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Miscellaneous Notes on the Reproductive Biology of Reptiles. 5. Thirteen Varieties of the Genus Lampropeltis, species mexicana, triangulum and zonata

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ABSTRACT

Certain aspects of courtship, copulation, oviposition and hatching, with data on the neonates are presented for thirteen varieties of kingsnakes, genus Lampropeltis: L. mexicana alterna, L. m. thayeri, L. triangulum amaura, L. t. annulata, L. t. arcifera, L. t. elapsoides, L. t. gentilis, L. t. hondurensis, L. t. nelsoni, L. t. sinaloae, L. t. syspila, L. triangulum ssp., and L. zonata parvirubra. Multiple egg clutches are reported for L. mexicana alterna, L. triangulum elapsoides, L. t. nelsoni, L. t. sinaloae and L. t. syspila. An undescribed L. triangulum from Puebla, Mexico produced three egg clutches in a single season. Two L. mexicana alterna morphs (alterna and blairi) were interbred and several pattern varieties present in the neonates are described. Geometric growth rate is calculated for L. mexicana alterna.

Although several taxonomic monographs (Blanchard, 1921; Blaney, 1977; Williams, 1978), a variety of reproductive summaries (Wright and Wright, 1957; Fitch, 1970; Miller, 1979; Zweifel, 1980; and others) and studies on pattern dimorphism (Klauber, 1936, 1939, 1944) are available dealing with the New World genus Lampropeltis, the reproductive biology of most king-snakes is still poorly known. We here report observations on courtship, copulation, egg-laying and hatching in three species of this widely distributed genus: L. mexicana (two subspecies), L. triangulum (ten subspecies), and L. zonata parvirubra. For certain forms, our observations supplement previous accounts.

It is well established that the normal reproductive mode of a large number of lizards includes the production of multiple clutches of eggs per season, but this capability has been demonstrated in few snakes.

Among the first colubrids shown to possess this characteristic were Boaedon lineatus, Boiga multomaculata, Pituophis m. melanoleucus, Ptyas mucosus, P. korros, Rhabdophis subminiata, Spalerosophis diadema and Xenochrophis vittata in addition to two viviparous species (Fitch, 1970; Naulleau, 1973). Since the review by Fitch (1970), multiple egg clutches have been observed in five ratsnakes, Elaphe g. guttata (pers. observation), E. o. obsoleta (Cohen, 1978), E. o. bairdi (Brecke et al., 1976), E. porphyracea nigrofasciata (Romer, 1979), Gonyosoma oxycephala (pers. observation), and two kingsnakes, Lampropeltis getulus (Lewke, 1979), and Lampropeltis mexicana alterna (Greatwood, 1978). In addition to presenting supportive data for L. getulus and L. mexicana alterna, we herein show evidence of this phenomenon in L. triangulum elapsoides, L. t. nelsoni, L. t. sinaloae, L. t. syspila and L. triangulum ssp.

Fitch (1970) and Iverson (1978) suggested that the lengthened breeding seasons apparent in a number of temperate zone species could well provide the capability of more than one clutch or brood per season. Aldridge (1979) however, concluded that this is unlikely because most temperate forms begin secondary vitellogenesis at a set time of the year. We contend that under optimum captive conditions, which may include adherence to natural cycles of photoperiod and temperature, the production of more than one clutch is quite possible in a number of species and appears dependant upon the availability of food and male snakes at the correct time of year. In nature, multiple egg clutches are probably more widespread than previously thought in temperate zone snakes, particularly in the southern portion of their ranges when food supply is plentiful.

Our experience has shown that staggered oviposition of a single clutch of eggs is an indication of infertility for most snakes. Williams (1978) recorded this for *L. t. syspila*, but did not indicate fertility status of the clutch. Other indications of infertility have included smaller average egg dimensions, non-adherency (in species where adherent clutches are normal), yellowish egg color (as opposed to white), a waxy odor, and soft egg texture instead of a full, turgid appearance.

MATERIALS AND METHODS

The observations in this account were carried out at the Dallas Zoo, Fort Worth Zoo (L. t. elapsoides, L. t. hondurensis and L. t. nelsoni) and in the collection of the senior author (L. mexicana alterna) unless otherwise noted. Most specimens were housed in glass-fronted fiberglass exhibit units or glass aquaria of varying sizes. All snakes were fed on laboratory mice unless otherwise noted. Individual L. zonata were maintained at 27–30 C during warm months, and were placed in hibernation from 1 December to 1 April. Hibernation room temperature was lowered 2 degrees C per day until 13 C was attained. Beginning 1 April, temperature was raised to 27 C at the rate

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| | 12 September | | | | | | |
|---|---|---|--|---|--|--|--|
| Number | 1976 (hatching) | 1 April 1978 | Daily kg of total length | Daily kg of weight | l April 1979 | Daily kg of total length | Daily kg |
| 1 (0701 070) | | | | | | India Indian | or weight |
| 4 (eggs 1979) 2 (eggs 1978) 4 (eggs 1979) Mean | 251 mm (9.7 g) 225 (8.2) 279 (10.5) 227 (6.5) 245 (8.7) | 780 mm (190.0 g) 600 (88.4) 627 (94.7) 623 (86.3) 657 (114.8) | .002 .0017301 .0014285 .0017407 | .0052469 .004194 .00388 .0045343 .0045337 | 910 mm (220 g) 755 (166.6) 763 (178.5) 800 (176.1) 807 (185.3) | .0004219 .0006301 .0005369 .0006849 .0005616 | .0004027 .0017424 .0017287 .0019506 .0013013 |

of 2 C per day. Adult and yearling L. mexicana alterna hibernated during the same months at 9-12 C (see Murphy et al., 1978). All other specimens were maintained year around at 23-32 C.

Gravid females were provided with plastic shoe boxes filled with damp sphagnum moss as a medium for oviposition. Egg measurements and weights were recorded to the nearest mm and 0.1 g with vernier calipers and a triple beam balance, respectively. Eggs were incubated at approximately 23–32 C in a vermiculite medium (Tryon, 1975). Neonates were measured for snout-vent length and total length using the squeeze box technique (Quinn and Jones, 1974), and weighed on a triple beam balance.

Geometric growth rates Kg (=instantaneous relative growth rates) were calculated for L. mexicana alterna by the method of Simpson et al. (1960).

