AN INVENTORY OF REPRODUCTION AND SOCIAL BEHAVIOR IN CAPTIVE GRAY-BANDED KINGSNAKES, LAMPROPELTIS MEXICANA ALTERNA (BROWN)

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ABSTRACT: Ritualized combat between *& alterna*-phase and *blairi*-phase *Lampropeltis mexicana* was observed. Courtship and copulatory sequences between a *blairi*-phase pair and *alterna*-phase pair were seen the following day. Unsuccessful courtship sequences between a *blairi*-phase *&* and *alterna*-phase *&* were recorded. No eggs resulted from these matings.

Additional agonistic interactions were observed between different blairi-phase & & , and both were involved in 14 courtship and copulatory behavioral patterns with 2 other blairi-

phase ♀♀.

Data for 2 clutches of eggs, incubation period, emergence and pattern of the neonates are presented and discussed. Comparisons are made between the combat, courtship and copulatory behavior of *L. mexicana* and other American colubrid snakes.

Although various authors have reported on the ecology and natural history of kingsnakes of the mexicana complex (see Gehlbach and Baker, 1962; Gehlbach, 1967; Raun and Gehlbach, 1972 for a review), descriptions have not included references to ritualized combat and courtship-copulatory behavior. Reproduction was reported by Tanzer (1970) who concluded that the variation of 5 sibling young which exhibited the pattern types of alterna and blairi suggested that the 2 presumed subspecies were polymorphs of the same taxon. Our observations include interactions with both alterna- and blairi-phase kingsnakes. Behavioral comparisons with congeners and other colubrid snake species studied to date indicate aspects which differ in part from kingsnakes of the mexicana complex.

MATERIALS AND METHODS

Nine Texas specimens of Lampropeltis mexicana alterna were available for study: male A dark alterna morph (total length 109.5 cm) was collected 26.5 km N and 2.4 km E Comstock, Val Verde County on 11 July 1968; male B dark blairi morph (total length 123.5 cm) was found 20.9 km N and 4.8 km W Comstock, Val Verde County on 15 August 1968; male C dark blairi morph (total length 86.2 cm) was collected 8.8 km N Langtry, Val Verde

County during September 1972; male D light blairi morph (total length 84.0 cm) was captured 8.8 km N Langtry, Val Verde County on 17 May 1973; female E dark blairi morph (total length 88.2 cm) was collected 1.6 km S and 8.0 km E Langtry, Val Verde County on 16 August 1968; female F light alterna morph (total length 100.0 cm) was taken 16.0 km N and 4.8 km W Comstock, Val Verde County on 11 July 1968; female G light alterna morph (total length 85.5 cm) was collected 16.0 km W Lajitas, Presidio County on 28 May 1973 while it was being attacked by a ringtail "cat", Bassariscus astutus (R. K. Guese, personal communication); female H dark blairi morph (total length 93.1 cm) was found near Langtry, Val Verde County during June 1973; female I dark blairi morph (total length 79.9 cm) was taken south of Shumla, Val Verde County on 18 May 1969.

Since 1968, various combinations of snakes A, B, E, F were tried in unsuccessful attempts to elicit reproductive behavior. During that period, the snakes were maintained indoors in glass-fronted fiberglass cages measuring $77 \times 50 \times 37$ cm with gravel substrate. The ambient temperature varied between 27° – 34° C and the relative humidity averaged 50%. Skylights provided a natural photoperiod. In 1975, the snakes

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were placed in an outdoor enclosure between May and September. The temperature varied between 27–35°C during daylight hours and dropped to between 18–27°C at night.

Snakes C, D, H, I were kept in cages within a room having a southern exposure; large windows provided a natural photoperiod. Water was always available but the cages were dry. The temperature was allowed to drop naturally and food was withheld after the end of November. During January and February, the low temperature averaged 9°C but increased as much as 4°C during a warm day. Generally, activity was noted whenever the temperature rose above 15°C. By mid-March, the range was 14°-18°C and increased movement was recorded. All snakes began eating laboratory mice during mid-April when the temperature began to average 22°C.

The combat interactions described below were recorded with still photographs taken sequentially at 2 to 3-s intervals.

OBSERVATIONS AND DISCUSSION

Ritualized combat was observed as follows: males A and B with females E and F present on 24 September 1975; males C and D with females H and I present on 20–27 May 1976. The snakes were maintained together for periods ranging from 2 weeks to >1 year. Terminology follows the usage of Carpenter et al. (1976) and that recommended by Charles Carpenter and James Gillingham (personal communication). A synopsis of an agonistic encounter lasting 305 min between males A and B is presented whereupon B was removed to avoid stress.

