

- . 1983. The influence of the ambient sex ratio and intermale competition on the sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Behav. Ecol. Sociobiol.* 13(4):307–313.
- . 1985a. Verzorging, balts en voortplanting van de groene watersalamander. *Lacerta* 43(7):130–135.
- . 1985b. Female availability and multiple courtship in male red-spotted newts, *Notophthalmus viridescens* (Amphibia): decisions that maximize male mating success. *Behaviour* 94(3–4):244–253.

Accepted: 8 June 1989.

Journal of Herpetology, Vol. 24, No. 2, pp. 217–221, 1990
Copyright 1990 Society for the Study of Amphibians and Reptiles

Reproductive and Combat Behavior of the Mexican Kingsnake, *Lampropeltis mexicana*

STEPHEN M. SECOR, *Department of Biology, University of California, Los Angeles, California 90024, USA.*

Descriptions of reproductive and combat bouts exist for members of the snake families Boidae (Barker et al., 1979), Colubridae (Brecke et al., 1976; Murphy et al., 1978), Elapidae (Leloup, 1964; Shine et al., 1981), and Viperidae (Leloup, 1975; Andren, 1981; Akester, 1983; Gillingham et al., 1983). The more recent of these studies have adopted the terminology and techniques of Gillingham et al. (1977) and Gillingham (1979) to describe and analyze the various reproductive behaviors. Similarly, the actions performed during combat have been described using the methods of Carpenter and Gillingham (1977) and Gillingham (1980). Applying standardized techniques to analyze reproductive and combat bouts allows meaningful comparisons among species. This study documents reproductive and combat bouts by Mexican kingsnakes, *Lampropeltis mexicana*, and compares them to similar data on other species.

For this study twelve adult, six males (\bar{x} = 66.4 cm SVL, 79.5 cm TL, and 137.2 g) and six females (\bar{x} = 77.5 cm SVL, 89.7 cm TL, and 269.0 g), *L. mexicana* were used. These snakes were maintained on a weekly diet of mice and juvenile rats and were exposed to a 2–3 month period of artificial hibernation prior to pairing.

To initiate courtship or combat, one snake was introduced into the cage of another ($61 \times 45.7 \times 30.5$ cm) or both were placed in a 75.7 liter aquarium. Courtship and combat bouts were recorded on video cassette and later replayed for description and analysis of behaviors. Sixteen courtship bouts, nine resulting in copulation, were taped during the spring of 1983 and 1984 and one combat bout was recorded during the spring of 1984.

The motor patterns performed by courting male *Lampropeltis mexicana* were: Touch (TO), Mount (MT),

Chase-Mount (CM), Dorsal-Advance Movement (DM), Forward-Body Jerk (FBJ), Writhe (WR), Tail-Search Copulatory Attempt (TSCA), and Intromission (IN). The definitions of these motor patterns are given in Gillingham (1979) and Secor (1987). The combat bout was described using the terminology (boldface in text) given by Carpenter and Gillingham (1977) and Gillingham (1980).

The number, mean duration, range of duration, and relative frequency of each motor pattern performed by male *L. mexicana*, pooled from all sixteen courtship bouts, are presented in Table 1. The following describes the general sequence of motor patterns performed during each of the three courtship phases developed by Gillingham et al. (1977).

The Tactile-Chase Phase (Phase I) began with the male's first courting contact (TO) with the female and ended with his first Tail Search Copulatory Attempt (TSCA) and averaged 2.2 min (range = 0.6–4.5, SD = 1.0, N = 12). When first paired, the male typically moved around the cage performing repeated volleys of tongue flicking. After approaching the female he tongue-flicked her sides and dorsum and initiated contact (TO). He then placed his chin upon her dorsum (MT) and moved towards her head (DM), while constantly tongue flicking (\bar{x} rate = 1.7 flicks/s, SD = 0.30, N = 46) (Fig. 1A). In the several instances that the female moved away from the male's advances, he was still able to maintain dorsal contact (CM). After obtaining dorsal alignment, he began a series of DM followed by WR. Occasionally, he performed a FBJ (\bar{x} = 1.4 jerks/s, SD = 0.17, N = 53) just prior to WR. The tactile-chase phase ended when the male was able to align the posterior portion of his body and tail with that of the female and perform a TSCA.