RESULTS AND DISCUSSION

L. mexicana alterna. Reproduction in this form has been treated recently by several authors (Assetto, 1978; Burchfield, 1976; Gehlbach and McCoy, 1965; Greatwood, 1978; Murphy et al., 1978; Tanzer, 1970). Murphy et al. (1978) provided data on two clutches of eggs and their hatchlings from matings in 1976. The results given herein represent the interactions of the same captive group of kingsnakes during 1977-79. Ten Texas specimens of L. mexicana alterna were involved: Female A, dark blairi morph (total length 970 mm) collected near Langtry, Val Verde County; female B, dark blairi morph (total length 800 mm) taken south of Shumla, Val Verde County; male A, dark blairi morph (total length 870 mm) collected 8.8 km N Langtry, Val Verde County (UTA-R7188); male B, light alterna morph (total length 925 mm) taken 7 km E Sanderson, Terrell County; male C, dark alterna morph hatched 4 October 1977 (parents male B, female A). In addition, three captive-bred 1976 hatched blairi morph females became reproductively active in 1978, and a fourth in 1979. Geometric growth rates of these females are presented in Table 1.

Although males and females were usually housed together, courtship did not occur before the first week in May of each year; this coincided with the first spring ecdysis in the male snakes. Female snakes were not receptive until after their first ecdysis of the season. Courtship paralleled that described by Murphy et al. (1978) with one major exception. On two occasions, male B was observed biting and chewing the dorsal neck region of a female immediately prior to copulation. Bites appeared to be hard, and chewing behavior was vigorous. Each bite lasted about 5 seconds. Murphy et al. (1978) noted one bite to a female during male combat, and concluded this to be a misdirected sexual response, as males frequently engaged in biting during this phase of social behavior. It appears, however, that biting is included in the courtship ritual of L. m. alterna. Interestingly, biting was noted only from a male of the alterna morph. Biting prior to copulation, presumably for the purpose of inducing a receptive response from females has been reported for *Elaphe subocularis* (Tryon, 1976), *E. v. vulpina* (Gillingham, 1974), *Lampropeltis getulus* (Lewke, 1979) and *L. triangulum* (Miller, 1978).

Homosexual behavior was noted between the males in March 1977. Male B was introduced to male A on 19 March. Dorsal advance movement and attempted copulation occurred within 15 minutes of introduction, and intromission took place on 24 March and 29 March. Male B appeared receptive insofar as he remained stationary and permitted intromission. Homosexual activity in snakes was discussed by Bogert and Roth (1966) and by Smith (1968). Although courtship behavior has been described between males of several forms, copulation is rare. Smith's (1968) conclusion that the captive snakes' discriminatory powers become dulled and confused may only partially explain this behavior. We feel that dominant-subordinate interactions should be considered. We have also observed intromission in males of a Malagasy boa, Acrantophis dumerili. In both cases, it was probable that intimidation experienced by a male introduced into the established living quarters of another might render the first temporarily vulnerable to such sexual advances.

Heterosexual copulation was recorded on 20 occasions between 5 May and 17 July, each lasting approximately 5–15 minutes. Most such occurrences took place at dawn and dusk, but some activity was noted throughout the night. On several occasions males copulated 2–3 times with one female or with a number of females during a 24-hour period. Frequently when several females were introduced, a male was seen courting one anteriorly while *in copulo* with another individual. Apparently, during receptive periods, anterior stimulation (i.e., tongue-flicking, jerking) by males is unnecessary for females to permit intromission.

Gravid females shed 6–9 ($\bar{x} = 7.5$) days prior to oviposition for 17 clutches. Egg-laying occurred 27–51 ($\bar{x} = 37.5$) days after the last observed copulation for six females (12 clutches). Incubation periods ranged from 57–68 ($\bar{x} = 61.9$) days for 16 clutches.

A total of 135 eggs (21 infertile) was produced. Clutch size ranged from 3-13 ($\bar{x} = 7.9$) for 17 clutches. Four first clutches from 1976 hatched females numbered nine, eight, four and three ($\bar{x} = 6.0$). Measurements for clutches with 100 percent fertility (13 clutches) are as follows: 100 fertile eggs, mean egg-length was 40.4 mm, mean egg-diameter was 21.8 mm, and mean egg-weight 11.4 g. Measurements in 1978 for 15 eggs (3 clutches) in 1976 hatched females were as follows: mean egg-length 47.2 mm, mean egg-diameter 35.0 mm, and mean egg-weight 12.3 g. In general, the largest and most elongate eggs were included in the smallest clutches (3, 4). The largest clutch previously reported for this species is 9 eggs (Murphy et al., 1978).

Female A produced two clutches in each of three consecutive years.

| Species | First clutch (date) | Copulation date (interval) | Second clutch (interval) | Source |
|-------------------------------------|------------------------|-------------------------------|--------------------------------|----------------------|
| Boaedon lineatus | 30 January | [] | 16 A | |
| Boiea multomaculata | E M. | | (o/) IIIdv or | Blackwell (1954) |
| 0 | Yew c | [] | 1 January (241) | Kopstein (1938) |
| Florida a militaria | 22 October | (<u>)</u> | 21 December (60) | |
| cuphe g. guildia | | | | This name |
| Elaphe obsoleta bairdi | 7 May | 13 May (6) | 31 1 (16) | 1 nus paper |
| Elaphe obsoleta obsoleta | 10 Luna | | (c+) aunc 17 | Brecke et al. (1978) |
| Flanke nornhyracco viceof | anne ei | <u>[</u>] | 17 August (59) | Cohen (1978) |
| and the polynymeter merojasciala | · 19, 20 April | () I | 6-8 August (109-111) | Romer (1979) |
| Jonyosoma oxycephala | 2 February | () | 31 May (118) | This namer |
| Lampropettis getulus (yumensis) | 4, 5 May | () | 8 July (65, 66) | I auto (1070) |
| Lampropettis getulus (californiae) | 20 May | () | 4 July (45) | This near |
| Lampropeltis mexicana alterna | 29 May | 17 June (19) | 27 Iuly (59) | Contract 110700 |
| | 26 June | 6 July (10) | Id August (30) | UICALW000 (19/8) |
| | 27 June | 11 July (14) | 18 August (38) | This paper |
| | 20 June | 26, 27 June (6, 7) | 6 August (47) | This namer |
| annandeia mining | 6 July | None occurred | 24 August (49) | This paper |
| Common della striangulum elapsoides | 9 May | () | 30 June (52) | This paper |
| Lumpropetits triangulum nelsoni | 29 June | () | 10 September (74) | This namer |
| Lampropeltis triangulum sinaloae | 4 July | 9 July (5) | 17 August (44) | This paper |
| Lampropeltis triangulum syspila | 7 May | | 15 T (20) | I IIIS paper |
| Pituophis melanoleucus melanoleucus | 12 March | | (cc) plint ct | I his paper |
| | 17 March | | 4 May (53) 4 November (732) | Fitch (1970) |
| | 18 March | () | 29 April (42) | |
| | 4 April | (<u> </u>) | 23 May (49) | |
| riyas mucosus | 1 | () | — (59) | Konstein (1038) |
| riyas korros | 1 | (<u> </u> | (UL) | |
| Rhabdophis subminiata | 28 June | | | Kopstein (1938) |
| | 2 October | | 15 November (44) | Kopstein (1938) |
| Spalerosophis diadema | 8 June | None occurred | 3 September (87) | Dmital (1047) |
| Xenochrophis vittata | 26 march | (<u>)</u> | 3 Mav (41) | Konstain (1020) |
| | 31 March | (<u> </u> | 27 Sentember (110) | (0061) Illaisdow |

Summary of multiple egg clutches in colubrid snakes.

