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## Ritualistic Combat of Male Gopher Snakes, *Pituophis melanoleucus affinis* (Reptilia, Colubridae)

BY CHARLES M. BOGERT<sup>1</sup> AND VINCENT D. ROTH<sup>2</sup>

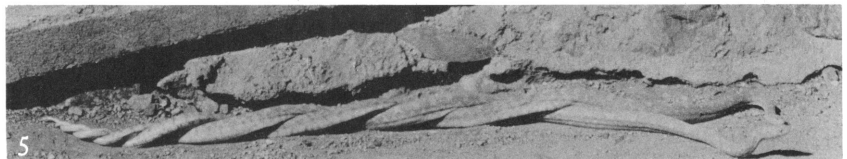
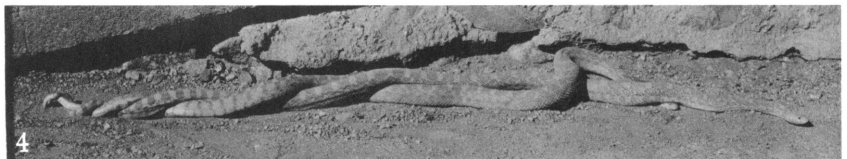
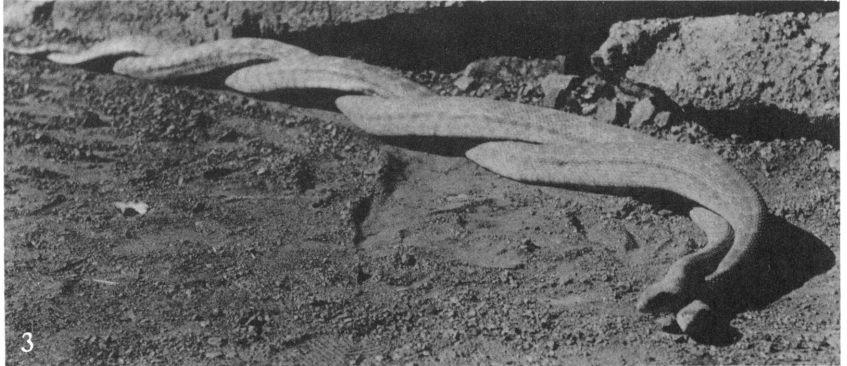
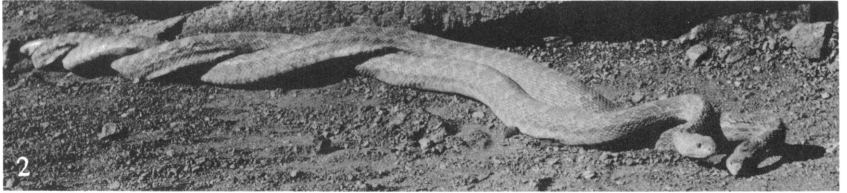
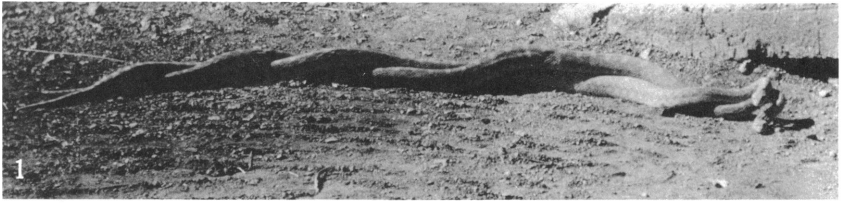
Ritualistic struggles between conspecific adult male snakes have been reported for representatives of various species, genera, and families. Shaw (1948) and Klauber (1956) have provided detailed accounts of the "male combat dance" of crotalids and viperids and summarized the information available. Shaw (1951) described comparable behavior in captive colubrids of three species and reviewed the literature dealing with "male combat" in colubrids and elapids. In the latter review Shaw noted the differences between courtship and male combat, both of which he described for *Pituophis m. melanoleucus*. He also described combat in snakes of two other American colubrid genera, *Elaphe* and *Lampropeltis*, and followed these descriptions with a review of the published accounts and a critical appraisal of the various hypotheses that have been offered to explain the behavioral significance of male combat. After noting the deficiencies and inaccuracies in the literature, Shaw concluded that much more extensive and detailed information would be needed before male combat among snakes could be explained satisfactorily.

Carr (1963) has stressed the ritualistic nature of courtship and territorial behavior in reptiles. Though Carr suggested that male combat may

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<sup>1</sup> Curator, Department of Herpetology, the American Museum of Natural History.

<sup>2</sup> Resident Director, the American Museum of Natural History Southwestern Research Station, Portal, Arizona.



FIGS. 1-5. Adult male gopher snakes, *Pituophis melanoleucus affinis*, engaged in combat. Sequence reveals modifications in the positions assumed by opponents during an interval when they moved forward approximately 2 meters.

be "a ceremonial way of contesting territory," or a display of prenuptial rivalry, he observed that the significance of such contests remained obscure. Klauber (1956), however, expressed a somewhat different opinion. Following his detailed review of the evidence, Klauber concluded that the male combat dance of rattlesnakes "stems from some sexual impulse, rather than from one based either on territorial defense or social domination."

Shaw (1951) also rejected territoriality or social domination in his discussion of male combat. He was inclined to believe that struggles between conspecific male snakes are often attributable to the homosexual behavior of one of the participants. There is evidence, however, that this behavior is more prevalent among captives than it is among snakes in their native environment. It is probable, therefore, that few combats observed in the field are motivated by homosexual activity. Shaw noted that other activities arouse combat behavior, and recent publications supply confirmatory evidence.

