

# Female Reproductive Cycles of Five Species of Snakes (Reptilia: Colubridae) from the Yucatan Peninsula, Mexico<sup>1</sup>

Ellen J. Censky and C. J. McCoy

Section of Amphibians and Reptiles, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213, U.S.A.

## ABSTRACT

Female reproductive cycles were studied in five species of colubrid snakes from the Yucatan Peninsula, Mexico (*Dryadophis melanolomus*, *Elaphe triaspis*, *Leptophis mexicanus*, *Oxybelis aeneus*, and *Stenorrhina freminvillii*). *Leptophis mexicanus* and *Oxybelis aeneus* reproduce annually during the rainy season (March–October and March–August, respectively). *Dryadophis melanolomus* also reproduces during the rainy season, but has a biennial cycle. *Stenorrhina freminvillii* lays two clutches of eggs annually during the dry season (November–April). *Elaphe triaspis* appears to have aseasonal (continuous) reproduction. Clutch size varies from  $\bar{x} = 3.1$  eggs (*D. melanolomus*) to  $\bar{x} = 11.6$  eggs (*S. freminvillii*). The timing of reproductive cycles of these species is compared with the climatic regime of the Yucatan Peninsula, and the significance of adaptation of reproductive cycles to geographic distribution and dispersal is discussed.

## RESUMEN

Se estudiaron los ciclos reproductivos en hembras de cinco especies de serpientes (Colubridae) de la Península de Yucatán, México (*Dryadophis melanolomus*, *Elaphe triaspis*, *Leptophis mexicanus*, *Oxybelis aeneus*, *Stenorrhina freminvillii*). *Leptophis mexicanus* y *Oxybelis aeneus* se reproducen durante la época de lluvia (Marzo–Octubre y Marzo–Agosto, respectivamente). *Dryadophis melanolomus* también se reproduce durante la época de lluvia, pero su ciclo es bienal. *Stenorrhina freminvillii* tiene dos puestas por año durante la época seca (Noviembre–Abril). *Elaphe triaspis* aparenta tener una reproducción sin ciclos (continua). El número de huevos varía de un promedio de 3.1 por puesta (*D. melanolomus*) a 11.6 (*S. freminvillii*). Se compara la relación de los ciclos reproductivos de estas especies con los ciclos climatológicos de la Península de Yucatán, y se discute la importancia de las adaptaciones de los ciclos reproductivos con la distribución geográfica y la dispersión de las especies.

SNAKE SPECIES THAT OCCUR in temperate zone climates have relatively uniform reproductive cycles that are constrained by seasonal temperature cycles (Shine 1985). Typically in these species ovulation occurs in late spring, eggs are laid in early summer, and young hatch or are born in late summer. In tropical climates, however, where seasonal fluctuations in temperature are minimal, no such constraint exists. Conjecture about the timing of reproductive cycles in tropical reptiles has been divided between aseasonal (continuous) reproduction (Fitch 1970) and cyclical reproduction constrained in some way by precipitation cycles (Fitch 1982). Actually, neither of these hypotheses appears to be universally true, and identifying the causes of cyclical reproductive patterns in tropical species remains a challenge to students of reptile biology (Vitt 1983b).

To approach this problem of cyclical patterns in tropical snake reproduction, with the goal of identifying adaptive modes, we studied five species from the northern Yucatan Peninsula, Mexico.

## MATERIALS AND METHODS

Five species of colubrids were studied: *Oxybelis aeneus*, *Leptophis mexicanus*, *Dryadophis melanolomus*, *Stenorrhina*

*freminvillii*, and *Elaphe triaspis*. These species were selected for study solely because they were the most numerous in our collection. About 90 percent of the specimens examined were collected at Piste, Yucatan, and Pueblo Nuevo X-Can, Quintana Roo, in the northern Yucatan Peninsula, over a period of one year (1967–1968). The remaining specimens were collected at various localities within 50 km of Piste, Yucatan.

Vegetation in the northern Yucatan Peninsula has been characterized as deciduous thorn forest (Paynter 1955). The climate is thoroughly tropical, with only slightly fluctuating high temperatures, and extremely seasonal rainfall (Lee 1980). Precipitation data from Valladolid, Yucatan, which lies between the principal collecting sites, shows that the months between November and April are very dry, with average monthly rainfall of 3.3 cm. Precipitation increases sharply in May (12.4 cm) to peak in June at 13.7 cm. The rainy season continues through July and August, and rainfall peaks again in September (16.5 cm). The month of October is moderately dry with 12.1 cm average precipitation (Contreras Arias 1959).

The five species studied are all oviparous. Measurements taken were snout–vent length (SVL), the number and diameter ( $\pm 0.1$  mm) of enlarged ovarian follicles, and number and dimensions (length and diameter) of oviducal eggs. The condition of the oviduct was noted in

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TABLE 1. Ovarian follicle and oviducal egg size ranges (in mm) and size classes in five species of colubrid snakes from the Yucatan Peninsula, Mexico.

