

COURTSHIP AND MATING BEHAVIOR OF THE SPECKLED KINGSNAKE, *LAMPROPELTIS GETULUS HOLBROOKI*

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ABSTRACT: The mating behavior of wild-caught speckled kingsnakes, *Lampropeltis getulus holbrooki*, was analyzed in a laboratory situation over a 3-yr period. Mating bouts were recorded on videotape and were divided into three phases for analysis: tactile-chase, tactile-alignment, and intromission and coitus. The behavioral motor patterns performed by the males include Touch, Mount, Chase, Chase-Mount, Dorsal-Advance Movement, Forward-Body Jerk, Writhe, Biting, Tail-Search Copulatory Attempt, and Intromission. The mean duration, relative frequency, relative duration, and the sequence of these actions were analyzed. The relative frequency and duration of Forward-Body Jerk and Writhe differed significantly between Phases I and II. The major behavioral motor patterns were performed in a sequential pattern with Writhe being performed most frequently. Male tongue-flick and Forward-Body Jerk rates increased from Phase I to Phase II. The percent of body contact and specific dorsal contact between the mating pair increased from Phase I to II, then decreased during Phase III. The average durations of phases and specific actions performed are compared with other forms of *Lampropeltis* and other species of snakes. The durations of the three courtship phases of *L. getulus holbrooki* are relatively longer than those observed in other colubrid snakes.

Key words: Behavior; Mating; Reptilia; Colubridae; *Lampropeltis*

STUDIES of the reproductive behavior of different species of lizards, snakes, and turtles have shown that reptilian reproductive behavior can be very active, intricate, and even "ritualistic" (for review see Carpenter, 1980; Carpenter and Ferguson, 1977). A number of studies document courtship and mating behavior of snakes, but many early accounts of these behaviors provided only anecdotal descriptions (Gloyd, 1947; Meade, 1932; Simonson, 1951). Other accounts (Blanchard and Blanchard, 1942; Noble, 1937; Oliver, 1956) emphasized identification of specific actions and made comparisons. Though these early studies provided the basic framework for later works, methods for describing the observed behaviors varied, making subsequent interspecific behavioral comparisons difficult.

Gillingham et al. (1977) and Gillingham (1979) described a method to split a complete courtship and mating bout into a triphasic behavioral schema and provided a basic terminology to label the specific actions performed by courting and mat-

ing snakes. The development of a standardized terminology and a triphasic behavioral schema facilitates comparing the reproductive behavior of different snake taxa. This format has since been used to describe and analyze the reproductive behavior of other species of snakes (Barker et al., 1979; Brecke et al., 1976; Gillingham, 1977; Gillingham and Chambers, 1980, 1982; Gillingham et al., 1983; Lewke, 1979; Murphy et al., 1978).

From 1982-1984, I studied the reproductive behavior of the speckled kingsnake, *Lampropeltis getulus holbrooki*. The objectives of this study were to (1) record courtship and mating bouts of these snakes, (2) analyze the different motor patterns applying the terminology developed by Gillingham (1979), (3) examine individual mating bouts using the triphasic behavioral schema, and make qualitative and quantitative comparisons of certain behavioral factors among the phases, and (4) compare the reproductive behavior of the speckled kingsnake with that of other snakes.

MATERIALS AND METHODS

The speckled kingsnake, one of seven members of the *L. getulus* complex, exists

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in a variety of habitats, primarily woodland and riparian. It ranges from southern Iowa, extreme western Tennessee and southwestern Alabama, west through southeastern Nebraska, Kansas, Oklahoma, and eastern Texas (Conant, 1975). The 24 (12 males and 12 females) speckled kingsnakes used in this study were wild-caught adults from Oklahoma, except two from northwestern Louisiana and one from northeastern Texas. Snout-vent length and total length of males averaged 103.8 cm (range = 82.5–128.4, SD = 13.2) and 116.9 cm (range = 94.5–144.8, SD = 15.1), respectively. Mean values for females were 84.2 cm (range = 67.8–101.5, SD = 11.6) and 95.6 cm (range = 76.8–115.5, SD = 13.5).

This study was conducted at the Animal Behavior Laboratory of the Department of Zoology, University of Oklahoma. Snakes were individually housed in either 10-gal aquaria (50.8 × 25.4 × 30.5 cm) or 55.9 × 30.5-cm fiberglass cages and were maintained on a weekly diet of young mice with water always available.

Temperature and light-period changes, as experienced during winter dormancy, are very important in controlling the reproductive cycle of many reptiles (Crews and Garrick, 1980; Duvall et al., 1982). Placing snakes in a cooled environment at the time of their natural hibernation is conducive to reproduction following removal (Huff, 1979, 1980; Laszlo, 1976). For this reason, snakes were artificially hibernated during the winter in either an outdoor hibernaculum (Gillingham and Carpenter, 1978) or a 3.66 × 4.88 × 2.74-m environmental chamber (Sherer model CER 1216). Snakes were placed in the hibernaculum in 1982 (7 January–27 February) and 1983 (13 January–27 February). Mean temperature within the hibernaculum was 7.46 C (SD = 1.71) in 1982 and 9.48 C (SD = 2.74) in 1983. The following year snakes were placed in the environmental chamber (11 December 1983–4 March 1984) and mean temperature during that time was 11.26 C (SD = 0.99). For each hibernating period, the L:D photoperiod was 0:24 h. Following hibernation, snakes were placed (if not al-

ready) in the environmental chamber and temperature and L:D photoperiod were gradually increased to a normal spring-time setting of 25 C with a L:D photoperiod of 14:10 h.