A typical bout lasted about 5 min from the time of contact to disengagement and many bouts were observed throughout the entirety of the combat.

Recognition—Investigation.—Both snakes investigated the cage until contact was made frontally (Fig. 1). Both snakes hovered ≈ 4 cm from the substratum and



Fig. 1.—Recognition—Investigation phase of ritualized combat posture in *Lampropeltis mexicana alterna*.

began a rapid volley of tongue-flicks (1/s). Each snake attempted to move anteriorly

along the body of its opponent.

Elaphe obsoleta bairdi (Brecke et al., Lampropeltis doliata (Shaw, 1951), Lampropeltis c. calligaster (Moehn, 1967), Lampropeltis getulus holbrooki (Charles Carpenter and James Gillingham, personal communication), Masticophis t. taeniatus (Bennion and Parker, 1976) and Pituophis melanoleucus (Shaw, 1951: Bogert and Roth, 1966) have been reported to engage in hovering-like activity. Vertical hovering-like behavior seems to be most prominent in Elaphe l. longissima (Stemmler-Morath, 1935). This behavior may be described as the act by one snake of raising its head and anterior trunk region over that of another, moving back and forth laterally or backwards and forwards (Charles Carpenter and James Gillingham, personal communication).

Alignment.—Both snakes continued to move in an anterior plane to accomplish longitudinal alignment of the bodies. Biting by both snakes in the region of the opponent's neck, midbody and tail occurred regularly, perhaps as a mechanism to facilitate alignment. When the snakes were in contact, either by being perpendicular to the lateral surface of the rival's body or through incipient dorsal advance movements, pronounced body jerks (forward jerk, jerk crawl) were apparent.

Some colubrid snakes perform body jerks during combat: Elaphe g. guttata and Lampropeltis doliata annulata (Shaw,

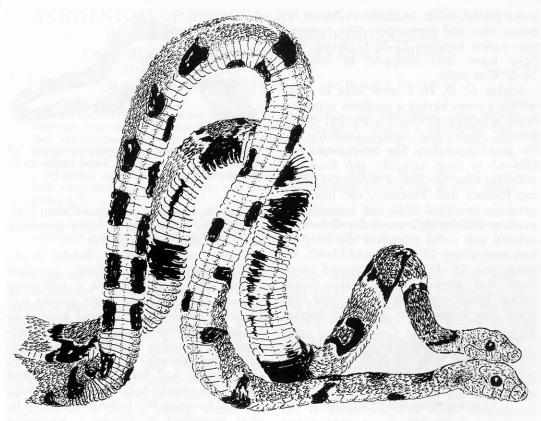


Fig. 2.—Solicitation Display in Lampropeltis mexicana alterna.

1951) and L. g. holbrooki (Charles Carpenter and James Gillingham, personal communication).

Drymarchon (Tinkle, 1951), Elaphe obsoleta bairdi (Brecke et al., 1976), Masticophis t. taeniatus (Bennion and Parker, 1976), Pituophis (Woodbury, 1941), Sonora e. episcopa (Kroll, 1971) and all 3 Lampropeltis species mentioned above have been reported to bite at some point during combat.

Charles Carpenter and James Gillingham (personal communication) have observed that male combatants of L. g. holbrooki at times had parts of the trunk or tail region lying or moving over the opponent.

Solicitation Display.—Each snake was in a hovering stance and the heads were about 2.5 cm apart and 4 cm above the substratum. Both snakes formed body bridges or bows by pressing their heads and 2–3 cm of the cervical region upon the substratum as *points d'appui* (Fig. 2). The bridges were generally at a 45° angle above the ground and touching seemed to stimulate bowing. Formation of bridges by the snakes seemed to be opportunistic as any available vertical surface, including the sides of the cage, was used to gain an advantage. Amplitude of the bows varied from 10–37 cm. Occasionally, the males formed bows as they touched the body of a female but females showed no inclination to develop bows.

Formation of bows by males when encountering females may be "... indiscriminate heterecious sexual behavior wherein sexual discrimination is subnormal. Bogert and Roth have made it plain that disruption of sensory cues so vital to sexual discrimination.