Our survey of the literature was prompted by the observations of the junior author, who obtained photographs of gopher snakes, *Pituophis melanoleucus*, in combat. Such struggles have been observed and reported in other races of this species, but the only illustrations of American colubrids in combat thus far published portray captives. The photographs herewith reproduced will augment our meager knowledge of combats between conspecific male colubrids. While trying to ascertain the behavioral significance of such combats and the nature of the situations that lead to such struggles, we have found it necessary to reappraise, and in some instances to reinterpret, the observations reported by others. As far as possible we have avoided citing accounts previously reviewed by Shaw (1951) and Klauber (1956), but it proved to be necessary to refer to the accounts covered in these earlier surveys that contained information particularly pertinent to some aspects of combat behavior we discuss below.

### FIELD OBSERVATIONS

The ensuing account describes the behavior of two large male Sonora gopher snakes, *Pituophis melanoleucus affinis*, observed in combat near Portal, Arizona. The Sonora gopher snake is comparatively abundant in the vicinity of the town, which is situated near the mouth of Cave Creek, at an elevation of nearly 5000 feet in the foothills of the Chiricahua Mountains. Snakes of the subspecies are encountered at higher elevations in this region, but they are more abundant below or along the edge of the foothills, especially in grassland and cultivated fields.

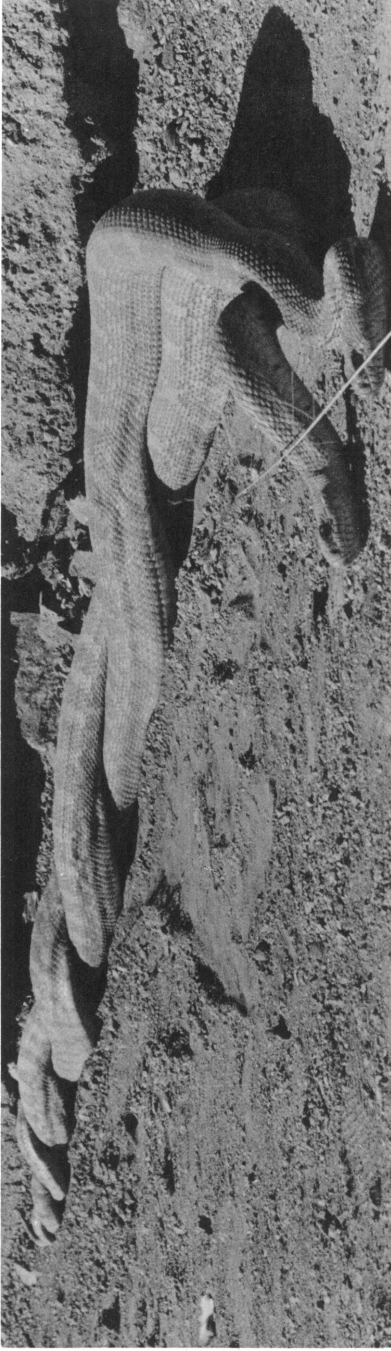


FIG. 6. Male gopher snake with head tilted and extended to one side as it endeavors to counteract the force exerted by its opponent.

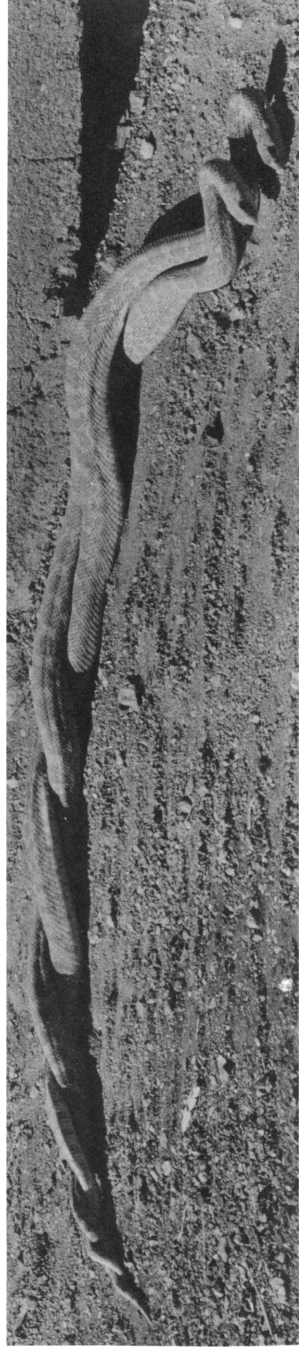


FIG. 7. Male gopher snakes tend to maintain tails and posterior portions of their bodies entwined while engaged in combat. Anterior portions of their bodies are more often loosely entwined, with heads nearly parallel, as illustrated.

Near Portal the floor of the canyon has been largely cleared of trees except for sycamores bordering the bed of Cave Creek. The cleared area affords suitable environments for many reptiles inhabiting the sparsely covered terrain of the San Simon Valley, which borders the eastern side of the mountains.

When first noted, on May 2, 1964, the gopher snakes were carrying on their ritualistic struggles on a grass-covered bank near a house above the main settlement in the canyon. At the time, approximately 3:00 P.M., the temperature of the air approached 26° C. The snakes were undoubtedly warmer, for it was a clear, cloudless day, and the substratum had been exposed to the sun during the preceding hours. Moreover, the snakes were in direct sunlight throughout the period of observation. They may have evaded direct sunlight earlier, for shrubs, rocks, and the few trees in the vicinity afforded shade. It seems probable that the snakes encountered each other not far from the patch of grass where they were first seen. Their struggle may have been in progress for some time prior to the arrival of the observer, of course, but there was no way of learning where or how the combat was initiated. Even with their bodies intertwined, and despite their inability to employ their normal locomotion, the snakes moved forward slowly, seemingly propelled by the force that each snake exerted on the coils of the other. This "corkscrew" propulsion led the snakes to advance more or less steadily in the same direction. Shortly after 4:00 P.M. the observer was asked to remove the snakes from the premises. During the preceding hour the snakes had moved approximately 9 meters from the grass to the gravel adjacent to the concrete runway of a grease rack.