Two weeks following removal from hibernation snakes were tested for courtship by placing a male and a female together in a 182 × 60 × 60-cm glass-fronted observation chamber located within the environmental chamber. The observation chamber had a sand substrate and was divided into three equal sections (60 × 60 × 60 cm) enabling multiple tests to be conducted simultaneously. For many of the trials, the male was placed within the observation chamber prior to introduction of the female. This procedure reduced the time that the male spent investigating the chamber when the snakes were paired. The pair was then watched for any signs of courtship behavior. If courtship was not initiated during the first 30 min, the pair or the female was removed and a new pair or female was introduced. Once a courtship bout began, the other snakes in the observation chamber were removed.

Courtship bouts were recorded using a color video camera (Panasonic WV-3320) and a portable VHS video cassette recorder (Panasonic NV-8410). The camera was connected to a time-date generator (Panasonic WJ-800) which inserted a time display into the camera signal on its way to the recorder. A verbal account of the snakes' activities was also recorded on the video tape. The recorded courtship bouts were replayed on a video cassette recorder (Panasonic NV-8320) for timing and description of the performed actions.

Snakes were tested from mid-March to mid-June, corresponding to that species' normal breeding season (Fitch, 1970). During the 3 yr of this study, 164 pairings were observed from which 24 bouts of courtship were recorded, 12 of which ended in copulation. These bouts of courtship were performed by six different males (four of which copulated) and nine different females (eight of which copulated).

A complete mating bout was divided into three phases: Phase I, tactile-chase; Phase II, tactile-alignment; and Phase III,

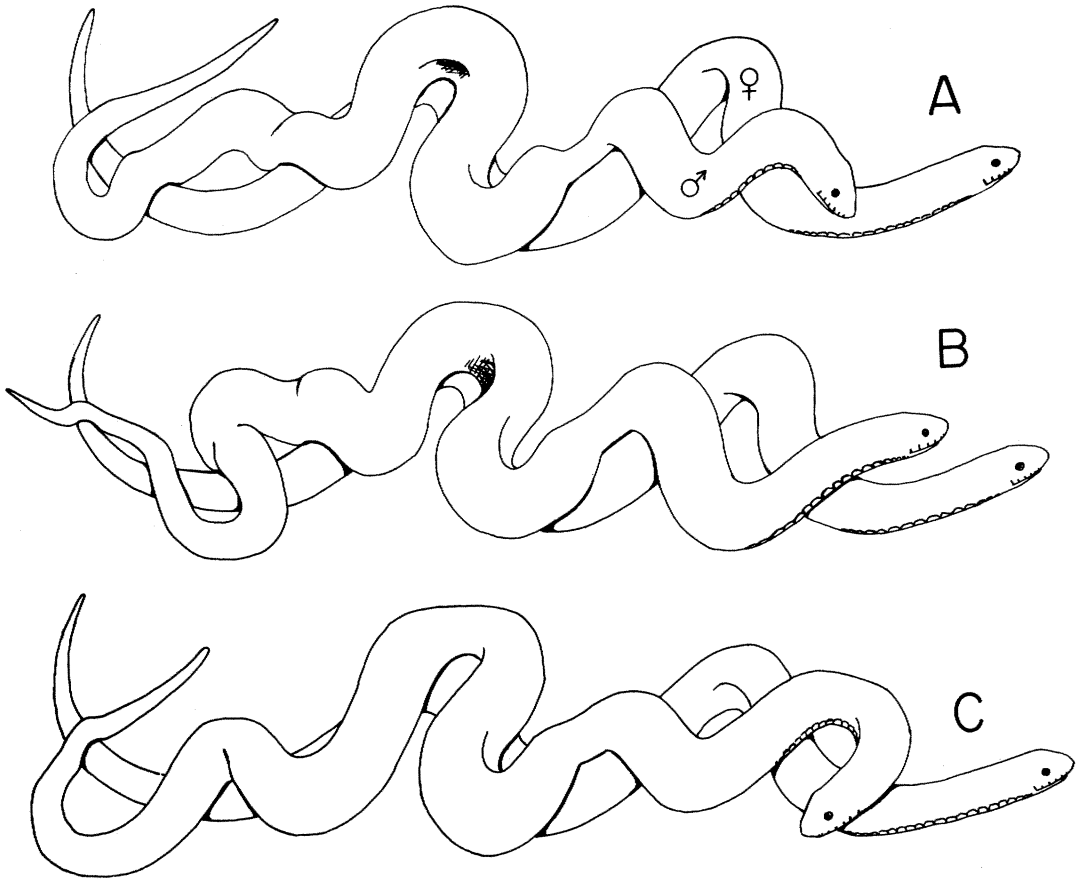


FIG. 1.—Positioning and sequence of movements (1-s intervals) by male *L. getulus holbrooki* performing the Forward-Body Jerk motor pattern.

intromission and coitus. Individual motor patterns of males were described using the terminology developed by Gillingham (1979). The average duration, relative duration, and relative frequency of each motor pattern were determined, and for each courtship bout they were compared between Phases I and II with a nonparametric, two-tailed Wilcoxon test (Sokal and Rohlf, 1981). The relative frequency of each motor pattern, for either Phase I or II, was determined by dividing the occurrence of each motor pattern by the total occurrence of all motor patterns. The relative duration of each motor pattern, for either Phase I or II, was determined by dividing the combined durations of each motor pattern by the combined durations of all motor patterns. Nonparametric comparisons were analyzed with a SAS

statistical package (SAS Institute Inc., 1982) and statistical significance was designated at $\alpha = 0.05$.