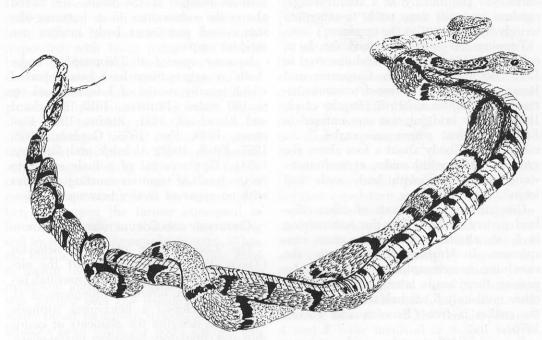


Fig. 3.—Topping attempt in Lampropeltis mexicana alterna.

nation often occurs in captivity" (Smith, 1968).

Orientation.—When one snake was out of position, the other tended to orient on the opponent's body bridge by moving in an anterior plane for realignment. At this stage, S-shaped lateral bends were loosely draped over the rival. No definite head orientation was apparent. When one snake was aligning on the opponent's body bridge or moving anteriorly along the dorsum, the lower snake tried to throw off the rival's head with violent body jerks.

Topping.—Body bridges were pressed down against the resistance of the opponent's body bridges; this behavior developed a "corkscrew" effect as the hovering or bridging attempts moved posteriorly down the longitudinal axes of the bodies (Fig. 3). Each snake attempted to maintain its head and anterior trunk upright to counteract the force of the opponent; hence the anterior portions of the bodies were less entwined. Bows were used to

press down the head and anterior trunk of the opponent and the snakes moved forward slowly in their efforts to maintain superior positions. This forward motion was accomplished through cephalocaudal waves. Bows were formed in 5-8 s and there were usually no multiple bows. Charles Carpenter and James Gillingham (personal communication) have observed that male L. g. holbrooki responded to contact by the opponent by bowing violently presumably to disorient the snake above. This pattern differs in part from L. m. alterna insofar as the anterior trunk bowing was used as an integral mechanism for topping. Both L. m. alterna combatants were consistent in trying to form the bows quickly, usually within a dorsoventral plane; then attempts were made in a lateral plane to use the bow to press down upon the opponent's bow of less amplitude. Successful placement of the bow included greater height with the position of the bow anterior to that of the rival. When one snake was positionally at a disadvantage, rigorous attempts were made to move anteriorly by orienting on the opponent's bow.

Topping has been described for L. c. calligaster (Moehn, 1967), and observed in L. g. holbrooki (Charles Carpenter and James Gillingham, personal communication) and Elaphe o. bairdi (Brecke et al., 1976). Body bridging was encountered in Elaphe obsoleta where one snake ". . . raised the midbody about a foot above the ground. The second snake, at such times would cover him with body coils and loops" (Rigley, 1971).

Comparisons of accounts of other colubrid genera suggest that the intertwining in L. m. alterna is one of the most conspicuous. In Masticophis t. taeniatus, the entwining is accomplished by the males passing their heads laterally over one another until only 5 cm behind the heads of the snakes is free (Bennion and Parker,

1976).

Recovery.—When either snake successfully pinned the head of the rival with a bow, the other tried to withdraw from beneath the coil quickly or turn over the

opponent with a counter action.

Submission.—Each snake attempted to turn the opponent onto its dorsum, thus effecting total immobilization. Superiority seemed to be established by snake (A) pursuing snake (B) around the cage and moving anteriorly along the body of B with its head pressed against the dorsum of B. B refused to engage in combat but instead tried to escape. A raised its tail and left some intermittent marks which were probably musk or uric acid. A superiority shift between males A and B was also noted.

Bogert and Roth (1966) in analyzing the postures assumed by male combatants, described 4 general types of ritualized behavior; the first refers to colubrids and is a situation where the rivals are ". . . with most of their bodies, or at least the posterior portions, entwined and extended behind heads more often in horizontal positions and scarcely raised above the substratum." Lampropeltis m. alterna differs from that account insofar as the heads are raised above the substratum in a hovering-like stance and prominent body bridges are

used for topping.

In some species of Thamnophis, snake "balls" or aggregations have been reported which usually consist of 1 female and up to 100 males (Ruthven, 1912: Blanchard and Blanchard, 1941; Breder, 1946; Finneran, 1949; Fox, 1955; Gardner, 1955, 1957; Fitch, 1965; Aleksiuk and Gregory, 1974). Displacement of a male seems to be the result of vigorous courting activities with no apparent rivalry between males.