Table 2.

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Fig. 1. A specimen of Lampropeltis mexicana alterna which shows characteristics intermediate between alterna and blairi morphs.

Copulation in May 1977 with male A resulted in a clutch on 20 June. Six and seven days later, copulation occurred twice when male B was introduced. A second fertile clutch was deposited on 6 August 1977. Female A(bred 21, 22 May) again produced a fertile clutch on 6 July 1978. However, the male was preparing for ecdysis and failed to show reproductive interest at this time. Nevertheless, 49 days after oviposition female A deposited a second clutch (all infertile) on 24 August.

On 6 and 11 July 1979, male C copulated with female A and C, respectively. Second clutches consisting of 9 and 5 eggs were produced on 14 and 18 August. The resulting hatchlings from female C represent the first secondgeneration offspring from this group of captive specimens. These data indicate that male as well as female L. m. alterna are capable of sexual maturity at 18–20 months of age, although males of some other genera mature earlier than females (see Shine, 1978, for a review).

Apparently, copulation is necessary for fertility with each clutch, but not for egg production in this species. An additional infertile clutch was reported previously for female A (Murphy et al., 1978). Multiple egg clutches for L. *m. alterna* have been recorded (Greatwood, 1978). A summary of multiple clutching in colubrid snakes reported to date is presented in Table 2.

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Interactions between *blairi* morph snakes (two clutches) produced 15 *blairi* morph hatchlings. Burchfield (1976) and Murphy et al. (1978) indicated similar results. Two additional reports of captive breedings (Assetto, 1978; Greatwood, 1978) did not distinguish pattern types. Although Tanzer (1970) presented information on both *alterna* and *blairi* morph hatchlings from a single *alterna* female, the present observations provide the first published information regarding captive breedings between *alterna* and *blairi* morph specimens. Several characteristics present in the neonates deserve description.

Male A and female A produced a clutch of eight *blairi* morph neonates. When bred with male B for her second seasonal clutch, however, the six hatchlings from female A fit the description for *alterna* morphs (Tanzer, 1970), and two were considered intermediates using the description by Gehlbach and Baker (1962). In order to further examine this relationship, male B was used in breeding with the five additional *blairi* morph females. For a total of 12 clutches (99 eggs, 10 infertile), 41 neonates (46 percent) were *alterna* morph (Fig. 1), 11 (12 percent) were *blairi* morph, and 37 (41 percent) were determined to be intermediates. Tables 3 and 4 present meristic and morphometric data for these hatchlings.

A number of specimens look similar to that pictured by Gehlbach and Baker (1962); it is therefore probable that their specimen resulted from *alterna* \times *blairi* interactions. One consistent feature of our snakes is the possession of *blairi* morph characteristics anteriorly (i.e., symmetrical head pattern, large nuchal blotch), and *alterna* morph characteristics posteriorly (red bands reduced or absent) (Fig. 1). One inconsistent feature is the presence or absence of alternating markings between major body bands. Table 4 summarizes this feature in the three pattern types. One snake in Figure 2 represents the *alterna* morph without those markings which have been heretofore described as a characteristic of this morph (Gehlbach and Baker, 1962; Gehlbach and McCoy, 1965; Tanzer, 1970). One snake described by Tryon (1979) superficially resembled both phases, but was not determined to be intermediate.

Offspring from breedings between male C and females A (mother) and C (sibling) include no intermediate snakes. *Alterna* morph characteristics are evidently predominant in this group of captive specimens, as seven of nine neonates were of this morph, and two were the *blairi* morph. Further breedings will be necessary before pattern inheritance is understood in L. m. *alterna*.

Klauber (1936, 1939) and Tanzer (1970) suggested reduced viability for intermediates in nature. While this may be a factor, the feeding and growth of our snakes were comparable to that of the *alterna* and *blairi* morphs. Of 114 neonates, seven died at hatching; two were *alterna*, three were *blairi*,

| Specimen | Egg number | Egg length | Egg diameter | Adherent clutch weight | Hatchling total length | Hatchling weight |
|--------------|------------|-----------------|-----------------|---------------------------|---------------------------|---------------------------------|
| l (female A) | 80 | 35-38 mm (36.6) | 21-23 mm (21.6) | 82.2 g (10.3) | 255-278 mm (263.4) | 6.8-8.7 P (7.1) |
| | 10 | 33-40 (37.0) | 22-25 (23.6) | 122.0 (12.2) | 243-276 (256.1) | 8.1-10.8 (9.2) |
| | a | 27 20 25 1 | | | (N = 7) | (L = N) |
| | ~ | (1.05) 46-26 | 19-24 (22.2) | 92.4 (10.2) | 261-286 (276.2) | 8.6-10.0 (9.3) |
| | c | 0000 CF LC | | | (N = 5) | (N = 5) |
| | • | (0.65) 74-16 | 23-24 (23.4) | 120.2 (13.3) | 258-276 (266.0) | 6.3-10.2 (9.1) |
| (female D) | : | | | | (N = 7) | (L = N) |
| (Iciliaic D) | 71 | 30-35 (32.5) | 22–23 (22.5) | 112.9 (9.4) | 232-275 (249.4) | 7.2-8.5 (7.9) |
| | 9 | | | | (N = 11) | (N = 11) |
| | 13 | 27-34 (30.5) | 20-24 (21.8) | 74.0 (N = 9) | 203-228 (216.6) | 4.3-8.0 (6 1) |
| | | (6 = N) | (0 = 0) | | (N = 5) | (N = 0) |
| 3 (female C) | ∞ | 39-44 (42.2) | 20-22 (21 2) | 02 2 (11 0) | 11 970, 000 310 | |
| 1976 hatched | 10 | 39 44 (41.6) | 71-73 (71 0) | (6.11) 2.00 | (1.00) 007-047 | 7.9-11.1 (10.0) |
| | \$ | 15 61 (50 0) | (6.12) (2-12 | (0.21) 0.021 | 255-285 (275.2) | 9.5-10.3 (9.9) |
| | n | (2.00) 10-0+ | 19-21 (20.0) | 66.3 (13.2) | 277-290 (284.0) | 10.0-10.8 (10.4) |
| (famela D) | , | | | | (N = 4) | (N = 4) |
| | n (| 52-61 (56.0) | 19-20 (19.6) | 41.4 (13.8) | 275-293 (288.3) | 10 1-10 6 010 20 |
| 19/0 natched | 6 | 34-41 (37.6) | 19-21 (20.0) | 82.4 (9.1) | 212-241 (227 2) | 62-74 (6 0) |
| 5 (temale E) | ∞ | 38-43 (40.1) | 20-21 (20.1) | 80.3 (10.0) | 232-245 (240 6) | (() + |
| 1976 hatched | | | | | (0.013) 013 203 | (0.0) (|
| 6 (female F) | 4 | . 45-54 (50.5) | 19-20 (19.2) | 40 2 (12 3) | 11211 101 37L | |
| 1976 hatched | 4 | 37-44 (39.2) | (20) | 39.0 (9.7) | 220-252 (237.3) | 7.8-10.5 (9.4) 6.3-7.1 (6.8) |
| | | | | | (N = 3) | (N = 3) |