The Tactile-Alignment Phase (Phase II) began with the male's first TSCA and ended with IN and averaged 12.7 min (range = 0.1–57.4, SD = 18.3, N = 9). Throughout this phase the male maintained most of his body in dorsal and lateral contact with the female. The predominant sequence of motor patterns was WR followed by TSCA and a subsequent rest period (\bar{x} duration = 30.7 s, SD = 24.0, N = 97). In the longer Phase II bouts, these motor patterns were performed repeatedly and at many times either DM or FBJ was performed immediately before WR.

The male started each TSCA by rapidly undulating his tail alongside the female's, followed by side to side twisting actions which would eventually juxtapose their vents (Fig. 1B). In two bouts, the first TSCA resulted in IN and for the others the male performed from 3 to 35 TSCAs prior to IN (\bar{x} = 8.3, SD = 10.0; for all bouts).

The Intromission and Coitus Phase (Phase III), the duration of copulation, averaged 9.0 min (range = 5.2–14.7, SD = 3.4, N = 9). Immediately prior to each IN, the female raised her tail 45° and gaped her cloaca. Neither snake moved during 74.8% of the time spent in Phase III (Fig. 1C). For the remaining time, male actions included sliding back, regaining dorsal position, and waving the tail back and forth (with and without pushing at the cloaca); while the female moved her entire body or just her head. Following seven terminations of coitus either one or both individuals raised their tails 30–90° above the substrate for 4–214 s (\bar{x} = 64.9, SD = 65.6).

In combat, following initial contact, male G (pre-

TABLE 1. Courtship motor patterns of male *Lampropeltis mexicana*. Data are pooled from sixteen courtship bouts.

Motor pattern	N	Duration (s) \bar{x} (SD)	Range (s)	Relative frequency	Phases
Touch	9	3.0 (1.3)	2-6	2.3	I
Mount	9	3.4 (1.3)	2-6	2.3	I
Chase-mount	5	9.0 (6.2)	2-19	1.3	I
Dorsal-advance movement	68	7.4 (4.1)	2-19	17.5	I, II
Forward-body jerk	54	30.1 (39.3)	5-202	13.9	I, II
Writhe	145	25.9 (22.5)	2-129	37.3	I, II
TSCA	89	12.7 (5.8)	3-32	22.9	II
Intromission	9	487.8 (250.5)	69-884	2.5	III

dominantly grey in coloration; 66.5 cm SVL, 83.5 cm TL, 162.0 g) **Aligned** himself alongside male R (red coloration; 67.0 cm SVL, 80.5 cm TL, 162.7 g) and proceeded to mount him (**Touch Mount**). As G advanced along R's dorsum, R responded by lifting parts of his body that were in contact with G (**Push-Bridge**). Immediately after, R moved out from under G's right side, raised his head and neck (bent in an S-shaped loop) above G and dropped it down on G's head and anterior body (**Dorsal Pin**). Male G simultaneously **Push-Bridged** against R, then moved to R's right side and reciprocated with a **Dorsal Pin** against R (Fig. 2). This exchange of **Dorsal Pins** and **Push-Bridges** continued throughout the bout resulting in their entire bodies becoming **Entwined**. Occasionally, one male would hold his head and neck above the other's head prior to lowering it down (**Hover**).

One min 50 s into the bout, G bit R about $\frac{3}{4}$ down R's body. After making five side to side twisting motions with his head, G released R. Five s later, R bit G for a duration of five s during which he performed 15 twisting motions. Three min, 14 s following contact, G **Retreated** from R, with R in pursuit. Up to that point there were 62 exchanges of dorsal head and neck positioning, occurring as rapidly as two/s. Just prior to separation, **Dorsal Pin** exchanges occurred so frequently that the males were spiralling in a corkscrew fashion. Prior to G's **Retreat**, male R held the dorsal position 52.4% of the time, while G held it the remaining time.