COURTSHIP AND COPULATORY BEHAVIOR

The "Coluber type" of mating behavior (Davis, 1936) describes in part the elements observed by us in the precoital behavior of L. m. alterna. Gillingham et al. (1977) developed a behavioral triphasic schema to describe the elements of courtship and copulatory behavior: tactile-chase. tactile-alignment, intromission and coitus. Terminology follows the usage of Gillingham (1976) and Gillingham et al. (1977). Three sequences were recorded between 25-28 September: male A and female G with copulation; male B and female E with copulation; male B and female F with precoital behavior, no copulation. Fourteen additional sequences between males C and D and females H and I were observed between 20 May and 9 June 1976. snakes were maintained together for periods ranging from 2 weeks to >1 year.

In many of the courtship and copulating sequences, combating males were present; hence the tactile-chase phases were interrupted by intermittent aggressive encounters and the duration of time could not be calculated accurately for this phase. The following account is a compilation of observed reproductive interactions with a

single pair of snakes.

Tactile-Chase.—This phase may be defined as that ". . . period of time from the onset of courtship activity until the first copulatory attempt" (Gillingham et al., 1977). Pre-coital behavior began with the male courting the female with a series of body jerks as he contacted her; the female responded with body jerks. The female began to exhibit flight behavior whereupon the male pursued and tried to align by dorsal advance movements, either sagittally, parasagittally or laterally. The female began slight body twitching and vigorous side-toside twitching of her tail regularly occurred throughout this phase. The male showed active tongue-flicking (1/s). The female crawled slowly away from the male and remained quiescent until he encountered her, whereupon the former attempted to force the female to abandon her resting coil by initiating vigorous body jerks. When the female began to crawl, the male tried to mount by moving anteriorly along the middorsal line of the female until his head was aligned over the female's head. The male's head remained stationary over the female's head while his body jerked. The male began to align his body posteriorly over the female's middorsal line while adpressing her head to the substratum. The male's tail did not encircle the female's tail as he tried to align the cloacae. longest tactile-chase phase lasted 50 min. In reproductive encounters involving 2 males in combat with a female present, the duration of time from the male's incipient dorsal advance movements toward the female to the onset of the tactile-alignment phase was very brief, varying from 7-9 s. Receptivity of the female appeared to be indicated by an uplifted tail for in those instances where the female did not raise her tail, copulation was not accomplished. Biting of the female by a male was noted in 1 instance, but this may have been a misdirected response stimulated by the presence of an additional male.

Lampropeltis triangulum sinaloae engaged in the tactile-chase phase for 2.5–9.0 min ($\bar{x} = 5.5$), according to Gillingham et al. (1977). Averages for this phase of 5.0 min, 12.5–13.0 min, 10.3 min and 45 min have been recorded for Elaphe guttata (Gillingham, 1976), Elaphe v. vulpina (Gil-

lingham, 1974, 1976), Elaphe obsoleta (Gillingham, 1976) and Elaphe obsoleta bairdi (Brecke et al., 1976), respectively.

The side-to-side twitching movement of the tail exhibited by the female *L. m. alterna* corresponds in part to that described for *Pituophis* (Shaw, 1951) and *Elaphe g. guttata* (Holman, 1960) except that our various female *L. m. alterna* did not show as prominent a behavioral pattern.

Tactile-Alignment.—Gillingham et al. (1977) refer to this phase as the onset of the first copulatory attempt or "tail-search copulatory attempt (TSCA)." This phase occupied 3 min with a single pair of snakes and varied between 2–15 s with 2 males and a female. Cloacal gaping by various females was observed in some instances. Low intensity caudocephalic waves by the males were observed. The male's tail never passed beneath the venter of the female. Snakes A and F were involved in 8 Tail Search Copulatory Attempts with no intromission.

In Lampropeltis triangulum sinaloae, an average of 10 TSCA was recorded before intromission and this phase lasted 33 min (Gillingham et al., 1977). Gillingham (1976) listed an average of 4.5 min in Elaphe guttata, 9.9 min in E. vulpina and 18.3 min in E. obsoleta.

Intromission and Coitus.—This phase was recorded in 16 instances and varied between 4-15 min. The heads of the snakes were usually separated. In a typical postcopulatory sequence, the male (B) retracted his hemipenis and both snakes crawled slowly away from each other with the tails raised to a 45° angle from the substratum. The tails were slowly lowered (2.5 min) as the snakes crawled about the cage. Snakes A and G remained in copula for 4 min; when the male withdrew, a bloody mucoid liquid was trailing from the female's cloaca. In all cases, the female's venter rested upon the substratum whereas the male's body rested on the ventrolateral portion in order to effect penetration of the hemipenis without encircling the tail of the female (Fig. 4).