Table 3. Meristic data on eggs and hatchlings of *Lampropeltis mexicana alterna* (3 alterna morph, 2 2 blairi morph). Means are in paren-

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| | alterna morph (48) | blairi morph (13) | intermediate (37) |
|---|--------------------|-------------------|-------------------|
| Pre-anal bands (x̄) Number of dorsal | 15–21 (17.8) | 12-19 (15.6) | 13–19 (16.0) |
| alternating markings (x̄) | 0–14 (6.0) | 0-5 (1.0) | 0–10 (2.2) |
| Number with markings (%) | 42 (.87) | 6 (.46) | 28 (.75) |
| Total length (x̄) (mm) | 203–297 (258.4) | 249-293 (268.5) | 207–285 (251.1) |
| Weight (x̄) (g) | (N = 47) | (N = 11) | (N = 34) |
| | 4.3-10.8 (8.6) | 8.3-10.8 (9.8) | 4.7-10.5 (8.0) |
| | (N = 47) | (N = 11) | (N = 34) |

Table 4. Meristic and morphometric data for hatchlings of *alterna* morph, *blairi* morph and intermediate patterned *Lampropeltis mexicana alterna* (14 clutches).

and two were intermediates. The sex ratio for all snakes was approximately 50 percent as determined by hemipenial eversion.

L. mexicana thayeri. Three specimens were collected between La Angostura and San Juanito, Nuevo Leon, Mexico by W. Garstka. Two females, A and B, and one male were bred in captivity in three consecutive years, 1977–79 (W. Garstka, pers. comm.). Three individual copulations were noted and all occurred after dark. Intervals between the last observed copulation and oviposition for three clutches were 23, 33 and 34 days. The 25 hatchlings were 12 males and 13 females. The width of the red body bands varies considerably (Fig. 3). Reproductive data for L. m. thayeri are presented in Table 5.

L. triangulum amaura. A female, from the vicinity of Monroe, Ouachita Parish, Louisiana, was placed with a male of unknown provenance. Although courtship and copulation were not observed, a clutch of four adhering eggs was laid on 26 January 1977. Egg-length ranged from 40–44 mm $(\bar{x} = 41 \text{ mm})$, egg-diameter ranged from 14–15 mm $(\bar{x} = 14 \text{ mm})$ and total weight of the clutch was 19.5 g (\bar{x} egg weight 4.8 g). Hatching occurred 11– 12 March after an incubation period of 44–45 days. Neonates ranged in snout-vent length from 170–184 mm ($\bar{x} = 177 \text{ mm}$), tail length was 33–36 mm ($\bar{x} = 34 \text{ mm}$), and weight from 4.0–4.3 g ($\bar{x} = 4.1 \text{ g}$). Neonates first ate Leiolopisma lateralis and gradually switched to newborn mice.

R. M. Hubbard (pers. comm.) found a gravid female on 14 July 1976 near Shepherd, San Jacinto County, Texas. Nine adherent eggs were deposited 3 August 1976. Mean egg-length was 25 mm. Eight of the nine eggs hatched (one egg infertile) on 14 September 1976 after 42 days incubation. Total lengths of the eight neonates ranged from 190–200 mm.

A wild-caught female from near Moss Lake, Cooke County, Texas, laid a clutch of three adherent eggs which hatched 26 August. Data on ovipo-

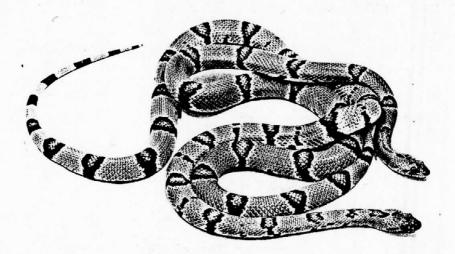


Fig. 2. Specimens of Lampropeltis mexicana alterna (alterna morph) with and without dorsal alternating markings between major body bands.

sition and measurements of eggs and hatchlings were not provided (J. E. Joy, Jr., pers. comm.).

Williams (1978) reviewed the scanty reproductive information available for this taxon. Clark (1949) reported a clutch of three eggs in a female taken on 5 July. Meade's (1940) five inch (125 mm) hatchling is apparently the smallest recorded specimen.

L. triangulum annulata. A male collected near Sarita, Kenedy County, Texas, bred (date not recorded) with a female from Aquilares, Webb County, Texas. A clutch of two eggs was deposited on 21 August 1978. Hatching occurred 31 October and 3 November (70, 73 days) (J. E. Joy, Jr., pers. comm.).

A male collected near Laredo, Webb County, Texas bred with a female from Bruni, Webb County, Texas, but copulation was not observed. Five eggs were laid on 26 April 1980. Egg-length was 47–62 mm ($\bar{x} = 53$), diameter 16–18 mm ($\bar{x} = 17$) and weight 12.0–13.2 g ($\bar{x} = 12.5$). Four neonate males emerged on 23 June and measured 245–255 mm ($\bar{x} = 249$) total length and weighed 9.9–10.4 g ($\bar{x} = 10.1$).

Burchfield (1979) described a clutch of four eggs produced from a captive breeding. The female parent was captive-hatched and two years of age at the time of oviposition. Incubation was 61 days.