Body lengths were measured from the video monitor screen at 30-s intervals with a measuring wheel. These measurements included male and female body length, length of male in contact with the female, length of female in contact with the male, length of male that was dorsally positioned on the female, and the portion of the female that had dorsal male contact. Percentages of body contact and specific dorsal contact for both the male and female snakes were determined. The mean percentages for the four categories of body contact for each phase of each of the measuring bouts were calculated and analyzed (Kruskal-Wallis test; Sokal and Rohlf, 1981) to determine if there were signifi-

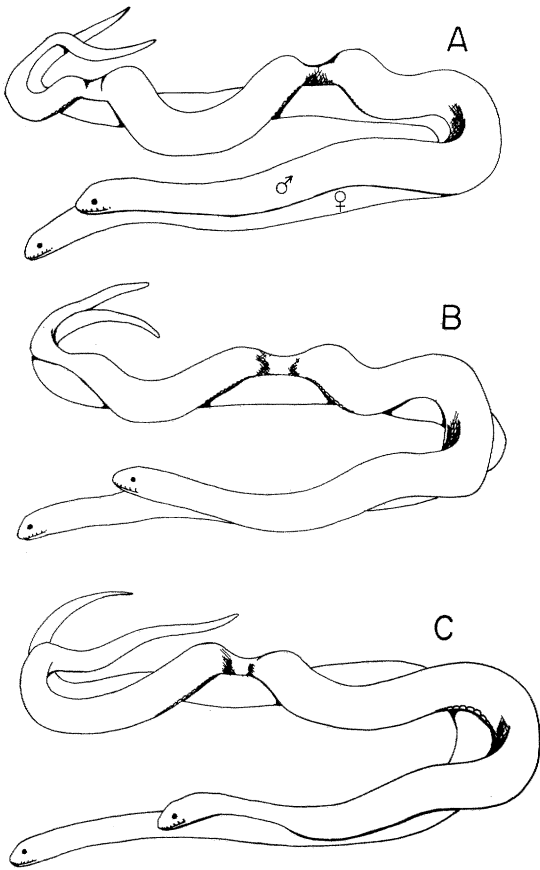


FIG. 2.—Positioning and sequence of movements (1-s intervals) by male *L. getulus holbrooki* performing the Writhe motor pattern.

cant differences of the bout means among the three phases.

Rates of tongue flicks and Forward-Body Jerks by the male were determined from the recordings and compared between Phases I and II. To test if the occurrence of successive actions was independent of preceding actions, the individual courtship motor patterns for each bout were arranged sequentially and paired. A sequence analysis was performed by setting up a contingency table of paired events and testing the rows and columns with a G-test of independence (Sokal and Rohlf, 1981). The mean duration of the three courtship phases of other collubrid snakes and their dominant courtship motor patterns were compared to those of the speckled kingsnake.

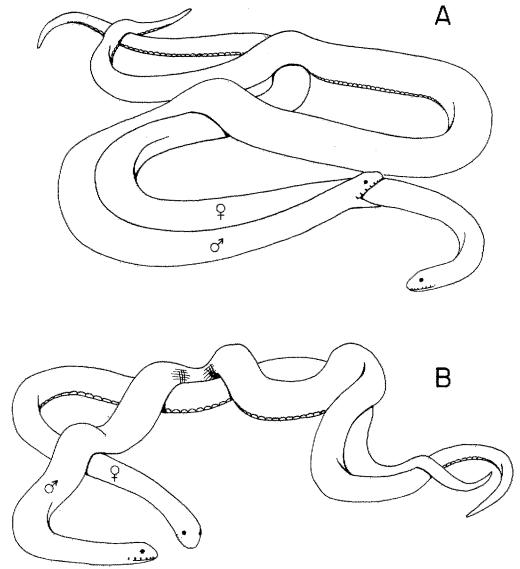


FIG. 3.—(A) Biting hold during courtship exhibited by male *L. getulus holbrooki*. (B) Typical positioning by male and female *L. getulus holbrooki* during copulation.

MOTOR PATTERNS

The following are the basic motor patterns performed by courting *Lampropeltis getulus holbrooki* males (following Gillingham, 1979). Letters in parentheses represent abbreviations used in the text. **Touch (TO)**—Male approaches female and contacts her trunk using his snout. **Mount (MT)**—Male places his head on female's dorsum and keeps his chin in contact with her. **Chase (CH)**—Rapid pursuit by male of fleeing female while not in contact with her. **Chase-Mount (CM)**—Male follows fleeing female while maintaining chin and/or trunk contact with her dorsum. **Dorsal-Advance Movement (DM)**—Anteriorly directed movement of mounted male with chin adpressed to medial or lateral dorsum of the female. **Forward-Body Jerk (FBJ)**—Male rhythmically jerking his body forward 1–2 cm while in contact with the female (Fig. 1). **Writhe (WR)**—Rhythmic sliding, twisting, and turning movements performed while completely mounted on the female (Fig. 2). **Biting (BY)**—Male grasps female in neck or trunk region with subsequent release (Fig. 3A). **Tail-Search Copulatory**

TABLE 1.—Mean, range of duration (s), relative frequency, and phases (in which they occur) of the courtship motor patterns of male *L. getulus holbrooki*.

Motor patterns	n	\bar{x} (SD)	Range	Relative frequency	Phase
Touch	22	6.0 (8.3)	1–39	1.49	I, II
Mount	16	11.7 (8.1)	2–31	1.08	I, II
Chase	3	7.0 (2.0)	5–9	0.20	I, II
Chase-Mount	20	6.7 (4.5)	3–23	1.36	I, II
Dorsal-Advance Movement	212	4.9 (3.0)	2–24	14.38	I, II
Forward-Body Jerk	164	35.2 (29.1)	3–154	11.13	I, II
Writhe	715	18.0 (15.9)	2–180	48.51	I, II
Biting	78	47.1 (93.5)	2–578	5.29	I, II, III
TSCA	219	7.5 (2.2)	3–17	14.86	II
Intromission	25	2163.4 (2428.5)	128–7103	1.70	III
Rest	724	37.5 (33.0)	2–295	—	I, II

Attempt (TSCA)—Complex tail movements as male attempts cloacal juxtaposition and intromission. *Intromission (IN)*—Insertion of one hemipenis into the cloaca of the female.

RESULTS

The number, mean duration, range of duration, and relative frequency of the motor patterns, with the phases in which they occurred, are presented in Table 1. The number, mean duration, and range of duration of each of the three courtship phases are presented in Table 2.