Following the initial establishment of dominance, the snakes continued to spar for short intervals with G each time **Retreating** from R. Both snakes continued to bite each other (\bar{x} duration = 4.5 s, SD = 2.7) and twist (\bar{x} rate = 2.6 head twists/s, SD = 0.8, N = 13). The twist rates of the two males did not differ significantly, though R (\bar{x} = 7.0 s, N = 6) held on significantly longer than G (\bar{x} = 2.4 s, N = 7; $z = 2.95$, $P < 0.01$). Throughout the bout, neither snake inflicted any noticeable damage to its opponent from biting.

Male *Lampropeltis mexicana* perform action patterns typical of the mating repertoire of colubrid snakes. As in the mating behavior of *Elaphe* spp. (Gillingham, 1979) and *L. getulus holbrooki* (Secor, 1987), these actions were performed in a nonrandom pattern, based upon a contingency table test for independence ($G = 123.0$, $df = 16$, $P < 0.001$). The high frequency of **DM** and **WR** performed during Phase I and II (54.8% of all motor patterns) was also found for *L. getulus holbrooki* (62.9%; Secor, 1987). Body jerks, which occurred most often during Phase II, are frequently performed

during courtship by male *Coluber* (Fitch, 1963), *Elaphe* (Gillingham, 1979), *Lampropeltis* (Gillingham et al., 1977; Murphy et al., 1978; Secor, 1987), and *Pituophis* (Perkins, 1943). *Lampropeltis mexicana*, like other *Lampropeltis*, did not perform caudocephalic waves during courtship, a motor pattern common to other colubrid genera (Secor, 1987).

The number of TSCAs performed prior to **IN** is contingent upon the male's ability to align the posterior portion of his trunk and tail with that of the female and the female's receptiveness to the male's advances. The females gaping their cloaca prior to **IN** undoubtedly conveys their receptivity to mating and possibly assists in hemipenial insertion. Cloacal gaping is a widespread phenomenon among mating snakes, having been observed in boids (Davis, 1936; Barker et al., 1979), colubrids (Noble, 1937; Murphy et al., 1978; Gillingham, 1979), and viperids (Armstrong and Murphy, 1979; Gillingham et al., 1983).

During copulation, male and female *L. mexicana* are usually immobile, unlike *L. getulus holbrooki* in which either or both sexes are active during 92.3% of Phase III (Secor, 1987). The relative time spent in motion during Phase III differs significantly between these two species of *Lampropeltis* ($z = 3.72$, $P < 0.001$). Copulatory movement, especially by the male, has also been observed for many other species and possibly functions to maintain body contact and to facilitate sperm passage. The functional significance of tail raising, which has also been noted for *Elaphe* (Gillingham, 1979), *L. getulus holbrooki* (Secor, 1987), and *L. triangulum* (Gillingham et al., 1977), is not known. For the male, it may facilitate hemipenis retraction and for the female it may assist in the passage of seminal fluid further into the oviducts.

Combat of *Lampropeltis mexicana* is similar to previously documented combat bouts of other species of *Lampropeltis*. Repeated sequences of raising the head and neck to a superior position and then lowering it onto the opponent, resulting in entwined bodies, is common among *Lampropeltis* and other colubrid snakes. The **Push-Bridge** response to opponent's contact is also employed by many other colubrid species. During their combat, I did not observe *L. mexicana* performing the body jerk motions which were noted for *L. alterna* (Murphy et al., 1978), *L. getulus* (Carpenter and Gillingham, 1977), and *L. triangulum* (Shaw, 1951).