The extent of the interlacing of bodies and tails varied from time to time, but the snakes were continuously intertwined throughout the period of observation. At times both snakes had the anterior portions of their bodies free. On such occasions one head was momentarily separated from the other when each snake crooked the free portion of its trunk outward from the main axis of the entwined bodies. At other times one snake elevated the trunk behind its head while the other extended a fold laterally. Ordinarily, however, the heads of both snakes were oriented in the same direction, regardless of whether the head of one or both snakes was elevated or pressed to the substratum. Despite the interlacing of their bodies, each snake attempted to maintain its head and body upright. Occasionally one snake exerted enough pressure on its opponent to force it to tilt its head, or the entwined bodies of both snakes rolled completely over. Both snakes rolled over together only when one snake managed to press a lateral fold to the substratum while the anterior part

of the other snake extended along the axis of the tightly entwined bodies behind it. The snakes quickly regained upright positions after rolling over, and they continued to exert pressure on each other as their entwined bodies advanced.

Throughout the struggle both snakes hissed repeatedly. The volume of sound thus produced was doubtless enhanced by the modifications of the epiglottis characteristic of snakes of the genus. Perhaps respiratory movements were accelerated as a result of muscular exertion as well as by the heat gained from their exposure to solar radiation. The sounds resulting from the forcible expulsion of air may have been little more than a by-product of respiratory cooling, although the normal defensive behavior of large gopher snakes commonly includes loud hissing. When attacked by mammals as small as weasels, or when approached by larger animals, gopher snakes often hiss or strike. Their jaws were never employed during combat, however, although the snakes had ample opportunity to bite each other. They behaved as though they were completely engrossed in their struggle. During the course of the hour at least a dozen people paused to watch the snakes, which were seemingly undisturbed, even when observers came within a meter of them.

As may be inferred from the photographs reproduced in the accompanying figures, the snakes were approximately the same size. Measurements obtained by straightening out the snakes on a flat surface indicated that each snake slightly exceeded the length of 2 meters that Klauber (1947) has given as the approximate maximum for the subspecies. The living snakes, one of which lacked the terminal portion of the tail, were sent to the Arizona-Sonora Desert Museum, where Mr. William H. Woodin ascertained that both were males. They were appreciably larger than the gopher snakes ordinarily encountered in the vicinity of Portal. No other snakes were noted in the vicinity of the two males near Portal, but, with attention centered on the snakes in combat, any females that might have been present could have evaded detection by seeking cover.

## DISCUSSION

### SIZE OF COMBATANTS

Snakes of other species observed in combat have not invariably been described as unusually large. Nearly all accounts refer to large snakes, or at least provide some indication that the combatants were sexually mature. All colubrids and elapids thus far seen in combat are relatively large representatives of their respective families, species that attain lengths of at least 1 meter. Struggles between large snakes would, of course, more readily attract attention. Male combat has not been reported for the

smallest vipers and pit vipers, but ritualistic struggles have been described for species that seldom exceed a length of 0.5 meter, *Vipera berus* in Europe and *Crotalus cerastes* in the United States. Unlike male colubrids, few of which raise the head much above the substratum while engaged in combat, viperids and crotalids frequently elevate the head by raising the anterior third or more of the body to a position that is nearly vertical, or even tilted backward. Consequently the "combat dance" of vipers and pit vipers is far more conspicuous.

#### TRENDS IN BEHAVIOR

The few elapids observed in combat also elevate the head. Information supplied by Grant (1956) suggests that at times during combat the anterior portions of the entwined bodies of mambas, presumably *Dendroaspis polylepis*, attain an upright position. "Sometimes their bodies were flat on the ground," according to Grant, but "the next instant the first four feet or so were held vertically and slightly arched back." Grant estimated the total length of the larger of the two combatants to have been 9 feet. His illustration, a sketch, which Grant said he prepared by projecting one frame from motion-picture film, portrays snakes with more nearly the anterior third of their bodies elevated and largely entwined, although each head is tilted away from the other. Leloup (1964) described male combat in *Dendroaspis jamesoni*, but the illustration provided depicts a combat between a male of this species and a male *D. polylepis* (identified erroneously as *D. angusticeps*). In this instance relatively small portions of both trunks are held in vertical position. Klauber (1956) cited accounts published as early as 1885 in which it was noted that male cobras (presumably *Naja*) sometimes fought, "while raised up anteriorly."

Precise information concerning male cobras in combat appears to be lacking. Fleay (1951), however, described and depicted the combat behavior of males of two distant relatives of the cobra, the large Australian elapids, *Pseudechis porphyriacus* and *Demansia textilis*. Males of both species apparently tend to elevate the head, and *Pseudechis* distends a cobra-like hood during combat. The relatively small portion of the trunk supporting the head, however, is seldom reared above the substratum at an angle greatly exceeding 40°. While engaged in their struggles, these Australian elapids ordinarily maintain the head in a horizontal position and sporadically entwine nearly the full length of their bodies. In these latter respects their combat behavior resembles that of gopher snakes or the Asiatic rat snakes, *Ptyas mucosus*, that Prater (1933) portrayed in combat. In contrast, the combat postures assumed by the African mambas

more closely approximate those of the vipers and pit vipers. Like the latter, the mambas not only raise the forepart of the trunk to a vertical position, but tilt the head backward or even upward, with their bodies loosely rather than tightly entwined.