Species	Class I	Class II	Class III	Class IV	Class V	Eggs
<i>O. aeneus</i>	<1.0	1.1–3.0	3.1–10.0	10.1–24.9	>25.0	>29.9
<i>L. mexicanus</i>	<1.0	1.1–3.0	3.1–8.0	8.1–33.3	>33.4	>37.0
<i>D. melanolomus</i>	<1.0	1.1–3.0	3.1–8.0	8.1–37.8	>37.9	>42.0
<i>S. freminivillii</i>	<1.0	1.1–3.0	3.1–7.0	7.1–11.9	>12.0	>14.9
<i>E. triaspis</i>	<1.0	1.1–3.0	3.1–8.0	8.1–33.5	>33.6	>35.0

nongravid females, as a stretched and flaccid oviduct indicates recent oviposition. We interpret stretched oviducts as marking a date of oviposition. The length of time that the oviducts remain flaccid after oviposition is not known, but our data indicate it must be less than a month in the species studied. Ovarian follicles were classified using a system similar to that of Zug *et al.* (1979). Five classes of follicles were recognized (Table 1). Juveniles contained only Class I follicles. Class I and II follicles were present in reproductively quiescent females. Class III, IV, and V follicles were found in reproductively active females. Clutch size was determined by counting either Class IV and V follicles or oviducal eggs. No individual female had more than one clutch of developing follicles, or a combination of enlarged ovarian follicles and oviducal eggs. Thus each symbol in Figures 1A, 2A, 3, 4A, and 5A represents the complete reproductive condition of one female.

Specimens examined are in the collections of Carnegie Museum of Natural History, the University of Colorado Museum, or the Field Museum of Natural History.

## RESULTS

*Oxybelis aeneus* is a medium-sized, very slender arboreal snake. The SVL of females we examined range from 290 mm to 896 mm. Males are smaller, with SVLs as large as 776 mm. The smallest female with enlarging follicles or oviducal eggs measured 650 mm SVL. Therefore, we considered all females 650 mm or larger SVL (88 of 107 females in the sample) to be adult.

Reproductive activity of female *O. aeneus* is compressed into a period of 12–13 wk (Fig. 1A). Vitellogenesis begins in March, and follicular growth is rapid. By May follicles reached a size of 10.0 mm (Class IV). Follicles were ovulated at a minimum size of 29.9 mm, between June and August. Class III follicles outnumbered Class IV and V follicles, indicating that some ovarian follicles underwent atresia. The presence of maximum-sized oviducal eggs in July samples and observations of individuals with stretched oviducts as late as September indicate a laying season of about 2.5 mo during the height of the rainy season. Females exhibited complete reproductive quiescence after laying for a period extending from July, August, or September nearly to the end of the following dry season.

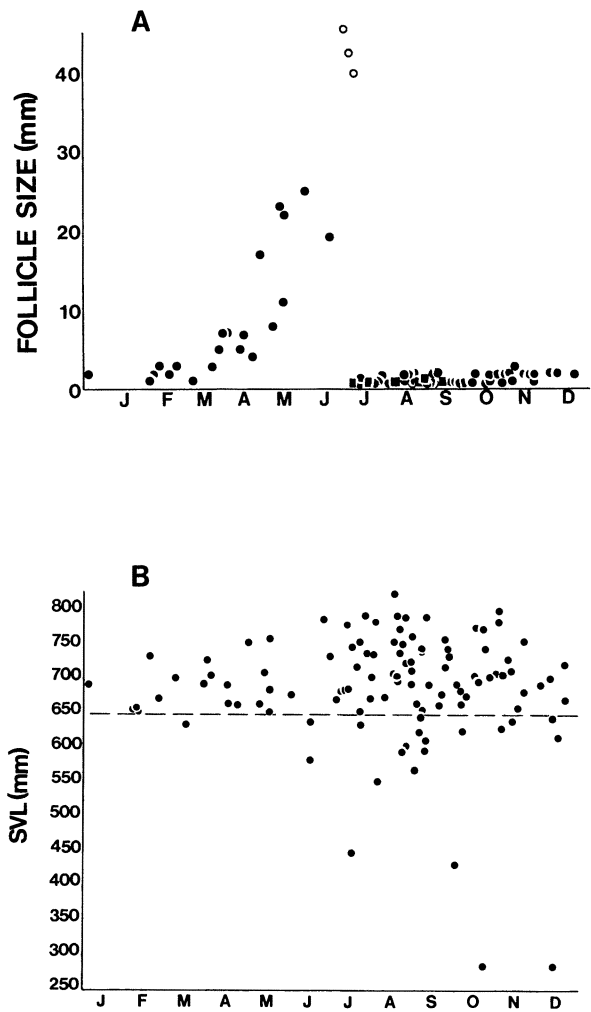


FIGURE 1. Reproductive condition and size of female *Oxybelis aeneus* plotted by date of collection. (A) Reproductive condition: Circles represent either the largest vitellogenic follicle (solid circle) or oviducal egg (open circle) recorded for each individual. Square symbols represent individuals with stretched oviducts. (B) Snout-vent length; the horizontal dashed line marks minimum size at maturity.