Phase I

The tactile-chase phase began at the moment of the male's first courting contact with the female and ended at the first **TSCA** (average duration, 14.8 min). This phase typically began with the male moving about the observation chamber, head slightly raised and tongue flicking. After contact (**TO**), the male would place his head upon the female's body (**MT**). This was accompanied by an increase in the male's tongue-flicking rate. If the male was responsive, he would follow the female's body with his head, placing more of his body upon hers (**DM**). The female usually reacted to the male's contact by fleeing,

coiling her body with sequential rapid whipping of her tail and occasional body jerking, or lifting that portion of her body in contact with the male 2–5 cm above the substrate. If the female moved away, the male would follow, either maintaining contact (**CM**) or not (**CH**). Once the female became stationary, the male would remount her if he had lost dorsal contact. After mounting, the male would proceed again with **DM**.

Once mounted, the male would commence a repeated series of **FBJ**'s and **WR**'s. If the female was not passive and continued to move away, the male would follow and continue his series of **CM** (or **CH** to **TO** to **MT**), **DM**'s **FBJ**'s, and **WR**'s. Following a sequence of these motor patterns, the male would usually lie still on or next to the female. This rest period (included in Table 1) would last until the male resumed courtship, usually stimulated by female motion. Once the male was able to align the posterior part of his body and tail with that of the female, he would perform a **TSCA**, ending Phase I.

Phase II

Averaging 28.5 min, the tactile-alignment phase began with the first **TSCA** and lasted until **IN**. The terminating motor

TABLE 2.—Mean and range of phase duration (min) in the reproductive behavior of *L. getulus holbrooki*.

Phase	n	\bar{x} (SD)	Range
I Tactile-Chase	21	14.8 (7.2)	5.9–32.3
II Tactile-Alignment	12	28.5 (24.3)	2.3–90.4
III Intromission and Coitus	12	86.7 (34.6)	22.4–154.0

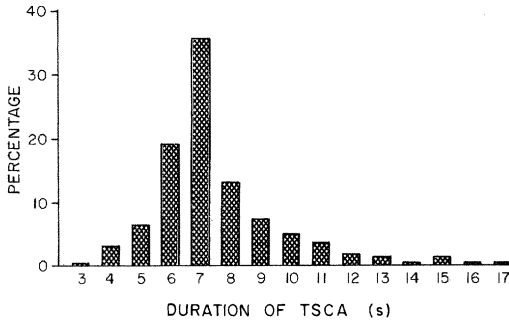


FIG. 4.—Percentages of Tail-Search Copulatory Attempts of different durations performed by male *L. getulus holbrooki*; $n = 219$ observations.

pattern of a typical Phase II action sequence, TSCA, would follow a series of DM's, FBJ's, and WR's. The TSCA began with short undulating movements of the male's posterior trunk and tail alongside the female's posterior region. He would repeatedly twist his tail beneath the female's tail, from both sides, causing the ventral sides of both tails to face each other. The male finished a TSCA with a quick, short, forward thrust of his cloaca towards the area of the female's cloaca. Intromission, when it happened, occurred at this time. The duration of a TSCA was usually very consistent ($\bar{x} = 7.5$ s, $SD = 2.2$, $n = 219$; Fig. 4) with 11.4% of the TSCA's resulting in IN. The mean number of TSCA's prior to IN was 4.3 (range = 1–16, $SD = 3.9$, $n = 25$). The remaining unsuccessful TSCA's were usually followed by a rest period (90.7% of unsuccessful TSCA's), after which the male resumed courtship.

The incidence of BY was greater in

TABLE 4.—Dominant actions performed by male and female *L. getulus holbrooki* at 15-s intervals during copulation.

Action	n	% of all intervals	% of intervals with action by indicated sex
Males			
No movement	530	25.5	—
Head movement	2	0.1	0.1
Biting	2	0.1	0.1
Body movement	427	20.6	27.6
Body and tail movement	114	5.5	7.4
Tail movement	950	45.8	61.5
Hemipenial thrust	41	2.0	2.7
Pulling	9	0.4	0.6
Females			
No movement	1452	70.0	—
Head movement	22	1.1	3.5
Gaping the mouth	6	0.3	1.0
Body movement	363	17.5	58.3
Body movement and pulling	88	4.2	14.1
Pulling	144	6.9	23.1

Phase II than in Phase I (Table 3). Of the 13 mating bouts in which BY occurred, only three had BY during Phase I. During BY, the male would grasp the female at a mean distance of 8.7 cm (range = 0.0–31.7 cm, $SD = 7.1$, $n = 66$) from her head and hold an average of 47.1 s. During BY, the male would lie still (59.5% of the combined biting duration), or perform WR (32.8%), TSCA (4.2%), or FBJ (3.5%).

Phase III

The intromission and coitus phase averaged 86.7 min, significantly longer in

TABLE 3.—Comparison between Phases I and II of the relative frequency and relative duration for eight motor patterns performed by male *L. getulus holbrooki*.

Motor patterns	Phase I			Phase II		
	n	Relative frequency	Relative duration	n	Relative frequency	Relative duration
TO	18	6.25	1.55	4	0.45	0.08
MT	14	4.86	7.30	3	0.34	0.28
CH	2	0.69	0.16	1	0.11	0.05
CM	3	1.04	0.47	17	1.93	0.61
DM	54	18.75	3.83	158	17.94	4.66
FBJ ^a	65	22.57	32.56	99	11.24	20.38
WR ^b	117	40.63	43.62	538	61.07	59.22
BY	15	5.21	10.51	61	6.92	14.72

^a Significant differences between Phase I and II in relative frequency ($z = -2.75$, $P < 0.01$) and in relative duration ($z = -3.14$, $P < 0.01$).