Unlike gopher snakes and most other colubrids for which combat is reported, snakes of the families Elapidae, Viperidae, and Crotalidae are not adapted to constrict their prey. Tight intertwining of bodies does

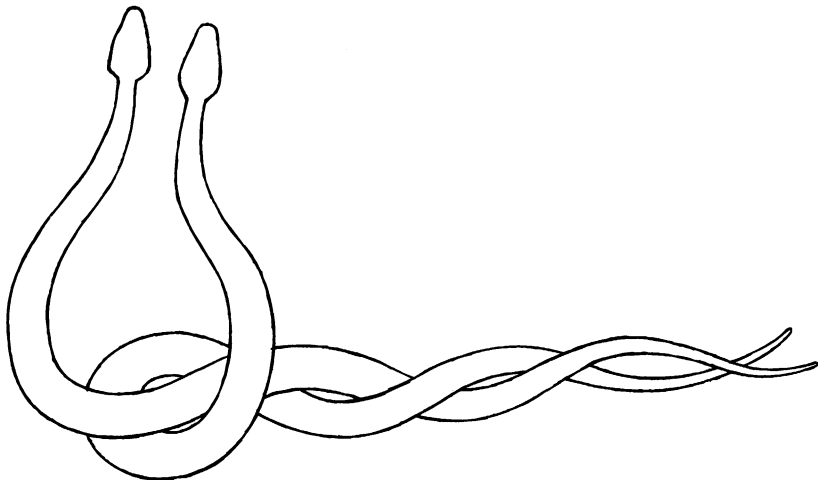


FIG. 8. Male Aesculapian snakes, *Elaphe longissima*, in the postures supposedly assumed during combat (as portrayed by Stemmler-Morath, 1935, who interpreted the posture as a "courtship"). The lyre-shaped configuration resulting from the elevation of the heads and trunks of males engaged in combat may be peculiar to this colubrid. While in combat, other colubrids rarely elevate the head much above the substratum.

not appear to be wholly dependent upon the ability to constrict, for Fleay (*supra cit.*) asserted that, when he observed *Pseudechis* in combat, both males were "writhing, hissing, struggling and exerting the greatest possible constriction on each other, and actually rolling slowly over and over *en masse*." Much the same sort of behavior was, of course, observed in *Pituophis*.

During the ritualistic struggles of the European colubrid, *Elaphe longissima*, each male elevates the anterior third of its body to a vertical position, while the posterior portions remain entwined. Viewed from the front, the upraised bodies of the two appear as a lyre-shaped configuration (fig. 8). Both heads are directed upward rather than with one facing the





FIG. 9. Postures characteristic of male colubrids engaged in combat, with tails and posterior portions of the bodies entwined and heads raised slightly above the substratum.

other, as they are commonly portrayed in the caduceus, which is supposed to have been inspired by the combat of this species. The unusual if not startling postures that males of this European species assume during combat attracted human attention at an early date (Klauber, 1956). If other colubrids, at least those similar in size, raise the body in comparable fashion, it seems probable that their combat behavior would have been observed and reported. *Elaphe longissima* among the Colubridae, and the mambas among the Elapidae, may be exceptional in attaining a vertical stance. An informant quoted by Wall (1921) described behavior, probably to be construed as male combat in *Ptyas mucosus* (as Shaw [1951] noted), during which the heads were raised a foot or more above the ground. Elevation of the head is not characteristic of *Ptyas*, however, as may be inferred from the illustration in Prater (1933) as well as from other accounts.

The information available, meager though it is, suggests some divergence of trends in the behavior associated with combat. Notwithstanding such behavior as that described for *Elaphe longissima*, which appears to be aberrant, four reasonably distinct patterns can tentatively be defined

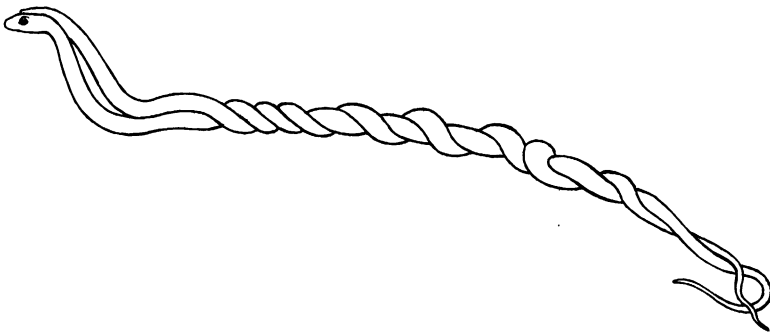


FIG. 10. Postures assumed by Australian elapids, *Pseudechis porphyriacus*, during combats between males of comparable size. Heads are commonly elevated during struggles that entail intertwining of bodies, but heads are not tilted to vertical position. (Based on illustrations published by Fleay, 1951.)

in terms of the postures assumed by the combatants, as follows:

1. Competing males 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. Such postures appear to be characteristic of colubrids (fig. 9).