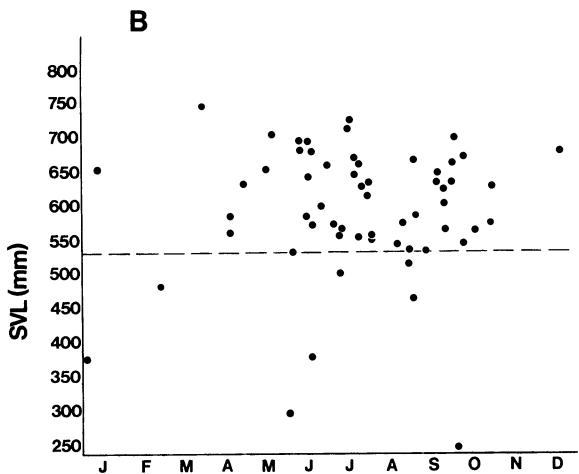
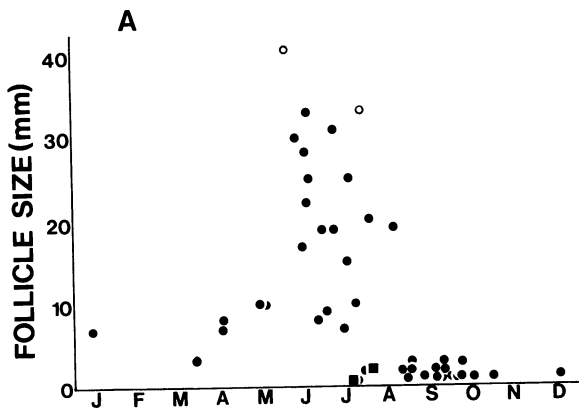


FIGURE 2. Reproductive condition and size of female *Leptophis mexicanus* plotted by date of collection. (A) Reproductive condition (symbols as in Fig. 1). (B) Snout-vent length; the horizontal dashed line marks minimum size at maturity.

Data on variation in clutch size and egg size are presented in Table 2. Although the clutch size range is limited (3–5 eggs), clutch size increases with body size (Spearman Rank Correlation Coefficient:  $r_s = .785$ ,  $N = 9$ ,  $P < 0.01$ ).

Females probably reach maturity at an age of 24 mo (Fig. 1B). The smallest specimen in the sample (290 mm), which we regard as a hatchling of the year, was collected on October 5. Juveniles reach a size of about 450 mm by the end of one year (15 July). By the end of the second year females reach adult size of 650 mm.

*Leptophis mexicanus* is also a medium-sized arboreal snake. SVL ranged from 262 mm to 756 mm in females, and males reached a maximum size of 800 mm SVL. The smallest female exhibiting reproductive activity measured

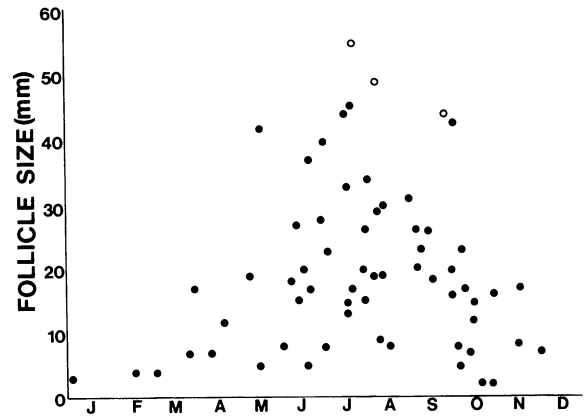


FIGURE 3. Reproductive condition of female *Dryadophis melanolomus* plotted by date of collection (symbols as in Fig. 1).

542 mm SVL; therefore all females 542 mm or larger (50 of 58 females in the sample) were considered adults.

The ovarian cycle of *L. mexicanus* is similar to that of *O. aeneus* in that the ovaries are quiescent during most of the dry season and vitellogenesis begins in March. However, *L. mexicanus* appears to have a longer reproductive season, extending from March or April to late October or early November (Fig. 2A), based on projections of follicular enlargement rates. Follicles were ovulated at a minimum size of 33.4 mm starting in June, and continuing probably through late August or early September. As in *O. aeneus*, Class III follicles outnumbered Class IV and V follicles, indicating follicular atresia. Eggs were laid during a period from the beginning of July, perhaps to late October, although positive data for the last two months of the period are lacking.

Table 2 gives data on variation in clutch and egg size. Clutch size in *L. mexicanus* ranged from 2 to 6 eggs and did not increase with body size ( $r_s = .338$ ,  $N = 19$ ,  $P > 0.05$ ).

Body size was plotted against month of collection for the sample of female *L. mexicanus* (Fig. 2B). The few specimens of immature size suggest a pattern. It appears that females reach maturity in 18 mo. The smallest specimen collected (262 mm SVL) was taken on 4 October. By 12 mo of age they grow to a minimum size of 450 mm, and by 18 mo they reach 580 mm.

*Dryadophis melanolomus* is a large, terrestrial, racer-like colubrid. Female SVL ranged from 260 to 976 mm. Males attained larger sizes, up to 1012 mm SVL. Females  $\geq 580$  mm SVL (68 of 74 females in the sample) were considered adults.