Biting, though not observed during courtship, was quite prominent in the combat of *L. mexicana*, and has been recorded during the combat of *L. alterna* (Mur-

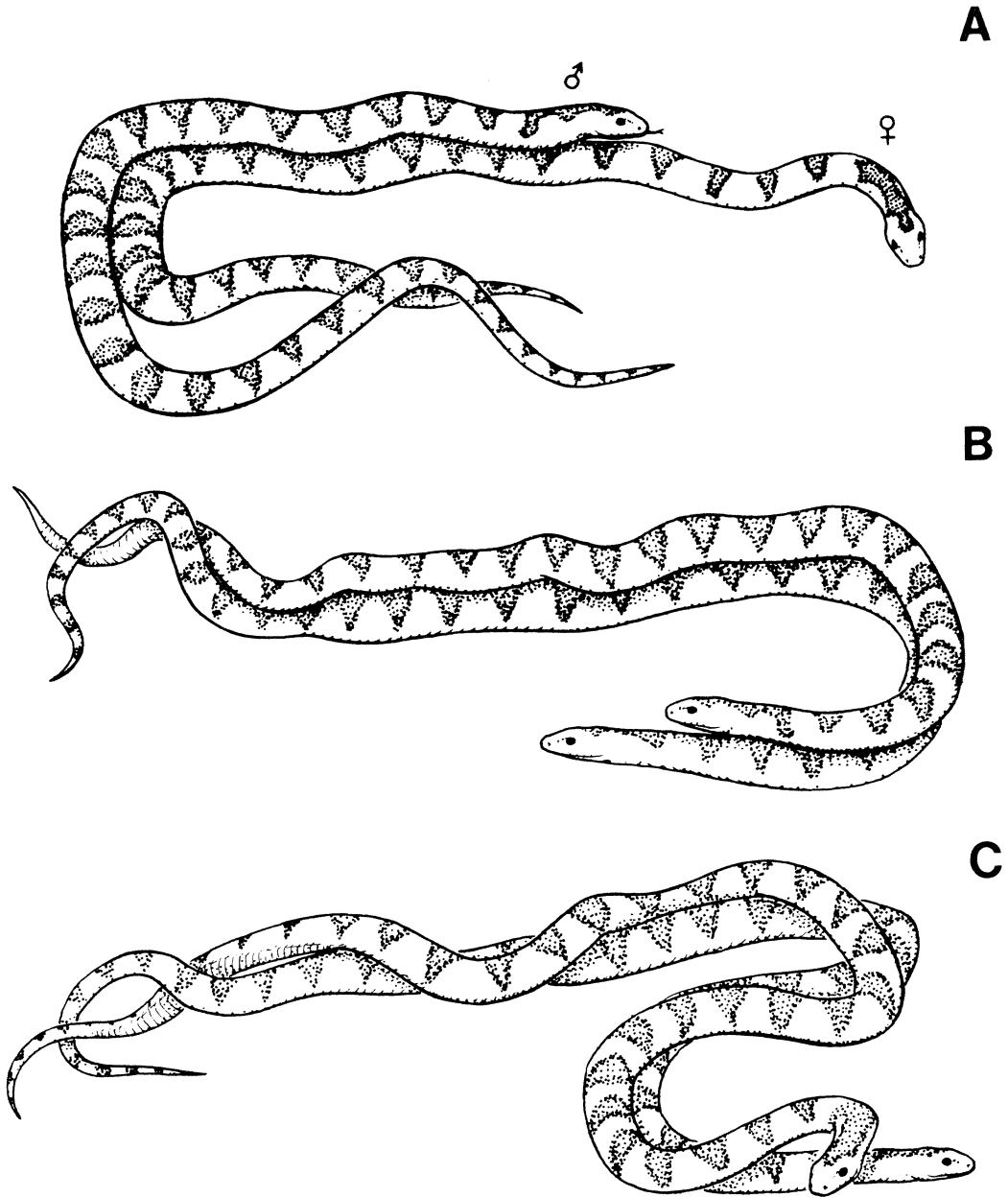


FIG. 1. Typical positioning of male and female *Lampropeltis mexicana* during (A) Phase I, (B) Phase II, and (C) Phase III of courtship.