2. Competing males with bodies intertwined, and heads in horizontal position, but elevated above the ground (fig. 10), as described for

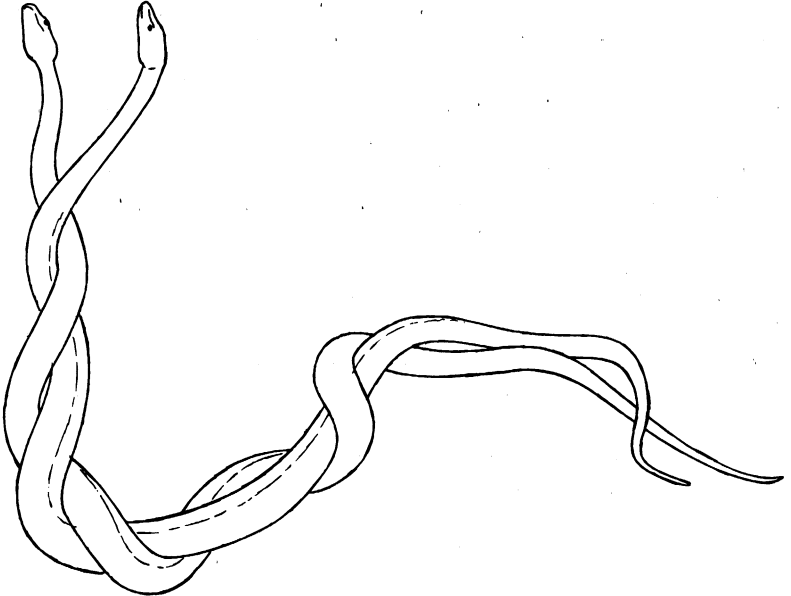


FIG. 11. Mambas, *Dendroaspis polylepis*, showing upraised bodies of males during combat, with anterior portions of the combatants upraised and entwined. Heads are momentarily vertical or tilted backward during combat, as in viperids and crotalids. (Redrawn from Grant, 1956.)

*Demansia* and *Pseudechis*, and perhaps characteristic of other large, un-specialized elapids.

3. Competing males with anterior portions of trunks upraised and intertwined, snouts tilted upward, or even oriented vertically. The tails and posterior portions of the trunk may be free or loosely but not tightly intertwined. Postures of the sort described and figured for mambas (fig. 11) differ from those of other elapids, and in some respects resemble those of vipers.

4. Competing males with anterior portions of the trunk upraised, and loosely intertwined from time to time, with head either tilted or in vertical position. Opponents may be oriented in the same direction or facing

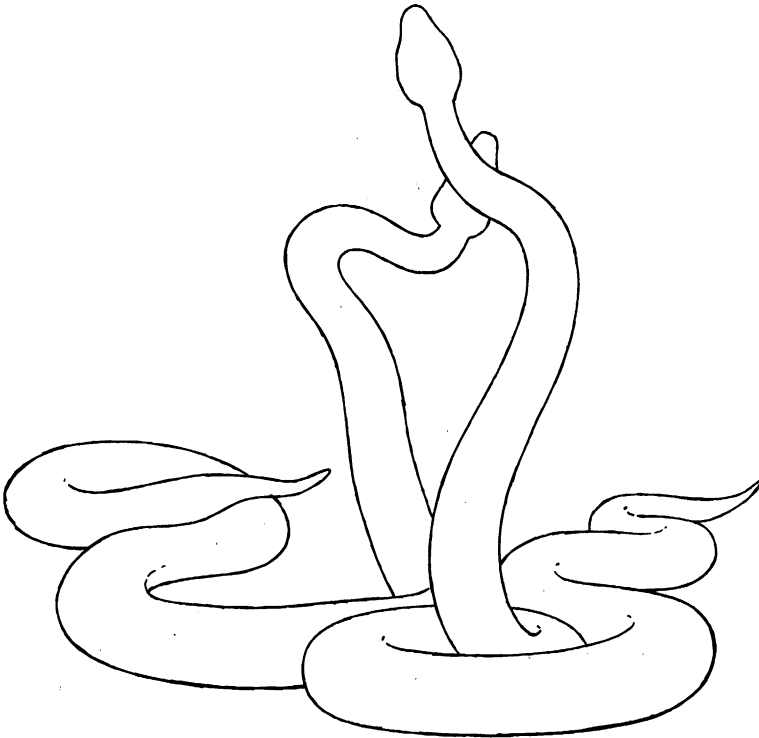


FIG. 12. Male viperids, *Vipera berus*, in postures commonly assumed when males are engaged in combat. The head and the forepart of the body are nearly vertical as each male thrusts the upraised portion of its body against that of its opponent.

each other, but intertwining of bodies is sporadic and largely restricted to anterior portions of the trunk. The vertical orientation of the head may be characteristic of viperids (fig. 12), but among crotalids (figs. 13 and 14) the head is more often tilted downward from the near-vertical position of the trunk.

Grant (*supra cit.*) described the mambas he photographed as "caressing each other with their long necks." Such terms would inaptly describe the behavior of colubrids, but, aside from their rapidity, the movements of mambas approximate those of vipers and pit vipers. Neither Grant nor Leloup (*supra cit.*) mentioned tightly intertwined trunks in mambas observed in combat, whereas the behavior that Fleay described for the Australian elapids, except for the more pronounced elevation of the head, closely parallels that observed in gopher snakes and other colubrids. Both *Pseudechis* and *Demansia*, however, may approach *Dendroaspis* in the rapidity of their movements during combat.