Vitellogenic follicles (Class III and Class IV) were found in specimens of *D. melanolomus* collected in almost every month of the year (Fig. 3). This seemingly continuous ovarian activity suggests a vitellogenic cycle of 12

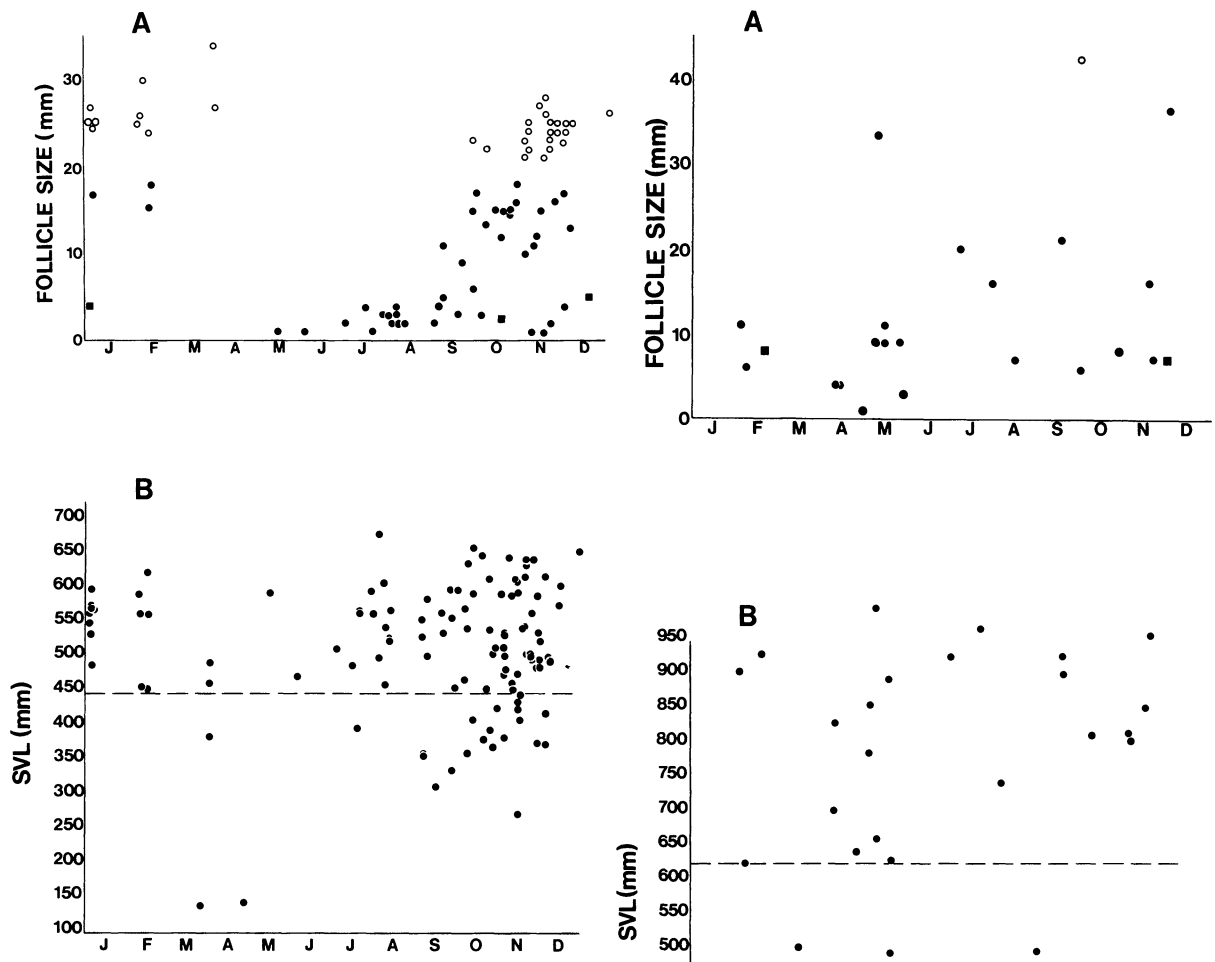


FIGURE 4. Reproductive condition and size of female *Stenorhina freminvillii* plotted by date of collection. (A) Reproductive condition (symbols as in Fig. 1). (B) Snout-vent length; the horizontal dashed line marks minimum size at maturity.

mo or more, with reproduction in alternate years. Another possible explanation would be multiple annual cycles, with rapid, almost continuous vitellogenesis. But the unimodal seasonal occurrence (November–January) of post-hatchlings in the sample does not support this latter interpretation. Follicles were ovulated at a minimum size of 42