^b Significant differences between Phase I and II in relative frequency ($z = 3.26$, $P < 0.01$) and in relative duration ($z = 2.48$, $P < 0.05$).

TABLE 5.—Comparison of mean percent of body and dorsal contact by *L. getulus holbrooki* in the three phases of courtship.

Position	Phase			Kruskal-Wallis (χ^2)
	I (21)*	II (18)	III (18)	
Male's body in contact with female	59.2	71.4	45.2	18.41***
Female's body with male contact	72.2	80.6	56.9	18.24***
Male's body dorsal contact with female	24.7	31.7	16.9	14.27***
Female's body, dorsal male contact	29.4	36.8	20.9	12.78**

* Numbers in parentheses are the number of bouts from which mean percentages were determined.

** $P < 0.01$, *** $P < 0.001$.

duration than either Phase I (Wilcoxon test: $z = 4.57$, $P < 0.001$) or Phase II ($z = 3.32$, $P < 0.01$). Figure 3B illustrates a typical copulation. During this phase, one or both snakes were usually active, though rarely as during Phases I and II. To analyze the actions during copulation, the predominant action(s) were noted for each 15-s interval of Phase III (Table 4). Timed intervals included actions performed by just the male (62.2% of the intervals), just the female (17.7%), both snakes (12.4%), or neither snake (7.7%).

Male action during Phase III involved varying amounts of body and/or tail movements. Male body movements (including forward motions, sliding, and regaining dorsal contact) entailed the whole body or a posterior fraction. Tail movements (the male slowly waving his tail back and forth) usually involved the entire tail and the extreme posterior region of the male's body. Other male Phase III actions included **BY**, movement of the head, pulling the female by the hemipenial connection, and hemipenial thrusting into the female's cloaca. Female action during this phase was primarily forward body motion and/or pulling the male at the hemipenial coupling. Additional female actions were moving the head and gaping the mouth.

In 24 observed hemipenial penetrations, the left and right hemipenes were used equally. The hemipenis used was determined by the side of the female's tail on which a **TSCA** was successful. Retraction of the male's hemipenis was observed in 18 copulations. Hemipenial withdrawal appeared to be voluntary by the male. In only one instance did the female move

(with slight pulling) at separation. Following most separations, both the male and female maintained their tails in a horizontal position against the chamber substrate. One male was observed in four instances to lift his tail (30–45° from the substrate) for a few seconds following hemipenial withdrawal.

Phase Comparison

The mean duration of eight individual motor patterns did not differ significantly between Phases I and II (Table 3). Touch and **MT** exhibited a noticeable decrease (nonsignificant) in both relative frequency and relative duration. Forward-Body Jerk exhibited a significant decrease in relative frequency and relative duration from Phase I to Phase II. The relative frequency and relative duration of **WR** increased significantly from Phase I to Phase II.

The percent of body contact and the percent of actual dorsal contact for both male and female snakes increased from Phase I to Phase II, then declined during Phase III. Bout means for the four percentages of body contact differed significantly among the three phases (Table 5). Tongue-flick rates were slightly greater during Phase II, though not significantly

TABLE 6.—Mean (SD) tongue-flick and Forward-Body Jerk rates (per s) of male *L. getulus holbrooki* during Phases I and II of courtship.

Action	Phase I	Phase II	Wilcoxon test (z)
Tongue flick	1.45 (0.51)	1.55 (0.43)	1.89 NS
Forward-Body Jerk	0.94 (0.25)	1.03 (0.24)	2.22*

NS $P > 0.05$, * $P < 0.05$.

		SUCCEEDING					TOTAL
		TOMT	DM	FBJ	WR	TSCA	
PRECEDING	TOMT	13	13	8	11	0	45
	DM	3	28	17	118	2	168
	FBJ	3	14	40	108	9	174
	WR	7	103	86	353	186	735
	TSCA	0	41	17	120	20	198
TOTAL		26	199	168	710	217	1320

FIG. 5.—Sequence analysis of courtship motor patterns using a $r \times c$ contingency table test for independence ($G = 226.08$, $df = 16$, $P < 0.001$).

so, and **FBJ** rates were significantly greater during Phase II (Table 6).

Sequence of Motor Patterns

The motor patterns used for the sequence analysis were Touch-Mount (**TOMT**), **DM**, **FBJ**, **WR**, and **TSCA**. These actions were arranged in a 5×5 contingency table and the number of succeeding-preceding pairs for every possible pair of the five motor patterns was entered producing a highly significant G -value (Fig. 5). Clearly these motor patterns are performed by male *L. getulus holbrooki* in a nonrandom sequence. A sequence diagram (Fig. 6) illustrates the relative transition of the performed motor patterns.

DISCUSSION

In this study, male *L. getulus holbrooki* performed continued series of identifiable motor patterns during their courtship of conspecific females. These actions enable the separation of their courtship and mating bouts into three behavioral phases as described by Gillingham et al. (1977). The duration of Phase I was strongly influenced by the actions of the male and female before the male's first **TSCA**. The male would perform a **TSCA** when he had aligned the posterior portion of his trunk and tail with that of the female's. In order for alignment, the female must show some

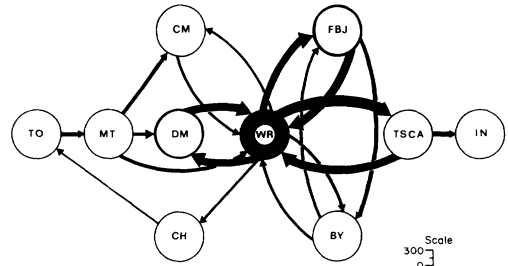


FIG. 6.—Sequence diagram of motor patterns performed by male *L. getulus holbrooki*. Thickness of lines and circles indicates frequency of transition.

receptivity by relaxing and straightening out at least that part of her body.