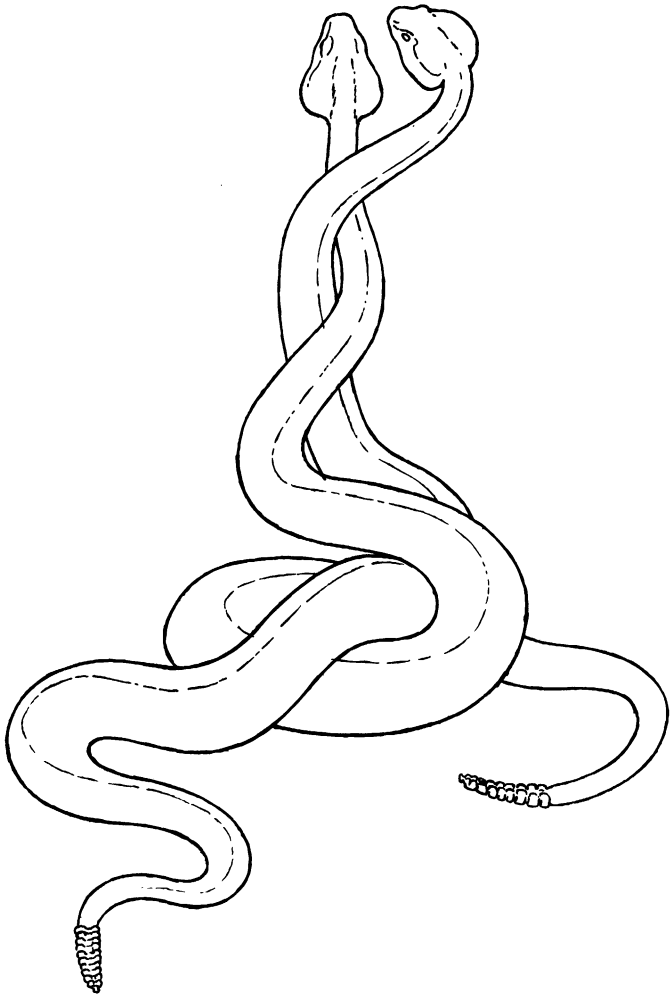


FIG. 13. Combat posture characteristic of male rattlesnakes, *Crotalus atrox*. Heads may be tilted toward the horizontal position or pointed upward when the upraised forepart of the body of each combatant is approximately vertical. Males may face each other, or their heads may be oriented in the same direction.

As Klauber (1956) observed, male combat may be of ancient lineage, "going back to the dawn of snake history," before genera and families had become differentiated. Thus far combat has been observed among snakes in only four families—the Colubridae, Elapidae, Viperidae, and Crotalidae. It may not be restricted to snakes in these families, but it

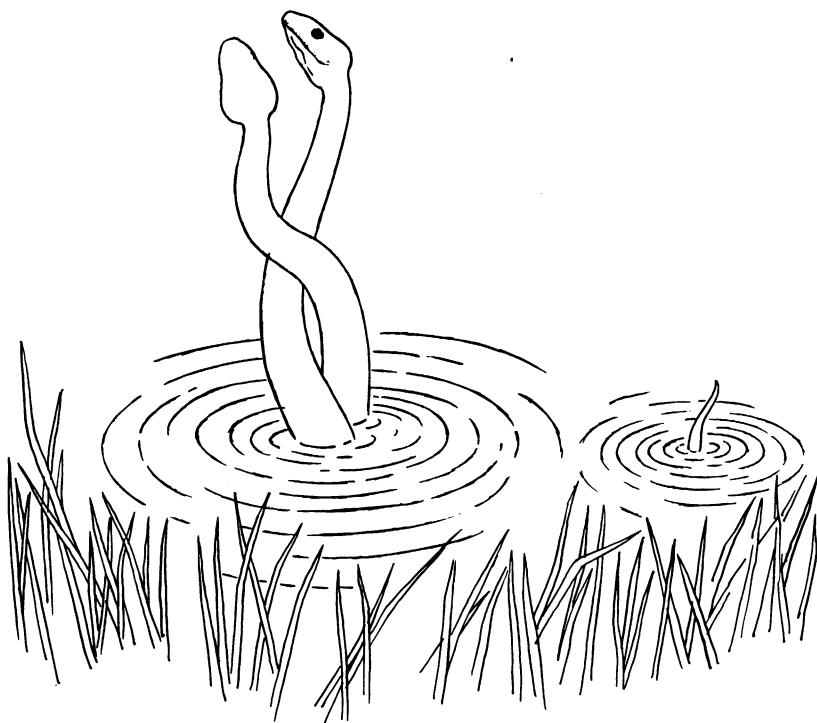


FIG. 14. Male water moccasins, *Agkistrodon piscivorus*, engaged in combat (re-drawn from Carr and Carr, 1942). The ritualistic struggles of such males, though carried out on the surface of pools, conform closely to those of crotalids in terrestrial situations.

has not been observed in the family Boidae, which contains several species of moderate dimensions as well as the largest snakes extant. Combats may or may not occur between fossorial snakes, particularly the specialized species assigned to the Uropeltidae, Typhlopidae, or Leptotyphlopidae, but chances are remote that such behavior would readily be observed in such secretive snakes. It is noteworthy, nevertheless, that ritualistic struggles during which combatants assume a near vertical stance, described by Deraniyagala (1958) as "pseudo-combat," occur between males in the family Varanidae, lizards that may well have descended from the same group of reptiles that gave rise to the snakes.

#### CONFLICTING INTERPRETATIONS

There are manifest shortcomings in field observations, which rarely

afford clues concerning the stimuli that initiate combat. Moreover, people who have the good fortune to witness combats under natural conditions rarely remain on hand to see the outcome of the struggle. Conditions approximating those of the native environments of many snakes are not easily duplicated in the laboratory, however, where snakes can more readily be observed. It is uncertain, therefore, whether studies of captives afford a reliable means of learning a great deal about the normal behavior of snakes. Nevertheless, careful, detailed observations of captives, such as those reported by Shaw (1948, 1951), afford more insight concerning the nature of combat behavior than most of the observations made in the field.