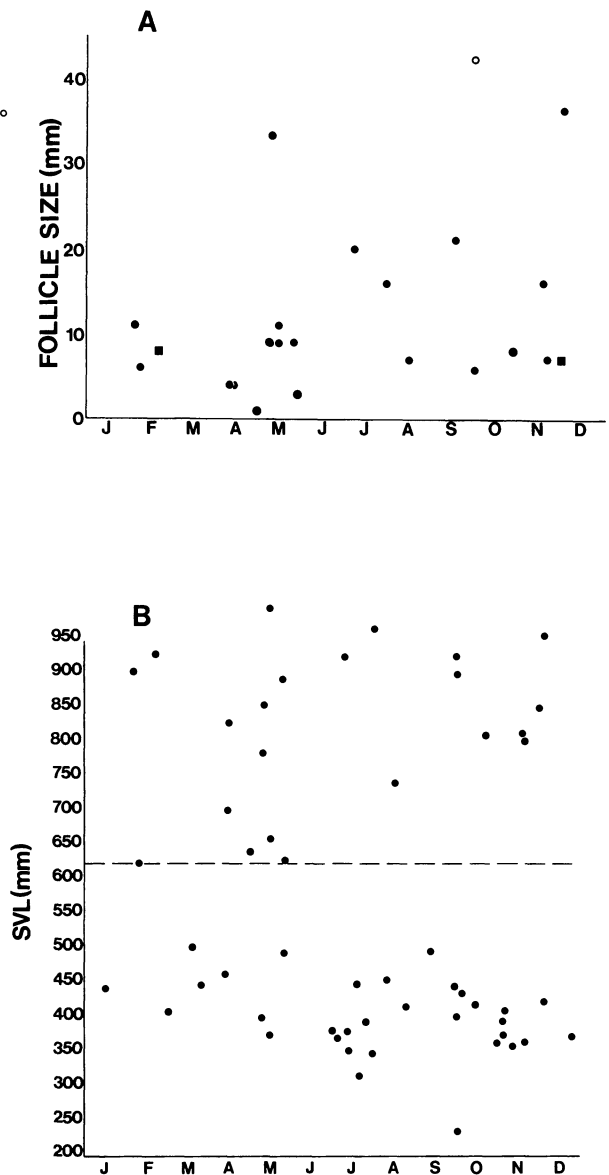


FIGURE 5. Reproductive condition and size of female *Elaphe triaspis* plotted by date of collection. (A) Reproductive condition (symbols as in Fig. 1). (B) Snout-vent length; the horizontal dashed line marks minimum size at maturity.

TABLE 2. Clutch and egg size data for five species of colubrid snakes from the Yucatan Peninsula, Mexico.

Species	Clutch size			Egg size (mm)		
	Range	Mean (SD)	N	Range	Mean (SD)	N
<i>O. aeneus</i>	3–5	3.6 ± 0.73	9	30–45	37.2 ± 5.1	11
<i>L. mexicanus</i>	2–6	4.8 ± 1.1	19	37–43	39.3 ± 3.7	3
<i>D. melanolomus</i>	2–5	3.1 ± 0.90	42	42–55	47.4 ± 4.2	7
<i>S. freminvillii</i>	5–19	11.6 ± 2.87	57	15–28	20.9 ± 3.1	384
<i>E. triaspis</i>	3–7	4.8 ± 1.42	11	35–42	38.5	2

mm, apparently beginning in July and continuing through October (Fig. 3). Eggs were probably laid between August and November. Class III follicles outnumbered Class IV and V follicles, indicating atresia of some follicles.

Data on variation in clutch and egg size are presented in Table 2. Clutch size varied from 2 to 5 eggs, and increased with body size ( $r_s = .631$ ,  $N = 39$ ,  $P < 0.01$ ).

The smallest specimen (260 mm) was collected on January 20, but unfortunately the sample contained too few immature specimens to allow prediction of growth rates and age at maturity. The data suggest, however, that at least 18 mo elapse before maturity.

*Stenorrhina freminvillii* is a medium-sized fossorial snake. Females in the sample ranged from 129 mm to 681 mm SVL. Males are larger, up to 714 mm SVL. Females reached maturity at 448 mm SVL. Of 121 females in the sample, 93 were adults.

Ovarian follicles began to enlarge in late July or early August (Fig. 4A). Follicles reached a minimum ovulatory size of 13.9 mm between September and March. In most reproductive specimens Class III follicles did not outnumber Class IV and V follicles, but two specimens had atretic follicles. Females with stretched oviducts were collected in October, December, and January, and hatchlings with yolk sac scars in March and April, indicating deposition of eggs between October and April during the driest part of the year.

Clutch size (5–19 eggs) increased with body size ( $r_s = .608$ ,  $N = 43$ ,  $P < 0.01$ ). Table 2 presents data on variation in egg and clutch size.

Females appear to mature in one year, as shown in the graph of body size versus month of collection (Fig. 4B). As eggs are laid beginning in October, hatchlings should start to appear in November. In 12 mo females reach a size of 490 mm SVL. Two specimens do not follow this pattern: one measuring 273 mm SVL from mid-November and another measuring 360 mm SVL from mid-July probably represent very early and very late season hatchlings, respectively.

*Elaphe triaspis* is a medium- to large-sized terrestrial snake. Females in the sample had SVLs of 247 to 996 mm. Males are smaller, reaching a maximum size of 821 mm SVL. Females reached maturity at 625 mm SVL, and a total of 23 of the 57 females were adults.