phy et al., 1978), *L. calligaster* (Carpenter, 1984), *L. getulus* (Carpenter and Gillingham, 1977; Clark et al., 1984), *L. pyromelana* (Martin, 1976), and *L. triangulum* (Shaw, 1951). Combat biting also occurs within the colubrid genera *Drymarchon* (Waide and Thomas, 1984), *Elaphe* (Brecke et al., 1976), *Masticophis* (Bennion and Parker, 1976; Hammerson, 1978), *Pituophis* (Shaw, 1951), and *Sonora* (Kroll, 1971). Combat biting by *L. mexicana* and other colubrids differs noticeably from courtship biting. Combatant males aggressively twist their heads from side to side while holding on to the

opponent's body. Courtship biting, documented for *L. calligaster* (Tryon and Carl, 1980), *L. getulus* (Lewke, 1979; Secor, 1987) and other colubrid genera (Secor, 1987), is generally longer (for *L. getulus holbrooki* \bar{x} = 47.1 s; Secor, 1987), and involves just the male grasping the female in his jaws. Combat biting is undoubtedly an aggressive action used to establish dominance or as a response to an opponent's advances. Courtship biting may function to restrain a fleeing female or to induce sexual receptivity (Gillingham, 1974).

In the combat bout reported here the males were

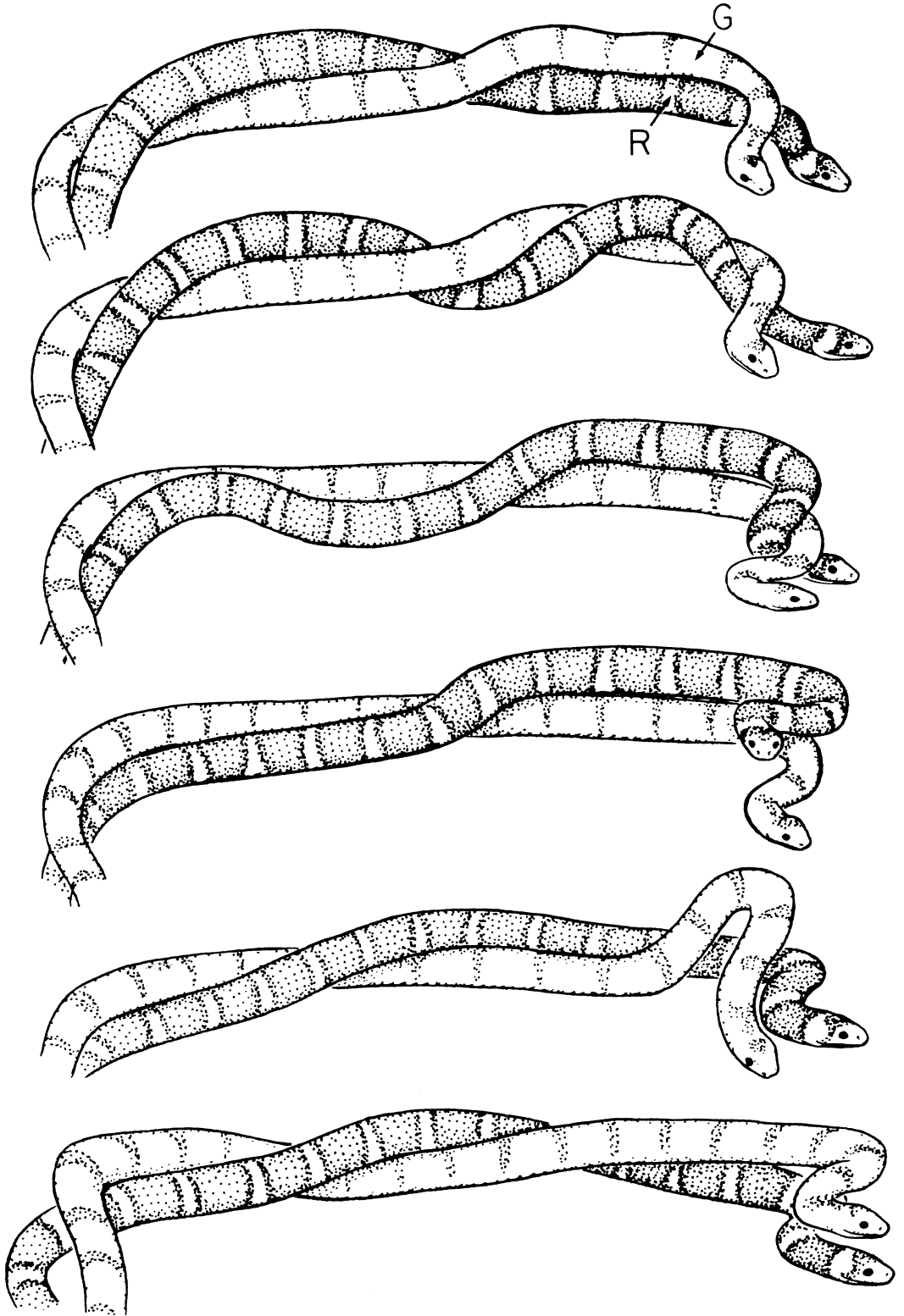


FIG. 2. The exchange of dorsal head and neck positioning during a 1.5 s sequence of combat between two male *Lampropeltis mexicana* (see text).

evenly matched in size, and for the first few minutes of combat neither was obviously dominant. During that period, each maintained superior position for about 50% of the time and each had bitten the other once. Following the initial retreat by G, R, the established dominant, maintained superior position most of the time while numbers of bites by each individual were essentially equal. Carpenter and Gillingham (1977) and Clark et al. (1984) also found that dominant males held the superior position over opponents for the majority of the duration of combat bouts.

Acknowledgments.—I thank Steven Osborne and Stuart Tennyson for allowing me to videotape the social behaviors of their snakes. The comments made by Jeffrey Howland, Claudia Luke, Laurie Vitt, and two anonymous reviewers on earlier versions of this manuscript greatly improved its quality. In addition, I am grateful to Charles C. Carpenter and the Department of Zoology, University of Oklahoma, for use of video equipment.