Werler (1951) recorded two clutches of five eggs laid 5 June and 12 July. Hatching occurred 50 and 47 days later, respectively. An additional wild caught female was known to have produced a fertile clutch in April (pers.

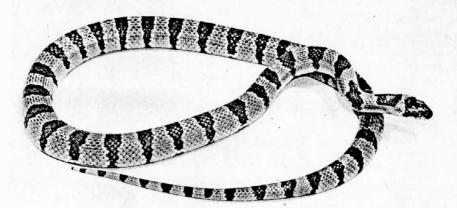




Fig. 3. Pattern variation in clutchmates of Lampropeltis mexicana thayeri.

obser., BWT). When considering the range of recorded ovipositional dates, the probability of multiple egg clutches in this form is particularly favorable.

L. triangulum arcifera. An adult pair were collected at Rancho San Francisco, Jalisco, Mexico at an elevation of 2075–2317 m. Ecological data for the collection site have been provided (Armstrong and Murphy, 1979). Eggs and hatchlings were produced each of four years as follows: Clutch 1.— Seven eggs were laid 16 May 1975; four hatched 22–23 July after 67–68 days incubation. Snout-vent lengths for the four hatchlings ranged from 202–218 mm ($\bar{x} = 207$ mm), tail length 23–25 mm ($\bar{x} = 23$ mm), and weight ranged

| | Date of copulation | Date of oviposition | Date of hatching (incubation period) | Egg number (number/ hatch) | Egg length (x) (mm) | Egg diameter (x) (mm) |
|-----------------|--------------------|---------------------|---|----------------------------------|------------------------|--------------------------|
| Female A | | | | | | |
| 1977 | — | 28 June | 14-18 September (78-82) | 8 (8) | 34-40 | 19-21 |
| 1978 | 20 May | 12 June | - | 7 (6) | (36.9) | (20.2) |
| 1979 | - 7 | 8 July | 14–19 September (68–72) | 7 (7) | (—) 30–46 (40.1) | () () |
| Female B | | | | | | . , |
| 1977 | 8 June | 11–14 July | 22–25 September (—) | 5 (2) | 38-51 | 19-21 |
| 1978 | 20 May | 23 June | infertile | 5 (0) | (43.0) | (20.2) |
| 1979 | - | 22 July | 25–27 September (65–67) | 5 (2) | (—) 43_45 (44.0) | (—) — (—) |

Table 5. Reproductive data for Lampropeltis mexicana thayeri.

from 6.3–6.8 g ($\bar{x} = 6.6$ g); Clutch 2.—Six eggs were deposited on 15 May 1977; all hatched 5-6 July after 51-52 days. Hatchling snout-vent lengths were 201–233 mm ($\bar{x} = 207$ mm), tail lengths 35–45 mm ($\bar{x} = 38$ mm), and weight averaged 8.8 g (7.6-10.4 g); Clutch 3.-Copulation was observed 17 March 1978. Four eggs were laid 83 days later on 8 June. Mean egg length was 39 mm (36–46 mm) and egg diameter was 18–20 mm ($\bar{x} = 19$ mm). Three snakes hatched (date unrecorded) with snout-vent lengths of 174-179 mm $(\bar{x} = 176 \text{ mm})$ and tail lengths of 29–37 mm ($\bar{x} = 33 \text{ mm}$). Mean weight was 5.9 g (5.4-6.9 g); Clutch 4.—Four eggs were laid 26 May 1979. Egg length ranged from 53–64 mm ($\bar{x} = 60$ mm), egg diameter from 20–21 mm ($\bar{x} = 20.5$ mm), and weight of the adherent clutch was 40.4 g ($\bar{x} = 10.1$ g). One egg hatched on 25 July 1979 after 60 days. Hatchling snout-vent length was 207 mm, tail length was 38 mm, and weight was 8.3 g; Clutch 5.-Copulation was recorded 21 April 1979. Seven eggs were laid 40 days later on 31 May 1979. Mean egg length was 38 mm (35-42 mm), mean egg diameter was 20 mm (19-20 mm), and weight averaged 10.3 g (72.7 g for adherent clutch of seven eggs). Three hatched on 1 August 1979 after 62 days incubation. Hatchling snout-vent length ranged from 205-220 mm ($\bar{x} = 212$ mm), tail length from 33–40 mm ($\bar{x} = 37$ mm), and weight from 8.0–8.7 g ($\bar{x} = 8.3$ g). Grand means across five clutches (17 neonates) is as follows: snout-vent length 174–233 mm ($\bar{x} = 205$ mm), tail length 23–45 mm ($\bar{x} = 34$ mm) and weight 5.4–10.4 g ($\bar{x} = 7.7$ g).

J. E. Joy, Jr. (pers. comm.) reported five clutches of from 4-8 ($\bar{x} = 6.1$) eggs laid 9 May to 16 June. Two snakes hatched after 68 days from a clutch laid on 15 May. One female oviposited in four consecutive years. All spec-

| Source | Locality | Date of oviposition | Clutch size | Female size (mm) | Hatching date (incubation period) |
|------------------------------|----------------------------------|---------------------|----------------|------------------------|--------------------------------------|
| Barten (1981) | Onslow County, North Carolina | 4 June | 5 | 492 | 5-6 August (63) |
| Palmer (1961) | Pitt County, North Carolina | - | 6 | - | 23 August (—) |
| Herman (1979b) | Jasper County, South Carolina | 6 June | 4 | 572 | 11 August (66) |
| This paper | Jasper County, | 9 May | 7 | 524 | 26 June (46) |
| | South Carolina | 30 June | 4 | | did not hatch |
| Groves and Sachs (1973) | Duval County, | 3 June | 7 | 438 | 7-8 August (59, 60) |
| | Florida | | 4 | 397 | 7-8 August (59, 60) |
| Groves and Assetto (1976) | Dade County, Florida | 8 October | 5 | — | — (—) |

Table 6. Reproductive data for Lampropeltis triangulum elapsoides.

imens were taken from the above locality. Herman's (1979a) report on an additional captive breeding is apparently the only available reproductive information published for this taxon.

L. triangulum elapsoides. An immature female and adult male were taken near Ridgeland, Jasper County, South Carolina. The pair was maintained together and cooled to 15 C from 25 October 1978 to 26 February 1979. Weight and total length measurements taken 1 March 1979 were as follows: female 524 mm, 42.3 g, male 492 mm, 37.9 g. Although no copulation was observed, the female deposited a clutch of seven adherent eggs on 9 May 1979. Eggs ranged in length from 21–31 mm ($\bar{x} = 26.1$ mm), in diameter from 12–13 mm ($\bar{x} = 12.2$ mm), and total clutch weight was 18.4 g (\bar{x} egg weight 2.6 g).