It is evident that cages encompassing areas no greater than 2 or 3 meters impose restrictions on the movements of all but the smallest snakes. Leloup (1964) avoided the shortcomings of small cages by observing the behavior of mambas maintained in the Congo under conditions closely approximating the normal environment. In pens that were 15 meters in length and 5 meters in width the snakes were, as described by Leloup, "semi-free." During the period of greatest sexual activity, as many as seven or eight males sometimes were attracted by a single female. Leloup noted that such assemblages can be attributed to the abnormal concentration of mambas in the enclosure. Behavior observed under such conditions may not be wholly normal. Aside from the presence of more males than might be expected under natural conditions, the behavior during courtship and mating that Leloup described for *Dendroaspis jamesoni* probably approximates that of mambas in their natural environment.

As interpreted by Leloup, male combat is associated with mating. The courtship of these mambas closely parallels that of most colubrids, although it is questionable whether the behavior of rival males is attributable to "jealousy," as suggested by Leloup. In the graphic but anthropomorphic terms of this author, when a rival intervenes, or "persists in his advances," the male momentarily abandons the female he has been courting and "throws himself upon his antagonist." Leloup doubted that the ensuing struggle between the two males is to be construed as a "dance or a symbolic combat." No biting is involved, however, for the snakes inaugurate the combat by entwining their bodies and raising the anterior portions to a vertical position. In the sparring that follows, each snake attempts to entwine its body around that of the other while seeking to avoid the compression of its own "respiratory region." As the feinting continues, the snakes engage in a sort of tilting match with choreographic qualities described by Leloup as "*assez captivante*." The

more robust or adroit male, unable to drag its opponent away from the female by force, manages nevertheless to direct its movements and thus to induce the competing male to remove itself some distance away. As interpreted by Leloup, the combat terminates with the loser "retaining his dignity," for he departs as though "he were no longer interested." The winner of the struggle returns to the female and resumes the courtship.

As described by Leloup, the behavioral significance of male combat becomes apparent. It would have selective significance as well, to the extent that such activities impose restrictions on the mating of weaker males. Leloup's explanation is both novel and plausible, although an alternate explanation warrants consideration in view of Shaw's (1951) interpretation of comparable behavior in *Pituophis*. Mambas are notoriously fast-moving snakes, however, that differ from gopher snakes in being able to move fairly rapidly even while entwined in combat, according to Grant (1956). Grant presumably observed *D. polylepis*, a species that may be faster than other mambas in its movements, particularly on the ground, where it is encountered as often as it is in trees. Leloup's account dealt primarily with *Dendroaspis jamesoni*, which is less frequently terrestrial and largely an inhabitant of forests. Nevertheless, mambas are conceivably capable of dispensing with rivals and resuming courtships without the prolonged delay presumably characteristic of *Pituophis*. It will be recalled that the gopher snakes observed in Arizona were engaged in combat for at least an hour. Their struggles, in progress when the snakes were encountered, might well have continued for a much longer period had they been unmolested.

Owing to their rate of progression, scarcely 9 meters per hour while in combat, the gopher snakes might not have shifted their positions any great distance had their struggles continued. Without more detailed information than that obtained when the two males were observed at Portal, it is conjectural whether their combat stemmed from an interrupted courtship. Woodbury (1941), however, has reported a combat between male gopher snakes belonging to another subspecies, *Pituophis m. deserticola*, during which a third snake, identified as a female, remained in the immediate vicinity but did not participate in the struggle. As reported by Woodbury, the males, with their bodies partly entwined, but their heads free, repeatedly struck at each other. When one of the observers seized the larger of the two males, the female, followed by the other male, promptly sought cover and escaped.

Had the observers allowed the males to continue their struggles, the larger snake, like the victor of combat between mambas Leloup described,

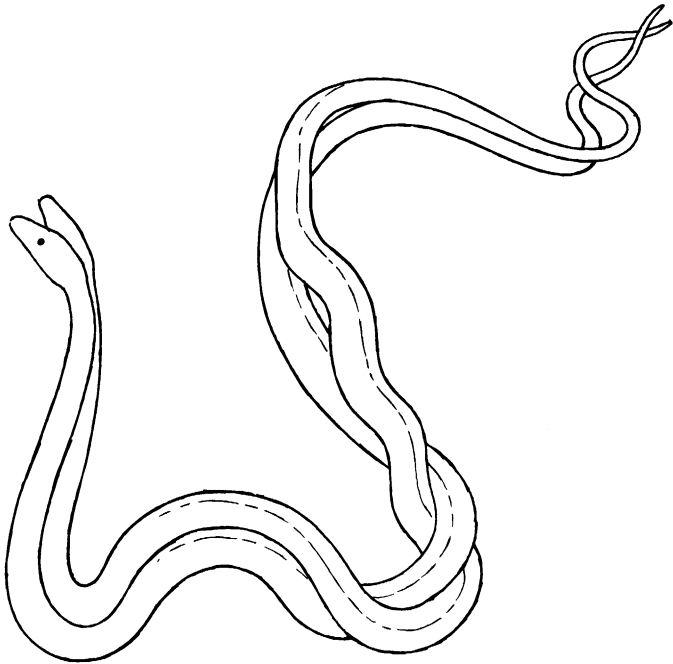


FIG. 15. Postures assumed by mambas when the male of one species, *Dendroaspis jamesoni*, is engaged in combat with a male of another species, *D. polylepis* (based on illustration in Leloup, 1964).

might have driven off its rival and returned to court the female. It is virtually certain that gopher snakes moving at speeds no greater than the males attained while in combat at Portal could, by means of olfactory cues, easily relocate any female they might have abandoned earlier.