Several steps may be involved in a female becoming receptive. Identification of the male as a conspecific by the types and sequences of the motor patterns he performs would be important, given that performance of motor patterns is species-specific. Even if the male is performing the necessary motor patterns, the achievement of female receptivity may also entail the correct positioning, timing, force, and repetition of the motor patterns. Continuing sequences of properly performed motor patterns by male *L. getulus holbrooki* may be necessary for inducing female receptivity. In this study, female receptivity was never quickly achieved, and males performed repeated series of motor patterns prior to the **TSCA** (Phase I) and throughout Phase II. For colubrids with a shorter Phase I (Table 7), species recognition from a relatively short sequence of motor patterns may be all the stimulus needed for female receptivity. The shorter Phase I duration for *L. mexicana* and *L. triangulum* resulted from the relative ease to gain female receptivity and the few motor patterns performed prior to a **TSCA**. Other species (*Elaphe obsoleta*, *E. vulpina*, and *Drymarchon corais couperi*; Table 7) may be like *L. getulus holbrooki*, and need additional tactile signals from persistent series of courtship motor patterns.

The length of Phase II (first **TSCA** to **IN**) also varied among colubrids (Table 7) and for *L. getulus holbrooki* depended on several factors. In order for a **TSCA** to

TABLE 7.—Comparison of mean duration (min) for the three phases of courtship in various colubrid snakes.

Species	Phase			Source
	I	II	III	
<i>Lampropeltis getulus holbrooki</i>	14.8	28.5	86.7	This study
<i>L. mexicana alterna</i> ^a	0.12–50	0.03–3	4–15	Murphy et al., 1978
<i>L. mexicana alterna</i> ^a	0.8	3.0	13.0	Personal observations
<i>L. mexicana mexicana</i>	2.7	3.8	12.0	Personal observations
<i>L. mexicana thayeri</i>	1.9	26.4	6.8	Personal observations
<i>L. mexicana campbelli</i>	1.9	—	—	Personal observations
<i>L. triangulum hondurensis</i>	2.5	6.9	18.8	Personal observations
<i>L. triangulum sinaloae</i>	5.5	33.0	20.6	Gillingham et al., 1977
<i>Elaphe guttata</i>	5.0	4.5	25.3	Gillingham, 1979
<i>E. obsoleta</i>	10.3	18.3	20.7	Gillingham, 1979
<i>E. obsoleta bairdi</i>	45.0	—	40.0	Brecke et al., 1976
<i>E. vulpina</i>	12.5	9.9	20.3	Gillingham, 1979
<i>Drymarchon corais couperi</i>	12.0	8.5	193.0	Gillingham and Chambers, 1980

^a Garstka (1982) promoted *L. mexicana alterna* (Gehlbach, 1967) to species-level, *Lampropeltis alterna*.

result in **IN**, there had to be proper body and cloacal alignment and female receptivity (with little resistance to hemipenial penetration). Unsuccessful attempts to penetrate by male *L. getulus holbrooki* were primarily due to the lack of proper cloacal alignment. When cloacal alignment was attained, unsuccessful penetration may have resulted from female resistance, keeping her cloaca closed and not allowing penetration.

Hemipenial movement during **IN** was hard to observe because the tails were tightly pressed together. To what extent the female influences penetration is unknown. The female could retard penetration by contracting her cloacal muscles, thus closing her cloacal orifice, or facilitate penetration by gaping her cloaca during **TSCA** as observed in members of the genera *Crotalus* (Armstrong and Murphy, 1979; Gillingham et al., 1983), *Elaphe* (Gillingham, 1979), *Lampropeltis* (Murphy et al., 1978; personal observations), *Python* (Barker et al., 1979; Davis, 1936), and *Thamnophis* (Munro, 1948; Noble, 1937; Pope, 1947). Cloacal gaping was never observed in female *L. getulus holbrooki*, and this may contribute to a longer time to attain **IN**. Male *L. getulus holbrooki* attempted to lift the female's tail with their tail during **TSCA** to gain access to her cloaca. Male *Thamnophis sirtalis* have also been noted to use their tail to lift the female's prior to **IN** (Blanchard and Blanchard, 1942).

Male *L. getulus holbrooki* usually perform different sequences of three motor patterns (**DM**, **FBJ**, and **WR**) before a **TSCA**. In this study, **WR** immediately preceded 85.7% of recorded **TSCA**'s. Gillingham (1979) noted for *Elaphe guttata* that Writhe-Bump (similar to **WR** with the addition of local dorsoventral trunk movement) preceded 96% of the **TSCA**'s. Caudocephalic Waves ("series of ventral or ventrolateral trunk contractions progressing in an anterior direction") preceded 94.5% and 90.7% of **TSCA**'s for *E. obsoleta* and *E. vulpina*, respectively (Gillingham, 1979). The Writhe-, Writhe-Bump-, or Caudocephalic Wave-**TSCA** relationship is an important sequence in the action pattern sequence of these snakes.

Most unsuccessful **TSCA**'s were followed by a rest period. Tail-Search Copulatory Attempt and the actions leading to it may tire the male. A rest period following a **TSCA** has also been noted for *Crotalus atrox* (Gillingham et al., 1983), *L. triangulum sinaloae* (Gillingham et al., 1977), and *Opheodrys aestivus* (Goldsmith, 1981).

Copulation (Phase III) by *L. getulus holbrooki* is considerably longer than that of other colubrids (Table 7). The time of insemination during Phase III (beginning, middle, or end) and its duration was not determined. I have observed, following coital separation in *L. getulus holbrooki* and *L. mexicana*, drops of semen extrud-

ing from the female's cloaca. This may result from insemination completing just prior to separation or be an overflow of semen. If the duration of insemination is similar among colubrids, then most of Phase III for *L. getulus holbrooki* and *Drymarchon corais couperi* is spent maintaining coitus.