Female ecdysis occurred 25 April, 14 days prior to oviposition. Hatching occurred 26 June 1979 after 46 days incubation. Seven neonates (four females, three males) measured 151-173 mm ($\bar{x} = 163 \text{ mm}$) in total length and weighed 2.8-4.1 g ($\bar{x} = 3.5 \text{ g}$).

The female was reintroduced to the male several days after oviposition. Although courtship and copulation were not seen, a second clutch of four adherent eggs was laid on 30 June 1979. Egg-length ranged from 31–33 mm ($\bar{x} = 32.3$ mm), egg-diameter from 11–13 mm ($\bar{x} = 12.0$ mm) and total clutch weight was 10.8 g (\bar{x} egg weight 2.7 g). The eggs discolored and developed mold two weeks into the incubation process. They were opened, and all contained dead embryos.

Williams (1978, for a review prior to 1974), Groves and Assetto (1976), Herman (1979b) and Barten (1981) published on reproduction in L. t. elapsoides. Herman's (1979b) report involved an additional captive breeding. Groves and Assetto (1976) speculated that a clutch laid 8 October might

| Source | Locality | Egg-laying | Clutch size | Hatching date (incubation) | Hatchling total length (mm) | x Egg dimensions (mm) | Female total length (mm) |
|------------------------------------|--------------------------|------------|----------------|--------------------------------------|---|-----------------------------|-----------------------------------|
| Hudson and Davis (1941) | Nebraska | July | 8-12 | - | - | 25 × 14 | _ |
| Iverson (1975) | Russell Co., Kansas | 27 June | 5 | 12–14 August (47–49) | 215, 235 | 34 × 14 | 590 |
| Iverson (1977) | Russell Co., Kansas | 29–30 June | 5 | 11–12 August (42–44) | 235 (x̄) | 38 × 16 | 620 |
| Marr (1944) | Ford Co., Kansas | - | 12 | -() | | 24 × 14 | 721 |
| Smith (1977) | Boulder Co., Colorado | 15 July | 4 | 29 August 1 September (45, 48) | 175, 186 | 43 × 19 | 650 |
| G. Carl (pers. comm.) | Weld Co., Colorado | 4 July | 4 | 25, 26 August (52, 53) | 173-185 ($\bar{x} = 181$) (N = 3) | 35 × 14 | - |
| R. K. Guese (pers. comm.) | Weld Co., Colorado | 7 July (2) | 4, 6 | — (—) | _ | - | — |
| J. E. Joy, Jr. (pers. comm.) | Weld Co., Colorado | 19 June | 4 | 19 August (61) | | - | - |

Table 7. Reproductive data for Lampropeltis triangulum gentilis.

have been a second seasonal egg-laying from their female. Because their snake was taken from near Miami, Dade County, Florida, at the extreme southern portion of the range, these data indicate that *L. t. elapsoides* is capable of multiple clutch production throughout much of its range. Table 6 presents reproductive data published to date on *L. t. elapsoides*.

L. triangulum gentilis. Three gravid females were collected 80 km NE Denver, Weld County, Colorado (R. K. Guese, J. E. Joy, Jr., pers. comm.). Two clutches of four and one clutch of six adhering eggs were deposited on 19 June 1977 and 7 July 1978 (two clutches). A clutch of four hatched on 19 August 1977 after an incubation period of 61 days. Measurements of eggs and hatchlings were not recorded.

Reproductive data available for L. t. gentilis are summarized in Table 7. Specific egg laying dates range from 19 June (J. E. Joy, Jr., pers. comm.) to 15 July (Smith, 1977). Clutch size ranged from 4–12 ($\bar{x} = 5.7$) eggs for seven clutches. G. Carl (pers. comm.) reported on a gravid female collected 26 June 1978. The female shed eight days prior to oviposition. Three of four eggs hatched and the neonates appeared ready to shed at hatching. Neonate ecdysis occurred on 31 August, four days after hatching. Knight and Collins (1977) reported on a gravid female collected on 31 May 1977 in Cheyenne County, in northwestern Kansas.

With an ovipositional span of slightly less than a month recorded for six clutches, it is probable that L. t. gentilis produces a single seasonal clutch in nature.

L. triangulum hondurensis. An adult pair from unknown localities was placed together in late March 1980. Reproductive activity was first seen after the female shed her skin on 3 April 1980. Copulation was noted shortly thereafter on 3 April and again on 20 April, but may have occurred at other times as the pair was maintained together. The female again shed on 21 May. Nine days later, on 30 May, a clutch of nine adherent eggs was laid. Egg diameter ranged from 24–27 mm (\bar{x} egg diameter = 25.5 mm), egg length from 50–62 mm (\bar{x} egg length = 56.7 mm) and weight of the total clutch was 242.9 g (\bar{x} egg weight = 26.9 g).

All eggs hatched on 4 August 1980 after 66 days of incubation. Snoutvent length ranged from 301-339 mm (\bar{x} snout-vent length = 318.2 mm), total length ranged from 358-395 mm (\bar{x} total length = 375.2 mm), and weight ranged from 20.9-24.4 g (\bar{x} weight = 22.5 g) for nine hatchlings. Sex ratio was four males and five females as determined by hemipenial eversion.

In males, the number of pre-anal red body bands ranged from 17–26 ($\bar{x} = 20$; adult male 22) and red tail bands from 4–7 ($\bar{x} = 5.2$). For females, these counts were 16–21 ($\bar{x} = 19.2$; adult female 17) and 4–6 ($\bar{x} = 4.6$), respectively. These counts fall within the ranges given by Williams (1978).

Two distinct color morphs were present. The adult female and four hatchlings (one male, three females) were typical of the description given by Williams (1978) for this subspecies. However, in the adult male and five hatchlings (three males, two females), the cream colored bands were invaded by orange pigment, giving the impression of an orange snake with black bands. This orange morph, commonly called the "tangerine phase," is well known in living collections but heretofore unmentioned in the literature, probably because most work to date has involved alcoholic specimens in which colors have faded. Figure 4 shows a juvenile specimen of each morph.