Reproductive activity of *E. triaspis* appears to be aseasonal or continuous (Fig. 5A). Specimens with enlarged ovarian follicles (30 mm or larger, Class IV) were found in March and November. A female with oviducal eggs was found in September. Females with stretched oviducts were taken in November and February. Dowling (1960) reported a female from Chichen Itza, Yucatan (adjacent to Piste), with two oviducal eggs in October. No seasonal pattern is evident in this reproductive activity, and we conclude that reproduction is continuous throughout the year.

Clutch size (3–7 eggs) did not increase with body size ( $r_s = .071$ ,  $N = 9$ ,  $P > 0.05$ ). Data on variation in clutch size and egg size are presented in Table 2.

A plot of body size against month of collection for *E. triaspis* shows no evidence of an annual juvenile class or classes (Fig. 5B). Instead, subadults of 300–500 mm SVL are evenly distributed throughout the year, further supporting the interpretation of aseasonal or continuous reproduction in this species. In rapidly maturing species the expectation is to find relatively few immature specimens, whereas slowly maturing species should show a larger proportion of immature specimens in a random sample (R. Shine, pers. comm.). Since our collection of *E. triaspis* contains a large number of immature individuals, we suggest that it is a late-maturing species, probably not reaching sexual maturity in less than 24 mo.

## DISCUSSION

Most studies of reptilian reproductive cycles have involved a single species, either from a single locality (Kofron 1983) or from various scattered localities (Zug *et al.* 1979). Comparative studies of reproduction in tropical reptile faunas (Saint Girons & Pfeffer 1971; Vitt 1980, 1982, 1983a, 1983b; Vitt & Lacher 1981; Vitt & Blackburn 1983; Vitt & Goldberg 1983; James & Shine 1985) have invariably demonstrated a variety of reproductive patterns in sympatric species. These five colubrid species from the Yucatan Peninsula are no exception showing a remarkable variety of reproductive patterns.

Three of the species reproduce during the wet season. *Leptophis mexicanus* and *O. aeneus* have very similar patterns. Vitellogenesis begins in both species in March (the end of the dry season), and eggs are laid during the wettest part of the year (July to August or September). Females are reproductively quiescent for the remainder of the year. This cycle is virtually identical to that of *Sibon sannicola* in the Yucatan Peninsula (Kofron 1983) and similar to the cycles described by Saint Girons and Pfeffer (1971) for *Boiga cyanea* and *Agkistrodon rhodostoma* in Cambodia.

*Dryadophis melanolomus* also lays during the wet season, but the ovarian cycle differs from that of the previous two species. *D. melanolomus* has a vitellogenic cycle of  $\geq 12$  mo. A large proportion of adult females lack vitellogenic ovarian follicles during the reproductive season, which we interpret as evidence for a two-year cycle. Such an extended cycle has been reported in numerous viperids (Saint Girons 1957, Fitch 1960, Tinkle 1962, Wharton 1966), but is less common in colubrids (Hebard 1951, Platt 1969). Bull and Shine (1979) hypothesized that such "low frequency of reproduction" (LFR) is associated with some "accessory" activity, such as breeding migration, egg brooding, or live bearing, none of which is known in *D. melanolomus*. A possible explanation for the observed LFR in *D. melanolomus* may be long adult survivorship

and consequent low rate of replacement in the adult population, an hypothesis which is further suggested by the low fecundity ( $\bar{x} = 3.2$  eggs/clutch) of this population. But demographic data are inadequate to unequivocally support this or any other explanation.

*Stenorrhina freminvillii* has a reproductive cycle that is timed to the dry season, with reproductive activity occurring from August through April. In addition, oviducal eggs are found over an extended period (6.5 mo). Two interpretations are possible for this prolonged period of reproductive activity: either individual females retain oviducal eggs for an extended period, which seems unlikely, or more than one clutch of eggs is produced by a female each season. The occurrence of numerous individuals with vitellogenic follicles throughout the reproductive season and the length of the reproductive season suggest production of two clutches annually. In addition, females fed throughout the reproductive season, including periods when oviducal eggs were present, presumably in anticipation of an immediate and subsequent period of vitellogenesis.

Vitt (1980) reported dry season reproduction in two species of *Philodryas* from the *caatingas* of Brazil. Saint Girons and Pfeffer (1971) also reported dry season reproduction in eight species of snakes from Cambodia. None of these species, however, produced multiple annual clutches. Saint Girons and Pfeffer (1971) attributed the dry season timing of reproduction in the aquatic and semiaquatic species they studied to increased accessibility of aquatic food organisms as a result of low water levels. *S. freminvillii* is an arachnid trophic specialist that feeds on tarantulas and scorpions (EJC, pers. obs.). If these arachnids are more abundant or more easily obtained by *S. freminvillii* in the dry season, then the seasonally increased food supply could sustain the prolonged dry season reproductive effort. Unfortunately, the only available data on seasonal cycles in food abundance are circumstantial, based on stomach contents of sampled snakes.