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Fig. 4.—Copulation between & D and & H Lampropeltis mexicana alterna.

The coital position of the tails for Lampropeltis may apparently vary from no encircling of the tail by the male in L. m. alterna to ". . . the last part of their tails being entwined" in Lampropeltis doliata oligozona (Meyer-Holzapfel, 1969).

Tanzer (1970) discussed cloacal hemorrhaging in the *mexicana* complex and McCoy and Gehlbach (1967) felt that it was a physiological side effect of defensive behavior in females. The tail-raising behavior after coitus exhibited by the participating *L. m. alterna* corresponds to the pattern found in *Lampropeltis t. sinaloae* (Gillingham et al., 1977) and *Elaphe* (Gillingham, 1976).

The males of certain natricine snake species form copulatory plugs which prevent insemination by conspecific rivals (Fitch, 1965; Devine, 1975). Devine (1975) suggested that male combat or other behavioral patterns may lessen the selective advantage of a plug. Highly

Table 1.—Behavioral elements in colubrid snake courtship and copulation.

Biting or absence of biting

Coluber constrictor (Wright and Wright, 1957) Elaphe obsoleta (Noble, 1937; Gillingham, 1976)

E. o. bairdi (Brecke et al., 1976)

E. o. quadrivittata (Brecke et al., 1976)

Elaphe subocularis (Tryon, 1976)

Elaphe v. vulpina (Carpenter, 1947; Simonson, 1951; Gillingham, 1974)

Lampropeltis getulus californiae (Wright and Wright, 1957)

L. g. holbrooki (Meade, 1932)

L. triangulum sinaloae (Gillingham et al., 1977)

L. t. syspila (Fitch and Fleet, 1970)

Masticophis t. taeniatus (Bennion and Parker,

Masticophis t. taeniatus (Bennion and Parker, 1976)

Pituophis melanoleucus (Perkins, 1943; Shaw, 1951) Sonora e. episcopa (Kassing, 1961; Kroll, 1971)

Duration of coitus

Coluber constrictor (Noble, 1937; Fitch, 1963) Elaphe guttata (MacMahon, 1957; Holman,

1960; Gillingham, 1976)

Elaphe obsoleta (Mansueti, 1946; Johnson,

1950; Gillingham, 1976) E. o. bairdi (Brecke et al., 1976)

Elaphe v. vulpina (Gillingham, 1974, 1976)

Lampropeltis getulus holbrooki (Noble, 1937) L. triangulum sinaloae (Gillingham et al.,

1977) Sonora e. episcopa (Kroll, 1971)

Storeria dekayi (Noble, 1937)

Thamnophis brachystoma (Pisani, 1967)

Thamnophis butleri (Noble, 1937)

T. s. sirtalis (Fitch, 1965)

T. s. parietalis (Munro, 1948)

tenuous evidence of this is suggested by the short interval (10 min) between the copulations of males C and D and female H on 20 May although the female was not examined after copulation.

Table 1 lists elements of courtship and copulatory behavior known in colubrid snakes as compiled from published accounts, and which serve as a comparison with behaviors in *L. m. alterna*.

EGG-LAYING, EGGS AND HATCHING BEHAVIOR

On 29 March 1975, an additional young male alterna-phase kingsnake was introduced to females

Table 2.—Data on hatchling Lampropeltis mexicana alterna.

Egg No.	Date hatch		Length (mm)			Red bands			Tail length
		h Wt (g)	Total	Tail	Subcaudals	Body	Tail	Total	Total length
Clutch 1			le me /	max vi	.noleslof/Wei			agh, wire	and distribution
1	10 Sep	6.5	227	33	57	10	2	12	14.5
2	10 Sep	7.8	246	40	62	12	1	13	16.2
3	10 Sep	7.0	222	35	57	11	2	13	15.7
4	11 Sep	8.2	225	36	61	12	1	13	16.0
5	10 Sep	10.2	261	43	54	13	2	15	16.4
6	9 Sep	7.7	223	35	56	11	2	13	15.6
		\bar{x} 7.9	234	37	57.8	11.5	1.6	13.1	15.7
Clutch 2									
7	10 Sep	10.5	279	44	63	14	1	15	15.7
8	9 Sep	7.5	230	38	58	12	2	14	16.5
9	10 Sep	8.3	258	40	62	12	1	13	15.5
10	10 Sep	9.1	256	40	59	13	1	14	15.6
11	11 Sep	9.7	251	36	56	13	2	15	14.3
12	10 Sep	10.6	267	40	56	11	2	13	14.9
13	10 Sep		243	35	57	13	1	14	14.4
14	12 Sep		257	39	56	12	2	14	15.1
		\bar{x} 9.4	255	39	58.3	12.5	1.5	14	15.2
	Gr	and \bar{x} 8.8	246	38.1	58.1	12.0	1.5	13.6	15.4