L. triangulum nelsoni. One male, and two females from unknown localities reproduced in five consecutive years (described, in part, by Tryon and Hulsey, 1976). Courtship and copulation were not observed. However, the females produced clutches of six moderately adherent eggs each on 18 June and 8 July 1977. One clutch measured 42–46 mm ($\bar{x} = 44$ mm) in egg-length, mean egg-diameter 19 mm, and egg weight ranged from 10.0–11.7 g ($\bar{x} =$ 10.4 g). Five eggs hatched after 53–56 days on 31 August–2 September. Five neonates had total lengths ranging from 265–276 mm ($\bar{x} = 271$ mm) and weights of 7.7–8.9 g ($\bar{x} = 8.2$ g). Although measurements were not taken on the 18 June clutch, three snakes hatched on 11 August (54 days). Mean total length was 254 mm (245–267 mm) and mean weight was 8.0 g (6.5–9.2 g).

In 1978 one female produced a clutch of seven non-adherent eggs on 29 June, and an additional clutch of four, three of which were laid on 10 Sep-

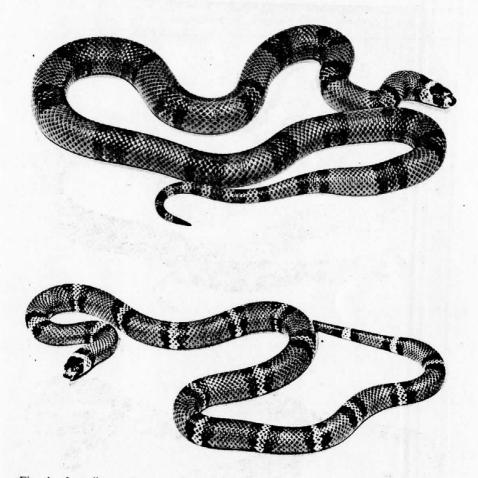


Fig. 4. Juvenile specimens of Lampropeltis triangulum hondurensis showing pattern morphs within single clutch.

tember. One egg was retained and deposited on 25 September. All later proved to be infertile.

This is apparently the first confirmation of multiple egg clutches in L. t. nelsoni. Kardon (1979) published on an additional captive breeding. Clutch sizes were four and three from two females.

L. triangulum sinaloae. A male collected 4.8 km S Mazatlan, Sinaloa, Mexico, and two females, (1) taken 11.2 km E Guamuchil, Sinaloa, Mexico, and (2) received from an unknown locality were available. Female 1 laid seven eggs on 18 June 1978 which hatched 25-26 August after 68-69 days of incubation. Female 2 produced clutches on 4 July and 17 August 1978.

| | Egg length (x) (mm) | Egg diameter (求) (mm) | Clutch weight (x) (g) | Hatchling s–v length (x) (mm) | Hatchling tail length (x) (mm) | Hatchling weight (x) (g) |
|-----------------------|------------------------|-----------------------------|-----------------------------|----------------------------------|--------------------------------------|-----------------------------|
| Clutch 1 | | | | | | |
| (N = 7) | 42-57 (48) | 21-23 (22) | 103.9 (14.8) | 231-241 (235) | 35-44 (40) | 9.7-11.3 (10.7) |
| Clutch 2 | | | | () | | 2.7-11.5 (10.7) |
| (N = 8) | 41-51 (44) | 20-23 (21) | 96.5 (12.0) | 184-246 (226) | 30-47 (39) | 6.1–11.1 (9.0) |
| Clutch 3 | | | | | | 0.1-11.1 (9.0) |
| (N = 4) | 53-61 (55) | 16-20 (17) | 48.2 (12.0) | 232–255 (247) | 42-45 (44) | 6.7-9.9 (8.8) |
| Clutch 4 | | | | | | 0.7-2.2 (0.0) |
| (N = 8) | 36-45 (41) | 20-22 (20) | 91.5 (11.5) | 213-245 (225) | 35-43 (37) | 9.7-11.3 (10.2) |
| Grand means across | | | | ۰. | | |
| clutches | | | | | | |
| (N = 27) | 36-61 (46) | 16-23 (20) | (12.5) | 184-255 (231) | 30-47 (39) | 6.1-11.3 (9.8) |

Table 8. Reproductive data for eggs and hatchlings of Lampropeltis triangulum sinaloae.

Clutch interval was 44 days. Mating for the first clutch was not observed. However, the pair was seen *in copulo* on 9 July 1978, five days after oviposition. Copulation was observed (female 1) on 28 April 1979, and 49 days later on 14 June female 1 laid a clutch of eight adherent eggs. All eggs hatched on 29 August 1979 after 76 days of incubation. Reproductive data on eggs and hatchlings are given in Table 8.

Williams (1978) mentioned that no previous reproductive information was available for this taxon. Courtship behavior was described by Gillingham et al. (1977). Kardon (1979) provided data on a clutch of four eggs and resulting hatchlings. This is the first confirmation of multiple egg clutches for L. t. sinaloae.

L. triangulum syspila. One male and three females were collected near Stanley, Johnson County, Kansas. A second male was taken at La Cygne, Linn County, Kansas. These snakes produced six captive-bred clutches of from 3–7 eggs ($\bar{x} = 5.5$ eggs) from 1975–77. Ovipositional dates for single clutches were 24 March, 18 April, 8 June and 13 June. One female produced a clutch of three fertile eggs on 7 May 1977, and a second clutch of six infertile eggs 39 days later on 15 June. All fertile eggs hatched with incubation periods ranging from 59–61 days ($\bar{x} = 60.6$ days) (J. E. Joy, Jr., pers. comm.).

J. T. Collins and G. R. Pisani (pers. comm.) discovered a gravid female (snout-vent length 543 mm, tail length 77 mm) near Lone Star Lake, Douglas County, Kansas, in June 1971. The female's weight was 61.1 g at 0930 hours, 2 July 1971. From 0936-1334 hours, 2 July, the female deposited seven eggs. Each egg was allowed to dry for 5-10 minutes, and the total clutch weight was 26.1 g ($\bar{x} = 3.7$ g). The female's weight after oviposition was 33.9 g.

Clutch weight (dry) was 42.7 percent of the female's pre-ovipositional weight. All eggs hatched 31 August-2 September 1971 after 61-63 days. Mean weight of seven neonates (four males, three females) was 3.2 g. Mean hatchling snout-vent length was 35.7 percent (34.1-37.0 percent) of the female parent's snout-vent length.

Published reproductive data for L. t. syspila were summarized by Williams (1978). Fitch and Fleet (1970) reported a copulating pair on 15 May. Previous reports indicate ovipositional dates have all been during June and July. It is problematical whether this taxon produces more than one clutch in nature, as three of our recorded dates are well before those reported for wild-caught snakes. Quite possibly, a number of taxa are capable of producing multiple egg clutches, but do so only under the most favorable conditions (captivity). Our clutch interval of 39 days represents the shortest reported to date. However, infertility of the second clutch may have been a factor.