The reproductive cycle of *E. triaspis* is unique among the species studied. Enlarged preovulatory follicles were recorded in May and November, oviducal eggs in September and October, and evidence of recent oviposition in November and February, indicating continuous, aseasonal reproduction. Many tropical snake species are known to have aseasonal reproduction (Dixon & Soini 1977, Duellman 1978, Zug *et al.* 1979), but most of them occur in relatively constant, aseasonal climates. On the other hand Vitt (1983b), reporting from a highly seasonal climatic regime in Brazil, found snakes with extended breeding seasons that may produce multiple clutches annually. Vitt hypothesized that in an area where the climate is favorable for reproduction the year around, availability of prey should dictate reproductive periodicity. Vitt found that in the *caatingas* of Brazil snake species that feed on lizards and mammals (*e.g.* *Philodryas*) have a shorter re-

productive season and a single annual clutch. If populations of food organisms in the Yucatan Peninsula respond to the seasonal climatic cycles in a way similar to those in the *caatingas*, then the mammal specialist *E. triaspis* (Duellman 1958, Dowling 1960) might be expected to have a highly seasonal reproductive cycle. A possible alternative explanation for the observed continuous reproduction in the Yucatan population of *E. triaspis* is that the absence of reproductive periodicity represents nonadaptive "evolutionary baggage" acquired under different climatic conditions (James & Shine 1985).

Growth rates and age at maturity in these species also exhibit a wide range of variation. *S. freminvillii* probably reaches maturity within 12 mo, *L. mexicanus* in 18 mo, and *O. aeneus* in 24 mo. Samples of the other two species are inadequate to determine age at maturity. However, available data suggest that *E. triaspis* probably reaches maturity in not less than 2 yr. On the basis of the large number of immature specimens in the sample and its large adult size, *D. melanolomus* probably requires at least 18 mo to reach maturity. These estimates fall within ranges known for other tropical colubrids. Zug *et al.* (1979) estimated sexual maturity at 2 and 3 yr for three Neotropical snake species, but stated that these may be underestimates. Kofron (1983) estimated 8 mo to maturity in *S. sanniola*, a very small species. Shine (1978) estimated age at sexual maturity of 12 mo for females of three species, 24 mo for another two species, and 3 yr in a third species of Australian elapids. He attributed the more rapid maturation of the first three species to year-round growth in a warmer climate. Possible correlates of early maturation of *S. freminvillii* are small size at maturity and continuous (aseasonal) activity and feeding. The other four species we studied mature between 18 and 24 mo, the larger species maturing later.

Table 2 gives data on variation in clutch size and egg size in the five species. In comparison with reported data for snakes, four of the five species have relatively low mean clutch sizes. Fitch (1970) reported an average of 7 eggs/clutch. These four species fall well below that figure, with clutches that average between 3.2 and 5 eggs. The smallest of the species studied, *S. freminvillii*, has the largest mean clutch size (11.6 eggs) and the smallest eggs (average length 20.9 mm). The other species' mean egg lengths range between 37.2 mm and 47.4 mm. *D. melanolomus* has the lowest mean clutch size (3.2 eggs) and the largest eggs (mean length 47.4 mm). Females of this species may also reproduce only in alternate years, yielding a very low reproductive potential.

Clutch size is also subject to geographic variation. Sexton and Heatwole (1965) reported a clutch of 4 eggs in *O. aeneus* from Panama, and Stebbins (1954) found 4 eggs in *O. aeneus* from Arizona. That these clutch sizes lie within the range of the Yucatan population (3–5 eggs) may indicate the absence of geographic variation in clutch

size in this species. We have no comparative data on clutch size from other populations of the other four species. However, comparing *E. triaspis* and *D. melanolomus* with their northern relatives (*Elaphe* and *Masticophis*, respectively) in the United States, we find smaller clutches in the tropical species. Clutch sizes for *Elaphe guttata* (9–13), *E. obsoleta* (6–44), and *E. vulpina* (7–29) (Wright & Wright 1957, Fitch 1985) all average larger than the Yucatan population of *E. triaspis* (3–7). *Masticophis* clutch sizes vary greatly for four species: *M. bilineatus*, 7; *M. flagellum*, 4–24; *M. lateralis*, 6–9; *M. taeniatus*, 3–12 (Wright & Wright 1957, Fitch 1985). *D. melanolomus* has a mean clutch size of 3.1 eggs (range 2–5). It is possible that selective pressure exists on the tropical species to produce smaller clutches with larger eggs and more clutches per year, as suggested by Zug *et al.* (1979). *E. triaspis* fits this pattern with aseasonal reproduction and the possible production of more than one clutch per year. But the fact that *D. melanolomus*, a species with low mean clutch size, reproduces in alternate years suggests more complex controlling factors.

We have found a variety of reproductive patterns in the five species we studied, as have others who have

compared reproductive cycles in tropical reptile faunas. This phenomenon indicates that individual species' responses to climatic cycles are not universal and that the causal factors responsible for initiation of reproductive activity are not well understood (Saint Girons 1985). The apparently low reproductive potential of four of the species studied and its relationship to the demography of the snake populations are phenomena that especially merit further investigation.

