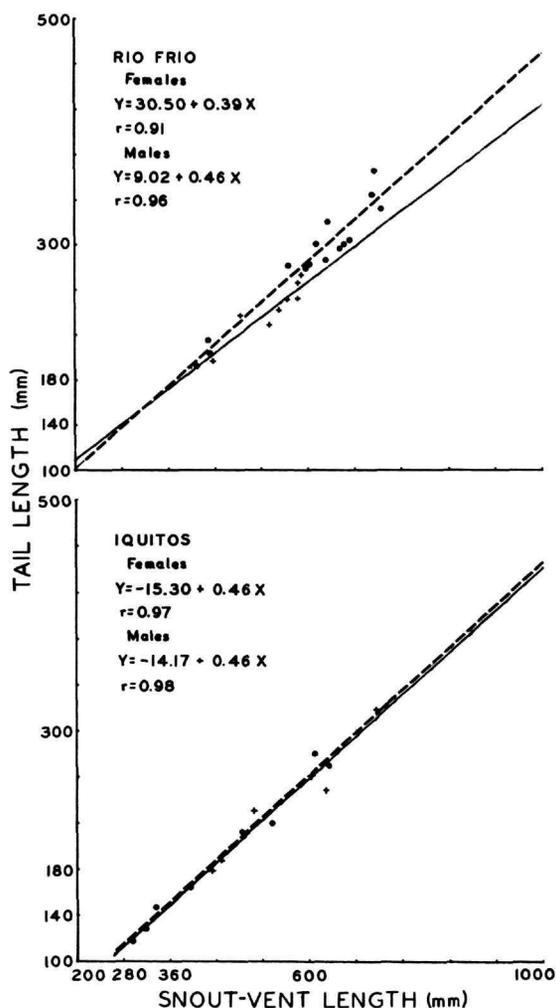


FIGURE 12.—Relationship of tail length to snout-vent length of *Imantodes cenchoa* in Río Frio (Costa Rica) and Iquitos (Peru).

GONAD POSITION.—The relative position of the gonads in *Imantodes* shows little sexual dimorphism. F values show borderline significance for our two larger samples; 8.02, df 1/27 for Ecuador (Napó), and 1.78, df 1/13 for Peru (Loreto). The gonads are situated 6 to 8 percent of snout-vent length from the vent.

TAIL BREAKAGE.—Tail break frequency in *Imantodes* is low but substantial. Combining localities, the incidence is 6 percent in females and 10 percent in males of all sizes, 9 percent in mature females, and 14 percent in mature males. Males of all sizes have a higher incidence of tail breaks in five of nine local samples, females in only one of nine; mature males have a higher incidence of breaks in four of the nine samples, females in two of nine. These differences are not significant ($\chi^2 = 0.95$ for all sizes of all localities; $\chi^2 = 0.40$ for adults of all localities); hence there is no evidence of differential predation of the sexes.

SEX RATIO

In six of the nine local samples for all sizes, males outnumber females ($\chi^2 = 3.64$ for combined nine samples). The same trend is observed when considering only mature snakes ($\chi^2 = 3.52$). The Panamanian sample differs in having a preponderance of females (13 females: 4 males, juveniles and adults; 7:2, only adults). Only the Chiapas and Río Bobonaza samples show an equality of sexes.

REPRODUCTION

CLUTCH SIZE.—The modal clutch size for oviducal eggs in *I. cenchoa* is two. Classes IV and V follicles show a modal clutch size of three in the two northern samples (Chiapas and Honduras), whereas the three southern samples (Ecuador and Peru) have modal sizes of two (Table 6). The range for all samples combined is one to three. The single instance of three oviducal eggs occurred in the largest female (snout-vent length 901 mm; Panama). Despite the inadequate sample size, this may suggest, as in *Coniophanes*, a positive correlation between body size and clutch size (Figure 13), although available data provide a regression slope of nearly zero. Potential clutch size in classes II and III ranges from 1–14 with 4–6 occurring most frequently in II and 1–3 most often in III.

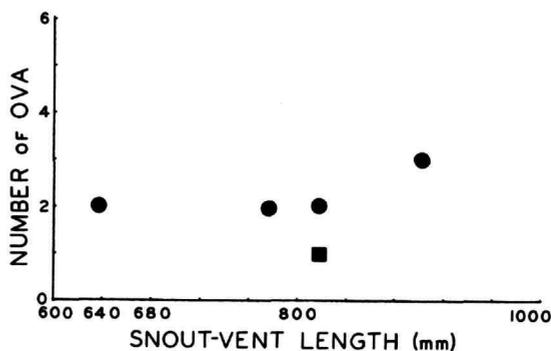


FIGURE 13.—Relationship of clutch size to body size in *Imantodes cenchoa*. (Circles = oviducal eggs; square = class V follicles; $Y = 0.30 + 0.03X$, $r = 0.72$, for only oviducal eggs.)