Tail lifting following separation was infrequently performed by either male or female *L. getulus holbrooki*. Postcopulatory tail raising was performed, for several minutes, by *Elaphe guttata*, *E. obsoleta*, *E. vulpina* (Gillingham, 1979), and *L. mexicana* (personal observations). *Lampropeltis triangulum sinaloae* lifted their tails for 60 s following coital separation (Gillingham et al., 1977).

Male movement during Phase III was confined to the posterior trunk and tail region. Tryon and Carl (1980) reported "intermittent waving and pulsating of the male's tail" during copulation by *L. calligaster rhombomaculata*. Forward thrusting at the cloacal region was also observed by Noble (1937) for male *Storeria dekayi* and *Coluber constrictor*. Copulatory tail movements were reported for male *Crotalus basiliscus* (Perkins, 1943), *C. ruber* (Perkins, 1943), *Elaphe obsoleta* (Johnson, 1950; Mansueti, 1946), and *L. triangulum sinaloae* (Gillingham et al., 1977). During copulation, both sexes of *Vipera berus* kept their tail upright; the female's was still, while the male waved his (Andren, 1981). These copulatory actions may be to gain better penetration and/or facilitate sperm release.

Movement by male *L. getulus holbrooki* during Phase III was usually in response to movement by the female and served to regain some body contact. If the female moved enough to put a strain on the male's hemipenis, the male would reposition himself to reduce the pulling strain. During copulation, female *L. getulus holbrooki* occasionally dragged the male by the hemipenial connection. Coital dragging has also been recorded for species of the genera *Coluber* (Fitch, 1963; Noble, 1937; Perkins, 1943), *Crotalus* (Armstrong and Murphy, 1979; Gillingham et al., 1983; Perkins, 1943), *Ophiopha-*

gus (Oliver, 1956), *Pituophis* (Shaw, 1951), *Storeria* (Noble 1937), and *Thamnophis* (Ball, 1978; Blanchard and Blanchard, 1942; Munro, 1948; Noble, 1937; Pisani, 1967).

The decrease in relative frequency of **TO** and **MT** from Phase I to II suggests that these two motor patterns are a specific feature of Phase I, when the male is initiating contact and gaining a mounted position. The decrease in the relative frequency of **DM** and **FBJ** coupled with the increase in relative frequency of **WR** imply that during Phase II the former two motor patterns are being replaced by **WR** which almost always preceded a **TSCA**.

The presence or absence of four motor patterns—Body Jerking, Writhe or Writhe-Bump, Caudocephalic Waves, and Biting—in the repertoire of courtship behavior of colubrid snakes are compared in Table 8. Body Jerking is common to many of these colubrids with the exception of *Drymarchon corais couperi*. In addition to *E. guttata*, Writhe-Bump was also performed by *D. corais couperi*. For most of these others, **WR** was a common feature in their mating behavior. Caudocephalic Waves, a frequent motor pattern in the mating behavior of a variety of colubrids, is not performed by mating male *Lampropeltis* nor male *Opheodrys aestivus*. Courtship biting was performed by males of the three subspecies of *L. getulus* and other colubrids, but was not documented in these studied forms of *L. mexicana* or *L. triangulum*. Biting by male *L. triangulum* could be expected in some instances of courtship since **BY** has been observed for *L. triangulum sypila* (Fitch and Fleet, 1970) and *L. triangulum annulata* (S. Tennyson, personal communication).

Biting by courting male *L. getulus holbrooki* was also reported by Meade (1932) and Noble (1937), and has been observed in other forms of *L. getulus* by Fitch (1949), Kennedy (1978), Lewke (1979), and Zweifel (1980). All of these studies described this action as a firm grasp of the female's body by the male, similar to what I observed. Courtship biting differs from male combat biting in *L. getulus hol-*

TABLE 8.—Comparison of the major motor patterns in the repertoire of courtship behavior of mating colubrid snakes.

Species	Body Jerking	Writhe/Writhe-Bump	Caudocephalic Waves	Biting	Source
<i>Lampropeltis getulus holbrooki</i>	Yes	Yes	No	Yes	This study
<i>L. getulus californiae</i>	Yes	Yes	No	Yes	Personal observations
<i>L. getulus getulus</i>	—	Yes	No	Yes	Kennedy, 1978
<i>L. mexicana alterna</i>	Yes	Yes	No	—	Murphy et al., 1978
<i>L. mexicana mexicana</i>	Yes	Yes	No	No	Personal observations
<i>L. mexicana thayeri</i>	Yes	Yes	No	No	Personal observations
<i>L. mexicana campbelli</i>	Yes	Yes	No	—	Personal observations
<i>L. triangulum hondurensis</i>	Yes	Yes	No	—	Personal observations
<i>L. triangulum sinaloae</i>	Yes	No	No	No	Gillingham et al., 1977
<i>Elaphe guttata</i>	Yes	Yes	Yes	Yes	Gillingham, 1979
<i>E. obsoleta</i>	Yes	Yes	Yes	Yes	Gillingham, 1979
<i>E. vulpina</i>	Yes	Yes	Yes	Yes	Gillingham, 1979
<i>Coluber constrictor</i>	Yes	—	Yes	Yes	Fitch, 1963; Wright and Wright, 1957
<i>Drymarchon corais couperi</i>	No	Yes	Yes	No	Gillingham and Chambers, 1980
<i>Opheodrys aestivus</i>	—	Yes	No	No	Goldsmith, 1981
<i>Pituophis melanoleucus</i>	Yes	Yes	Yes	Yes	Perkins, 1943; personal observations
<i>Regina septemvittata</i>	—	Yes	No	No	Ford, 1982
<i>Storeria dekayi</i>	—	Yes	Yes	No	Noble, 1937
<i>Thamnophis melanogaster</i>	—	—	Yes	No	Ball, 1978
<i>T. sirtalis</i>	—	—	Yes	No	Noble, 1937

brooki. Biting during combat is shorter in duration and includes a side to side chewing action by the biting snake, not observed during a courtship bite (personal observations). In this study, the incidence of **BY** varied among the bouts and among the individual males: male no. 78, 60 bites in eight bouts; male no. 24, nine bites in two bouts; and male no. 39, two bites in nine bouts. Lewke (1979) reported that in his study the majority of courtships that led to copulation included neck-biting (five out of seven copulations). Only five of the 12 successful copulations I observed included **BY**.