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## LITERATURE CITED

- BULL, J. J., AND R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. *Am. Nat.* 114: 296–303.
- CONTRERAS ARIAS, A. 1959. Bosquejo climatológico. In E. Beltran, (Ed.). Los recursos naturales del sureste y su aprovechamiento, pp. 95–158. Inst. Mexicano Recursos Naturales Renovables, Mexico, Mexico.
- DIXON, J. R., AND P. SOINI. 1977. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. II. Crocodylians, turtles, and snakes. *Contrib. Biol. Geol. Milwaukee Pub. Mus.* 12: 1–91.
- DOWLING, H. G. 1960. A taxonomic study of the ratsnakes, genus *Elaphe* Fitzinger. VII. The *Triaspis* section. *Zoologica* (New York) 45: 53–80.
- DUCELLMAN, W. E. 1958. A preliminary analysis of the herpetofauna of Colima, Mexico. *Occas. Pap. Mus. Zool. Univ. Mich.* 589: 1–22.
- . 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 65: 1–352.
- FITCH, H. S. 1960. Autecology of the copperhead. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 13: 85–288.
- . 1970. Reproductive cycles of lizards and snakes. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 52: 1–247.
- . 1982. Reproductive cycles in tropical reptiles. *Occas. Pap. Mus. Nat. Hist. Univ. Kans.* 96: 1–53.
- . 1985. Variation in clutch and litter size in New World reptiles. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 76: 1–76.
- HEBARD, W. B. 1951. Notes on the life history of the Puget Sound garter snake, *Thamnophis ordinoides*. *Herpetologica* 7: 177–179.
- JAMES, C., AND R. SHINE. 1985. The seasonal timing of reproduction: a tropical-temperate comparison in Australian lizards. *Oecologia* 67: 464–474.
- KOFRON, C. P. 1983. Female reproductive cycle of the neotropical snail-eating snake *Sibon sanniola* in northern Yucatan, Mexico. *Copeia* 4: 963–969.
- LEE, J. C. 1980. An ecological analysis of the herpetofauna of the Yucatan Peninsula. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 67: 1–75.
- PAYNTER, JR., R. A. 1955. The ornithogeography of the Yucatan Peninsula. *Bull. Peabody Mus. Nat. Hist.* 9: 1–347.
- PLATT, D. R. 1969. Natural History of the hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 18: 253–420.
- SAINT GIRONS, H. 1957. Croissance et fécondité de *Vipera aspis*. *Vie et Milieu* 8: 265–286.
- . 1985. Influence des facteurs de l'environnement sur les cycles annuels et reproducteurs des reptiles. *Bull. Soc. Zool. Fr.* 110: 307–319.
- , AND P. PFEFFER. 1971. Le cycle sexuel des serpents du Cambodge. *Ann. Sci. Nat. Zool.* 12th ser. 13: 543–571.
- SEXTON, O. J., AND H. HEATWOLE. 1965. Life history notes on some Panamanian snakes. *Caribb. J. Sci.* 5: 39–43.
- SHINE, R. 1978. Growth rates and sexual maturation in six species of Australian elapid snakes. *Herpetologica* 34: 73–79.
- . 1985. The reproductive biology of Australian reptiles: search for general patterns. In G. Grigg, R. Shine, and H. Ehmman, (Eds.). *Biology of Australasian frogs and reptiles*, pp. 297–303. Surrey Beatty and Sons, Chipping Norton.

- STEBBINS, R. C. 1954. Amphibians and reptiles of western North America. McGraw Hill Co., Inc., New York.
- TINKLE, D. W. 1962. Reproductive potential and cycles in female *Crotalus atrox* from northwestern Texas. *Copeia* 2: 306-313.
- VITT, L. J. 1980. Ecological observations on sympatric *Philodryas* (Colubridae) in northeastern Brazil. *Pap. Avulsos Zool. (Sao Paulo)* 34: 87-98.
- . 1982. Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habitat. *Can. J. Zool.* 60: 3113-3120.
- . 1983a. Reproduction and sexual dimorphism in the tropical teiid lizard *Cnemidophorus ocellifer*. *Copeia* 2: 359-366.
- . 1983b. Ecology of an anuran-eating guild of terrestrial tropical snakes. *Herpetologica* 39: 52-66.
- , AND D. G. BLACKBURN. 1983. Reproduction in the lizard *Mabuya heathi* (Scincidae): a commentary on viviparity in New World *Mabuya*. *Can. J. Zool.* 61: 2798-2806.
- , AND S. R. GOLDBERG. 1983. Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. *Copeia* 1: 131-141.
- , AND T. E. LACHER, JR. 1981. Behavior, habitat, diet, and reproduction of the iguanid lizard *Polychrus acutirostris* in the *caatinga* of northeastern Brazil. *Herpetologica* 37: 53-63.
- WHARTON, C. H. 1966. Reproduction and growth in the cottonmouths, *Agkistrodon piscivorus* Lacépède, of Cedar Keys, Florida. *Copeia* 2: 149-161.
- WRIGHT, A. H., AND A. A. WRIGHT. 1957. Handbook of snakes of the United States and Canada. Comstock Publ. Assoc., Ithaca, N.Y.
- Zug, G. R., S. B. Hedges, and S. Sunkel. 1979. Variation in reproductive parameters of three Neotropical snakes, *Coniophanes fissidens*, *Dipsas catesbyi*, and *Imantodes cenchoa*. *Smithson. Contrib. Zool.* (300): iii, 1-20.