Fitch (1970) reports a gravid female from Iquitos, Peru, containing two oviducal eggs. Egg size (oviducal) in our sample (9) ranges from 21.2 to 37.2 mm long, with a mean of 30.7 ± 5.13 mm.

REPRODUCTIVE CYCLE.—In the Ecuadorian and Peruvian samples (Figure 11), the occurrence of hatchlings throughout the year probably indicates continuous reproduction. Although the northern sample (Mexico to Panama) collectively shows similar trends, individual localities lack a sufficient number of hatchlings to draw conclusions (Table 7). Owing to the seasonal nature of rainfall at some of the sample localities, e.g., Panama Canal Zone, a seasonal reproductive cycle might be found in these populations. The presence of gravid females during late April and mid-June in Guatemala (Stuart, 1948) and of hatchlings during July and August in adjoining Chiapas, Mexico, indicates an extended reproductive season. It correlates well with the long wet season of that area, May through November (Stuart, 1948).

Discussion and Summary

Our two primary questions on reproduction—regional variation in clutch size and seasonality of reproduction—remain inadequately answered. The opportunistic nature of museum collections does not currently permit us to obtain large and year-round samples from single localities. A few old and large collections of single snake species are available, but all too often they lack collecting dates or the viscera have been removed. Surprisingly and dis-

TABLE 6.—Summary of clutch size in local samples of *Imantodes cenchoa* (abbreviations explained in Table 2)

Locality	Class IV Follicles					Class V Follicles					Oviducal Eggs				
	N	R	\bar{X}	SD	M	N	R	\bar{X}	SD	M	N	R	\bar{X}	SD	M
Mexico															
Escuintla	2		3		3	0					0				
Honduras															
Ulua R.	1		3		3	0					1		2		2
Portillo	2	1-3	2.0	1.41	-	0					0				
Total	3	1-3	2.3	1.15	3	0					1		2		2
Panama															
Canal Zone	0					0					1		3		3
Ecuador															
Santa Cecilia	4	1-2	1.5	0.58	-	1		1		1	1		2		2
Limoncocha	1		2		2	0					0				
Rio Bobonaza	1		1		1	0					1		2		2
Total	6	1-2	1.5	0.55	-	1		1		1	2		2		2
Peru															
Iquitos	1		2		2	0									
Grand Total	12	1-3	2.0	0.85	2	1		1		1	4	2-3	2.3	0.50	2

TABLE 7.—Monthly distribution of non gravid-mature and gravid females and hatchling *Imantodes cenchoa* (abbreviations same as Table 3 except hatchlings are less than 327 mm snout-vent length with or without yolk-sac scar)

Locality	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	N
Mexico							6 2-H	1 1-H		2			9
Honduras	1		1-0 1-H	1							1-H		3
Costa Rica		1	2		3			2				1 1-H	9
Panama	1-H		1	1		1		3				1	7
Ecuador	2 1-0		1	1	2	1	2 1-0 1-H	1	3		1 1-V		17
Peru		1		1 1-H	1		1	1 1-H				1	6

appointingly, we have discovered that, all too frequently, snakes from recent collections have been poorly prepared and preserved and not uncommonly held in captivity before being preserved. Both practices lead to inaccuracies in the initial data gathering and the final interpretations. In spite of these difficulties, museum collections with or without recently collected specimens can con-

tribute to an improved understanding of snake reproduction.

Coniophanes fissidens, *D. catesbyi*, and *I. cenchoa* are small or, at most, moderate-sized snakes. Their modal clutch sizes of three, two, and two eggs, respectively, are a reflection of their short and/or narrow body cavities. Perhaps the possession of small clutch sizes makes them poor candidates for

demonstrating regional variation in clutch size. We suspect, however, that life history adaptations, such as growth rate, size at sexual maturity, and average adult life span, will produce locally different reproductive patterns. Differences in clutch sizes will be as apparent in "small clutch" species as in "large clutch" species owing to the lower variance of "small clutch" species. We think our inability to recognize the presence or absence of regional variation results from our small sample sizes.

Coniophanes fissidens is the smallest of the three species examined, yet it has the largest clutch. This is accomplished by having the shortest egg length, mean of 22.4 mm. In *D. catesbyi* and *I. cenchoa*, mean egg length is 27.7 and 30.7 mm, respectively; egg length increases directly with body length. This suggested trend is provocative. How closely are egg length and volume associated with body size, intra- and interspecifically? Presumably egg (fertile) size is relatively constant within a species but increases with increasing body size in species comparisons. The larger egg will result in a larger hatchling, whose chance of survival is presumably enhanced by its larger size. Nonetheless, egg size must have an upper limit (plateau) where the advantages of large hatchling size are outweighed by the female's need to limit energy expenditure in egg production and/or to invest energy in egg number rather than size. Fitch's data (1970, figs. 12, 14) show that few subtropical or tropical snakes invest heavily in large clutch sizes (80 percent of snakes with clutch size of 12 or less) no matter what the adult body size of the species. The indication is that there is selective pressure for larger eggs or fewer eggs per clutch but more clutches per year.