L. triangulum ssp. A yearling male and two females were taken from 5.7 km SSW Zapotitlan, Puebla, Mexico, in desert terrain at an elevation of 1500 meters. This trio was seen courting on 31 March 1978, and both females produced clutches on 25 April, 55 days after observed courtship.

One clutch of six eggs averaged 21 mm (21–23 mm) in diameter, 44 mm (41–52 mm) in length, and mean egg weight was 13.6 g (weighed in two clusters of 28.2 and 53.4 g). Two neonates hatched on 17 June (53 days) possessing snout-vent lengths of 212 and 232 mm ($\bar{x} = 222$ mm), tail lengths of 35 and 40 mm ($\bar{x} = 37.5$ mm) and weights of 6.5 g and 10.0 g ($\bar{x} = 8.4$ g).

The second clutch of four eggs averaged 19–20 mm ($\bar{x} = 19$ mm) in diameter, 48–56 mm ($\bar{x} = 52$ mm) in length, and weight of the adherent clutch was 51.1 g (\bar{x} egg weight 12.8 g). Three snakes hatched with snout-vent lengths of 210–234 mm ($\bar{x} = 218$ mm), tail lengths of 34–40 mm ($\bar{x} = 36$ mm), and weights of 6.4–10.0 g ($\bar{x} = 8.1$ g).

In 1979, one female produced three clutches of eggs. This female was observed copulating on 28 April 1979, and a clutch of seven eggs was laid 32 days later on 30 May. Egg length ranged from 40–50 mm ($\bar{x} = 45$ mm), egg diameter from 20–23 mm ($\bar{x} = 21$ mm), and weight of the adherent clutch was 99.0 g (\bar{x} egg weight 14.1 g). All eggs hatched 61 days later on 30 July. Hatchling snout-vent lengths ranged from 235–251 mm ($\bar{x} = 245$ mm), tail lengths from 36–43 mm ($\bar{x} = 40$ mm), and weight from 10.2–11.9 g ($\bar{x} = 11.2$ g). Breeding occurred during the first week of June 1979, and the second clutch was deposited on 19 July, consisting of three eggs and one infertile mass. Measurements for the three eggs were as follows: egg length ranged from 39–42 mm ($\bar{x} = 40$ mm), egg diameter from 21–22 mm ($\bar{x} = 21$ mm), and clutch weight was 34.5 g (\bar{x} egg weight 11.5 g). One neonate emerged 64 days later on 22 September 1979 and had a snout-vent length of 228 mm, tail length of 38 mm, and a weight of 9.0 g. Breeding for the third clutch

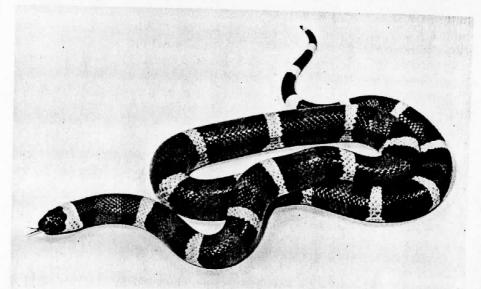


Fig. 5. Juvenile specimen of Lampropeltis triangulum ssp. from Puebla, México.

occurred on 24 July 1979. Six eggs plus one infertile mass were laid on 4 September, 42 days after observed copulation. For six eggs, mean egg length was 42 mm (38–50 mm), mean egg diameter was 21 mm (21–22 mm), and mean egg weight was 12.2 g (adherent clutch weight 73.5 g). All eggs spoiled shortly into incubation but were opened and found to contain dead embryos.

Grand means across five clutches (26 eggs) were as follows: egg length ranged from 38–56 mm ($\bar{x} = 45$ mm), egg diameter ranged from 19–23 mm ($\bar{x} = 21$ mm), and mean egg weight for five adherent clutches was 13.0 g. For 13 hatchlings, snout-vent length ranged from 210–252 mm ($\bar{x} = 234$ mm), tail length ranged from 35–43 mm ($\bar{x} = 38$ mm), and weight from 6.4– 11.9 g ($\bar{x} = 9.8$ g).

Figure 5 shows a juvenile of this undescribed taxon. Features immediately apparent include distinct banding and increased width of the white bands. The taxonomic status of this snake is presently under investigation (H. Quinn, pers. comm.).

L. zonata parvirubra. Two adult specimens were available, a male hatched 13 May 1969 from a clutch laid by a female gravid when collected in Fish Canyon, San Gabriel Mountains, Los Angeles County, California, and a female acquired 27 April 1971 from the same locality.

Three adherent eggs were produced on 13 May 1978. Egg diameter ranged from 16–18 mm ($\bar{x} = 17$ mm), length ranged from 40–45 mm ($\bar{x} = 43$ mm), and adherent clutch weight was 24.2 g (\bar{x} egg weight 8.0 g). Hatching oc-

curred on 30 June after 48 days incubation. Hatchlings ranged from 199–215 mm ($\bar{x} = 206$ mm) in snout-vent length, and had tail lengths of 35–41 mm ($\bar{x} = 39$ mm). Weight ranged from 5.7–6.4 g ($\bar{x} = 6.1$ g).

A clutch of four adherent eggs was deposited on 29 May 1979. Mean egg length was 41 mm (40–44 mm), mean egg diameter was 17 mm (17–18 mm), and mean egg weight was 8.6 g (adherent clutch weight 34.7 g). Three males hatched on 22 July 1979 after 54 days of incubation. Hatchling total lengths ranged from 260–272 mm ($\bar{x} = 265$ mm), and weight ranged from 6.4–7.7 g ($\bar{x} = 7.1$ g).

Grand means across both clutches (seven eggs) were as follows: egg length ranged from 40-45 mm ($\bar{x} = 42$ mm), egg diameter from 16-18 mm ($\bar{x} = 17$ mm), and mean weight of eggs from adherent clutches was 8.4 g. For six hatchlings, total length ranged from 240-272 mm ($\bar{x} = 254$ mm) and weight from 5.7-7.7 g ($\bar{x} = 6.6$ g). The neonates began feeding on small Uta stansburiana and gradually switched to newborn mice.

Reproductive data are scanty on this comparatively well known species. Zweifel (1952) mentioned a clutch of eight eggs for *L. z. parvirubra*. Cunningham (1959) noted three eggs in a female taken 18 July. Stebbins (1954) gave 61 days as the incubation period for one clutch.

Body/tail triad counts for the adult pair herein were 35/7 (male) and 35/5 (female). For six hatchlings these were 34/6, 34/6, 35/6, 33/7, 39/6 and 39/7.

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