Lewke (1979) and Gillingham (1974) proposed that **BY** functions to induce the receptivity of the female and its performance may depend on whether the female is receptive or not. If the female is receptive, then **BY** may not be needed, but if she is not, then **BY** may be a behavioral adjustment that may bring about female receptivity. This may have occurred in *L. getulus holbrooki*, since the majority of the **BY**'s occurred during Phase II, possibly in response to the female's continued unreceptive behavior.

Biting during copulation was only once

observed in this study for *L. getulus holbrooki* (485 s). Coital biting has also been reported in *Elaphe vulpina* (Carpenter, 1947; Gillingham, 1974, 1979; Simonson, 1951), *L. calligaster rhombomaculata* (Tryon and Carl, 1980), and *Pituophis melanoleucus* (Perkins, 1943).

Biting during courtship appears to be performed only by non-natricine colubrids. Besides those already noted (Table 8), courtship biting has been reported for other colubrids (Burchfield et al., 1982; Carpenter and Ferguson, 1977; Tryon, 1976). I did not encounter accounts of courtship biting in boids, crotalids, and elapids. Courtship biting in these snakes may be selected against because of the injury that would be inflicted by the elongated teeth and fangs possessed by these snakes, and the possible envenomation by the venomous species.

In addition to the appropriate series of courtship motor patterns, body contact (specifically dorsal contact) may be an important stimulus to induce female receptivity. The weight of the male, together with the amount of contact, may add to the effects of the motor patterns in quieting the female and gaining **IN**. An in-

crease in contact during Phase II would facilitate TSCA occurrence and success. Once in copulation (Phase III), the need to retain constant body contact is diminished and contact may only be needed at the cloacal region to maintain coitus.

An increase of male tongue-flick rate from Phase I to II was also observed by Gillingham (1979) in *Elaphe guttata*, *E. obsoleta*, and *E. vulpina*, and by Gillingham et al. (1977) in *L. triangulum sinaloae*. The mean tongue-flick rates of those species were higher (1.5–4.6 flicks/s) than that of *L. getulus holbrooki* (1.47 flicks/s). The mean tongue-flick rate of male *Python molurus* (0.91 flicks/s) is slower than that of *L. getulus holbrooki* (Gillingham and Chambers, 1982). Gillingham (1979) postulated that tongue flicking, normally having an olfactory role, may provide tactile stimulation during courtship, though there is no experimental evidence of this. The majority of the tongue flicks by male *L. getulus holbrooki* were directly above or lateral to the female's dorsum without actually making contact. Tongue flicking by male *L. getulus holbrooki* is probably most important for species and sex identification, and may be important in determining the reproductive state of the female. Crews and Garstka (1982) hypothesized that in *Thamnophis* a blood-borne pheromone (vitellogenin), which passes through the skin, acts as an attractant and communicates the reproductive readiness of the female.

Body Jerking, a component in the courtship of many snakes (Table 8), differs in its rate and motion among those species. Gillingham (1974, 1979) referred to this action by *Elaphe* as "Forward-Jerking" and indicated that "Each jerk consisted of two opposite motions: first the dorsal part of his body was thrown forward 1–2 cm; and second, the ventral part was thrown backward the same distance repeatedly." The **FBJ** performed by male *L. getulus holbrooki* did not include the backward motion. Mean Body Jerk rate by male *L. getulus holbrooki* ($\bar{x} = 0.99$ jerks/s) was lower than those recorded for male *Elaphe guttata*, *E. obsoleta*, and *E. vulpina* (mean for these species: 1.6

jerks/s; Gillingham, 1979). Body Jerking by male *Crotalus atrox* was limited to the head and neck region and occurred more frequently ($\bar{x} = 2.79$ jerks/s; Gillingham et al., 1983).

A sequence analysis of the transitions of the motor patterns for *L. getulus holbrooki* demonstrates that these motor patterns did not occur at random and that there existed a pattern to their performance. Nonrandom sequences of performed motor patterns were also recorded for *Elaphe guttata*, *E. obsoleta*, and *E. vulpina* (Gillingham, 1979). The general performance of behavioral acts by many reptiles has been described as being stereotypic (Carpenter and Ferguson, 1977). It would then be expected that *L. getulus holbrooki* or any other snake would perform its motor patterns nonrandomly. The existence of a "ritualized" courtship appears common among many colubrids and differences in this behavior would enhance the reproductive isolation of these species.

In order to be reproductively successful, a male snake must locate a female, and recognize her as the same species presumably by chemoreception through tongue flicking. He then must perform the appropriate repertoire of actions, which for the speckled kingsnake would include **DM**, **FBJ**, **WR**, and **BY**, for the purpose of gaining female receptivity so that she will straighten out her body and allow copulation. Without the use of limbs, a male snake performs his own species-specific set of motor patterns and, together with olfactory cues, this tactile communication ensures proper intraspecific recognition and pairing of the male and female snake.

Standardized methods to identify and quantify the reproductive behavior of snakes are now available. These methods facilitate the separation and analysis of different temporal and behavioral components of courtship and mating, which for *L. getulus holbrooki* exhibit similarities and differences to those of other colubrid snakes. The information gained from quantitative and qualitative comparisons of snake behavior could be used to assist

in understanding the phylogeny of different snake taxa. In addition, this information together with the knowledge of the habitats and social organization of snake species, should provide insight into the existence of any relationship between serpent reproductive behavior and their habitat and/or social organization.

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