H and I for approximately 1 month but no courtship behavior was apparent. At 1000 on 23 July 1975, female H was found coiled around a clutch of 9 moist, soft, slightly adherent eggs. Incubation techniques have been described earlier (Tryon, 1975) and the temperature varied between $25\,^\circ-33\,^\circ\mathrm{C}$. Measurements and weights are as follows: length 33.0-38.0 mm, $\bar{x}=34.8$; diameter 18.0-21.0 mm, $\bar{x}=19.0$; weight 7.0-7.6 g, $\bar{x}=7.2$. All eggs were infertile.

A plastic box filled with damp sphagnum moss was placed in the enclosure on 7 June 1976; on 7 July at 1700 h, female I was coiled beneath the sphagnum around 7 strongly adherent eggs (clutch 1). Two days later at 1500 h, female H was ovipositing and, by 1700 h, she laid 5 additional firm, white, strongly adherent eggs for a total of 8 (clutch 2). Measurements and weights are as follows: (clutch 1) length 36.0-41.0 mm, $\bar{x}=39.0;$ diameter 17.0–21.0 mm, $\bar{x}=20.0;$ weight of adherent egg mass 65.2 g, $\bar{x}=9.3;$ (clutch 2) length 38.0–45.0 mm, $\bar{x} = 41.0$; diameter 22.0-24.0 mm, $\bar{x} = 23.0$; weight of adherent egg mass 104.5 g, $\bar{x} = 13.0$. The grand means across fertile clutches were: length 40.0 mm, diameter 21.0 mm, weight 11.3 g. On 14 July, an egg from clutch 1 was discovered to be infertile. Two of the clutches reported for L. m. alterna earlier, 5 (Gehlbach and McCoy, 1965) and 6 (Tanzer, 1970) were smaller than our clutches.

On 7 September, egg 12 was compressed on the upper side and egg 13 was in the same con-

dition the next day. By 1800 h on 9 September, eggs 6 and 8 had been longitudinally slit and both snake's heads were protruding from the shells just past the eyes. Egg 1 developed 2 drops of moisture on the upper surface of the shell which increased to >20 drops over a 3-h period. At 2235 h, a dorsolateral slit was cut by the neonate, followed by a smaller slit a minute later. Two longer longitudinal slits were made on the upper surface of the egg during two 10-min increments and the hatchling's snout protruded at 2256 h. It appeared that the hatchling's snout moved in a longitudinal plane from right to left within the unslit egg. Only 2 eggs exhibited shrinkage prior to hatching, and moisture on the surface of the shell was seen in only 1 instance. By 1800 on 10 September, 5 of the eggs from clutch 1 and 6 of the eggs from clutch 2 were slit; all were slit by 1200 h on 12 September. The hatchlings remained in the eggs from 12–24 h before emerging and no egg teeth were visible. Incubation periods ranged between 62-64 and 60-63 days for clutches 1 and 2 respectively. All hatchlings immediately burrowed beneath the Measurements vermiculite upon emergence. (Quinn and Jones, 1974) and weights were taken on 12 September. Meristic data are presented in Table 2. The basic coloration of the hatchlings from clutch 1 corresponded to the light blairi phase pictured by Conant (1975, plate 32). In clutch 2, the gray saddles were intermediate in color between the 2 blairi-phase specimens represented by Conant (1975). Although all 14

hatchlings fit the description for the blairi phase of L. m. alterna (Tanzer, 1970), most of those from clutch 2 have alternating black markings laterally along the length of the body. Several have solid black heads and black venters with light blue-gray dorsal and lateral ground color. Only 1 of the young from clutch 1 tends to have a black head; the others have light gray heads with some symmetrical to irregular black markings.

Most of the hatchlings drank water soon after hatching. Within 24–48 h after hatching all snakes were becoming dull in preparation for shedding which took place 8–10 days of age.

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