Of the three species examined, only the data for the Peruvian *D. catesbyi* and Ecuadorian/Peruvian *I. cenchoa* are sufficient to indicate continuous or aseasonal reproduction. At the other localities for these two species and all localities for *C. fissidens*, the data are insufficient to discriminate between continuous and seasonal reproduction; however, we intuit the Central American samples, particularly the Mexican ones, to have seasonal reproduction for *Coniophanes* and *Imantodes*.

Our bias is to assume cyclic or seasonal reproductive patterns in subtropical and tropical snakes unless data indicate otherwise. Fitch (1970) and other biologists have the opposite bias. No matter what the researcher's preference, we must all be

aware of the potential diversity in reproductive cycles at a single site and the potential of a species for modifying its pattern at different locations. The first point is demonstrated by the recognition of six reproductive patterns in Cambodian snakes (Saint Girons and Pfeffer, 1971): (1) polyestrous with aseasonal reproduction, (2) polyestrous with midwet season reproduction, (3) monoestrous with spring reproduction, (4) monoestrous with early summer reproduction, (5) monoestrous with early fall reproduction, and (6) double period of reproduction (data can also be interpreted as monoestrous with winter or dry season reproduction). The snakes of the Iquitos region, Peru, show both continuous and seasonal reproduction (Dixon and Soini, 1977, table 1); data are insufficient for finer subdivisions. The modification of scheduling pattern by a tropical colubrid at different localities is indicated by our data and those of others, although as yet not convincingly so.

Neill (1962) postulated seasonal reproduction for Belize snakes by estimating the age of posthatchlings on the basis of yolk-sac scar condition. His evidence suggested an August to October period for hatching and birth and a May to July period for fertilization and egg laying. The synchronization mechanism was assumed to be the cooler temperatures of December through February and the resulting period of inactivity. Henderson and Hoevers (1977) agreed with the reproductive schedule proposed by Neill but disagreed with the mechanism and its periodicity. They suggested the February to May dry season as the mechanism. Unwittingly, Henderson had presented data earlier (1974, table 1) that demonstrates that the period of inactivity is December through March, but he did not analyze these data. A comparison of the growth rates of Belize *Oxybelis aeneus* shows that the rate is 0.12 ± 0.15 mm/day during the dry season (December to March) and 0.62 ± 0.56 mm/day during the wet season (April to November)—a strong indication of reduced activity during the dry season.

The annual growth rate for *Oxybelis aeneus* (calculated from Henderson, 1974, table 1) is 0.87 ± 0.47 and 1.18 ± 0.75 mm/day in immature (less than 700 mm snout-vent length) females and males, respectively. These rates are considerably faster than our estimates of 1 mm/week for *Coniophanes fissidens*, 1 mm/week *Dipsas catesbyi*, and 3.5 mm/week *Imantodes cenchoa*. With the possible excep-

tion of *I. cenchoa*, our estimates of growth may be underestimates, for aside from *Carphophis vermis* (Clark, 1970), other snakes have a growth rate greater than 0.5 mm/day, e.g., *Tropidoclonion* (Blanchard and Force, 1930), Australian elapids (Shine, 1978).

Underestimates of growth will result in overestimates of age at sexual maturity. Our estimates are two to three years for these tropical snakes. Estimates for temperate-zone colubrids are usually no longer than these and often shorter. Three Australian elapids, *Unechis gouldii*, *Hemiaspis daemeli*,

and *H. signata*, reach sexual maturity in the surprisingly short time of one year (Shine, 1978). It seems doubtful that any tropical species will mature faster than these temperate-zone species.

The available evidence on reproduction in tropical snakes suggests that they are not very different from their temperate-zone conspecifics and congeners. Only the possibility of continuous reproduction and two or more clutches per year is available to tropical colubrids, but not all tropical localities will permit even these reproductive adaptations.

Appendix

Specimens Examined

The following list contains no museum catalog numbers, only the abbreviation of the museum followed by the numbers of specimens examined. The specimens were borrowed from the American Museum of Natural History (AMNH), Auburn University Museum (AUM), California Academy of Science (CAS), Carnegie Museum (CM), Costa Rican Expedition–University of Southern California (CRE), Field Museum of Natural History (FMNH), University of Kansas Museum of Natural History (KU), Natural History Museum of Los Angeles County (LACM), Museum of Comparative Zoology (MCZ), Texas Cooperative Wildlife Collection (TCWC), Florida State Museum (UF), University of Illinois Museum of Natural History (UIMNH), University of Michigan Museum of Zoology (UMMZ), and National Museum of Natural History (USNM, referring to the former United States National Museum).