LITERATURE CITED

- AKESTER, J. 1983. Male combat and reproductive behaviour in captive *Bitis caudalis* (A. Smith). *British J. Herpetol.* 6(9):329-333.
- ANDREN, C. 1981. Behaviour and population dynamics in the adder, *Viper berus* (L.). Unpubl. Ph.D. Dissertation. Univ. Gotenberg. Sweden.
- ARMSTRONG, B. L., AND J. B. MURPHY. 1979. The natural history of Mexican rattlesnakes. *Univ. Kansas Mus. Nat. Hist. Special Publ. No. 5.*
- BARKER, D. G., J. B. MURPHY, AND K. W. SMITH. 1979. Social behavior in a captive group of Indian pythons, *Python molurus* (Serpentes, Boidae) with formation of a linear social hierarchy. *Copeia* 1979(3): 466-471.
- BENNION, R. S., AND W. S. PARKER. 1976. Field observations on courtship and aggressive behavior in desert striped whipsnakes, *Masticophis t. taeniatus*. *Herpetologica* 32(1):30-35.
- BRECKE, B. J., J. B. MURPHY, AND W. SEIFERT. 1976. An inventory of reproduction and social behavior in captive Baird's ratsnakes, *Elaphe obsoleta bairdi* (Yarrow). *Herpetologica* 32(4):389-395.
- CARPENTER, C. C. 1984. Dominance in snakes. *In* R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag (eds.), *Vertebrate ecology and systematics—a tribute to Henry S. Fitch*, pp. 195-202. *Univ. Kansas Mus. Nat. Hist., Spec. Publ. 10.*
- , AND J. C. GILLINGHAM. 1977. A combat ritual between two male speckled kingsnakes (*Lampropeltis getulus holbrooki*: Colubridae, Serpentes) with indications of dominance. *Southwest. Natur.* 22(4): 517-524.
- CLARK, D. L., J. C. GILLINGHAM, AND A. REBISCHKE. 1984. Notes on the combat behaviour of the California kingsnake, *Lampropeltis getulus californiae*, in captivity. *British J. Herpetol.* 6(10):380-382.
- DAVIS, D. D. 1936. Courtship and mating behavior in snakes. *Field Mus. Nat. Hist. Zool. Series* 20(22): 257-290.
- FITCH, H. S. 1963. Natural history of the racer *Coluber constrictor*. *Univ. Kansas Publ. Mus. Nat. Hist.* 15(8): 351-468.
- GILLINGHAM, J. C. 1974. Reproductive behavior of the western fox snake, *Elaphe v. vulpina* (Baird and Girard). *Herpetologica* 30(3):309-313.
- . 1979. Reproductive behavior of the rat snakes of eastern North America, genus *Elaphe*. *Copeia* 1979(2):319-331.
- . 1980. Communication and combat behavior of the black rat snake (*Elaphe obsoleta*). *Herpetologica* 36(2):120-127.