The number preceding each locality is used to identify that locality on the species distribution maps (Figures 1, 2, and 3). The localities are listed from north to south for convenience, and where possible, the elevation of the locality is included.

Coniophanes fissidens

N = 343

Mexico

1. Veracruz: Cuautlapan, 18°52'N, 97°02'W
FMNH (5), UMMZ (1), USNM (3)
2. Veracruz: Catemaco, 18°25'N, 95°07'W, 360 m
TCWC (4), UMMZ (1)
3. Chiapas: Muste, Mpio, Motozintla, 15°22'N, 92°14'W,
500 m
CM (27)
4. Chiapas: Escuintla, 15°20'N, 92°38'W, <100 m
UMMZ (20)
5. Chiapas: La Esperanza (probably near Escuintla)
USNM (39)

6. Chiapas: Unión Juárez, 15°04'N, 92°05'W, 1300 m
UIMNH (1)
6. Chiapas: San Jerónimo, 15°03'N, 92°08'W, 600–800 m
UIMNH (62)

Guatemala

7. San Marcos: Finca La Paz, 14°49'N, 91°50'W, 1500–
2000 m
UMMZ (12)
8. Sololá: Olas de Mocá, 14°32'N, 91°15'W, 500–1000 m
FMNH (29)
9. Chiquimula: Porvenir, 14°29'N, 89°21'W, ca. 1100 m
FMNH (9)
10. Suchitepéquez, 14°25'N, 91°20'W, 200–500 m
UIMNH (90)

Costa Rica

11. Heredia: Río Frio/La Selva, 10°20'N, 83°53'W, ca. 100
m
CRE (7), UF (5)
12. Cartago: Turrialba, 9°54'N, 83°41'W, 500–1000 m
CRE (8), KU (5)

Panama

13. Chiriquí Boquete, 8°47'N, 82°26'W, 1000–1500 m
CAS (2), UMMZ (5)
14. Chiriquí: Progreso, 8°27'N, 82°50'W, <100 m
MCZ (1), UMMZ (2)

Ecuador

15. Pichincha: Santa Domingo de los Colorados, 0°15'S,
79°09'W, 560 m
CAS (3), UMMZ (1), USNM (1)

Dipsas catesbyi

N = 371

Guyana

1. Demerara: Demerara River 6°48'N 58°10'W, <100 m
UMMZ (5)

Ecuador

2. Napo: Santa Cecilia, 0°03'N, 76°58'W, 340 m
AUM (4), KU (21)
3. Napo: Limoncocha, 0°24'S, 76°37'W, 260 m
LACM (1), UIMNH (5)

4. Pastaza: Río Bobonaza, 2°36'S, 76°38'W, 250 m
USNM (20)

Brazil

5. Para: Belem, 1°27'S, 48°29'W, 100 m
KU (8)

Peru

6. Loreto: Alto Río, Curaray, 2°22'S, 74°15'W, 100 m
USNM (17)
7. Loreto: Pebas, 3°20'S, 71°49'W, 100 m
CAS (3), FMNH (8)
8. Loreto: Iquitos, 3°46'S, 73°15'W, 100 m
AMNH (205), TCWC (18)
9. Huánuco: Tingo María, 9°10'S, 76°00'W, 670 m
USNM (23)

Bolivia

10. Santa Cruz: Buenavista, 17°27'S, 63°40'W, 500 m
FMNH (10), UMMZ (23)

Imantodes cenchoa

N = 227

Mexico

1. Chiapas: Escuintla, 15°20'N, 92°38'W, < 100 m
LACM (5), UMMZ (17), USNM (8)

Honduras

2. Atlántida: Río Ulúa, 15°53'N, 87°44'W, 100 m
MCZ (16), UMMZ (5)
3. Yoro: Portillo Grande, 15°05'N, 87°15'W
FMNH (29)

Costa Rica

4. Heredia: Río Frío/La Selva, 10°20'N, 83°53'W, 100 m
CRE (4), UF (23)

Panama

5. Canal Zone: a composite, 9°10'N, 79°45'W, 100 m
FMNH (4), UF (9), UMMZ (5)

Ecuador

6. Napo: Santa Cecilia, 0°03'N, 76°58'W, 340 m
AUM (1), KU (29), UMMZ (1)
7. Napo: Limoncocha, 0°24'S, 76°37'W, 260 m
AUM (1), LACM (5), UIMNH (8)
8. Pastaza: Río Bobonaza, 2°36'S, 76°38'W, 250 m
USNM (6)

Peru

9. Loreto: Iquitos, 3°46'S, 73°15'W, 100 m
AMNH (35), TCWC (16)

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