- , C. C. CARPENTER, B. J. BRECKE, AND J. B. MURPHY. 1977. Courtship and copulatory behavior of the Mexican milk snake, *Lampropeltis triangulum sinaloae* (Colubridae). *Southwest. Natur.* 22(2):187-194.
- , ———, AND J. B. MURPHY. 1983. Courtship, male combat and dominance in the western diamondback rattlesnake, *Crotalus atrox*. *J. Herpetol.* 17(3):265-270.
- HAMMERSON, G. A. 1978. Observations on the reproduction, courtship, and aggressive behavior of the striped racer, *Masticophis lateralis euryxanthus* (Reptilia, Serpentes, Colubridae). *J. Herpetol.* 12(2): 253-255.
- KROLL, J. C. 1971. Combat behavior in male great plains ground snakes (*Sonora episcopa episcopa*). *Texas J. Sci.* 23(2):300.
- LELOUP, P. 1964. Observations sur la reproduction de *Dendroaspis jamesoni kaimosae* (Loveridge). *Bull. Soc. Roy. Zool. Anvers.* 33:13-27.
- . 1975. Observations sur la reproduction de *Bothrops moojeni* Hoge en captivité. *Acta Zool. Pathol. Antwerp.* 62:173-201.
- LEWKE, R. E. 1979. Neck-biting and other aspects of reproductive biology of the Yuma kingsnake (*Lampropeltis getulus*). *Herpetologica* 35(2):154-157.
- MARTIN, B. E. 1976. Notes on breeding behavior in a captive pair of sonoran mountain kingsnakes, (*Lampropeltis pyromelana*). *Bull. Maryland Herpetol. Soc.* 12(1):23-24.
- MURPHY, J. B., B. W. TRYON, AND B. J. BRECKE. 1978. An inventory of reproduction and social behavior in captive gray-banded kingsnakes, *Lampropeltis mexicana alterna* (Brown). *Herpetologica* 34(1):84-93.
- NOBLE, G. K. 1937. The sense organs involved in the courtship of *Storeria*, *Thamnophis* and other snakes. *Bull. Amer. Mus. Nat. Hist.* 73(7):673-725.
- PERKINS, C. B. 1943. Notes on captive-bred snakes. *Copeia* 1943(2):108-112.
- SECOR, S. M. 1987. Courtship and mating behavior of the speckled kingsnake, *Lampropeltis getulus holbrooki*. *Herpetologica* 43(1):15-28.
- SHAW, C. E. 1951. Male combat in American colubrid snakes with remarks on combat in other colubrid and elapid snakes. *Herpetologica* 7(4):149-168.
- SHINE, R., G. D. GRIGG, T. G. SHINE, AND P. HARLOW. 1981. Mating and male combat in Australian blacksnakes *Pseudechis porphyriacus*. *J. Herpetol.* 15(1):101-107.
- TRYON, B. W., AND G. CARL. 1980. Reproduction in the mole kingsnake, *Lampropeltis calligaster rhombomaculata* (Serpentes, Colubridae). *Trans. Kansas Acad. Sci.* 83(2):66-73.
- WAIDE, R. B., AND R. THOMAS. 1984. Aggression between two *Drymarchon corais melanurus* in Campeche, Mexico. *Herpetol. Rev.* 15(1):10.