Despite these possibilities, without more information than Woodbury could supply, the situation he described is explicable in other terms. As interpreted by Shaw (*supra cit.*): “. . . it may be presumed that the two males had been courting the female and then had become involved with each other in combat, the larger male having become confused and substituted the smaller male for the female in his courtship activities. Similar behavior in which two males originally courting a female, become confused and court each other, has been observed frequently in *P. m. melanoleucus* and usually leads to combat between the two males.”

Caged snakes are perhaps more readily confused than those in natural environments. If males of *Dendroaspis jamesoni* ever attempted to court other males in the “semi-free” conditions under which they were observed



by Leloup, he failed to mention it. In a brief discussion of sexual dimorphism, however, he admitted that it was not always easy to ascertain the sex of living individuals without disturbing them. Leloup was aware of the confusion that resulted when a few mambas of another species (*Dendroaspis polylepis*) from Tanganyika were placed in an enclosure containing a dozen *D. jamesoni*. Males of the latter species courted females of *polylepis* as readily, and as successfully, as they had courted conspecific females. Males of *D. polylepis* were observed in combat with males of *D. jamesoni* (fig. 15), but *D. polylepis* males did not attempt to court females of the other species. Leloup's account, however, would indicate that, despite the lack of discrimination displayed by *D. jamesoni* in selecting a mate of its own species, it nevertheless discriminated between congeneric males and females regardless of whether they were also conspecific. Leloup may have omitted pertinent details in describing the behavior of the two species of mamba, but many elements of the pattern of combat behavior he described for *D. jamesoni* have been reported for male vipers when their combat is closely associated with courtship activity.

Experienced observers of the European adder, *Vipera berus*, do not find it difficult to distinguish males from females. Volsøe (1944) has discussed variations in the secondary sex characters of this species and summarized the differences, including the obvious differences in color. Whether sexual dichromatism has any direct bearing on the behavior associated with the courtship and combat reported for these vipers remains to be demonstrated, but there should be no question concerning the sex of the individuals mentioned in the following account.

Prior (1933), who observed the European adders under field conditions in England, watched one male that had encounters with three males in succession, and resumed courtship with the same female after each encounter. When Prior first observed this male, it was in combat with a smaller male that suddenly writhed free of its opponent and fled, with the victor in pursuit. Shortly after it had returned to the "arena" adjacent to the female, this male suddenly elevated its head and the anterior portion of its body to the combat posture in response to the approach of another male. Apparently the approaching adder saw the upraised body of the other male and veered to one side without stopping. As it disappeared, the male that had been poised for combat reassumed its prone position and crawled over to the female, displaying the jerky movements that characterize the activities of males during courtship.

These activities were soon interrupted when a large male crawled out of the bramble nearby and approached the female, seemingly unaware

of the presence of the other male. The reaction of the courting male this time went beyond the ritualistic elevation of its head, for, according to Prior, it "coiled vehemently at [the intruder] with a flash of silver body" that put him to "a rather ignominious flight." The victor presumably followed in pursuit, for Prior stated that it "returned from this triumph" to attend the passive female, which had remained coiled in the same position throughout the three encounters.

The behavior described for these vipers evidently shares many of the features that Leloup reported for mambas. While in combat, male crotalids and viperids shift position from time to time but usually confine their activities to a limited area. Field observers, few of whom seem to have been as patient as Prior, rarely remain on hand to see the outcome of the combats they witness. Consequently it is uncertain whether the threatening display of the upraised trunk is often effective in discouraging intruders, or whether such displays may also serve as the "challenge" that leads to combat. Nor can it be stated with assurance that one combatant usually pursues or drives away the other following the combat. The use of muscular force ceases, however, when one of the snakes withdraws from the struggle, even though it may be pursued by the victor. Combat among male viperids or crotalids, therefore, leads to or precedes the departure of the loser, whereas among colubrids and elapids both males move away from the female during combat, but only the victor returns.

The information derived from these accounts strongly suggests that male combat may be closely associated with mating behavior. The accounts of Woodbury, Leloup, and Prior, when considered collectively, reveal basically similar elements in the behavior patterns of colubrids, elapids, and viperids during combat. The combats of male vipers are essentially the same as those of crotalids, and Klauber (1956) observed that "the dancing pattern seems to be the same for all species and subspecies of rattlers." Klauber cited instances in which a third rattlesnake, the sex of which was not ascertained, was observed in the vicinity of males in combat. He pointed out, however, that the presence of a female is not required to provide the stimulus for combat.

Klauber's statement is supported in several accounts. Each time mambas of one species, *Dendroaspis polylepis*, were fed, Leloup observed combats similar to those accompanying courtship. Occasionally such combats lasted a long time, and, though Leloup described them as "*absolument identiques*" with those associated with courtship, he went on to say that sexual discrimination played no part in these struggles. He did not explicitly state that females were seen in combat, and it is doubtful whether

they assumed the combat posture. Leloup added that in some instances one combatant was severely wounded or even eaten. Shaw (1951) noted that the excitement caused by feeding captive males of *Elaphe guttata* and *Lampropeltis doliata* often led to combat. One male of the latter species bit its rival, although no biting was observed in the other species. Authors occasionally mention males' biting each other during combat, but most observers, seemingly impressed by the failure of the combatants to inflict serious damage on each other, specifically mention the absence of biting.

It seems probable that snakes more often wound their adversaries when their bouts stem from the presence of food. Nearly the same postures or modes of behavior may be displayed by males, however, whether their combat is traceable to the presence of a female or to the presence of food. Without evidence that one male was carrying on a courtship immediately prior to the onset of a combat, the observer cannot safely interpret the struggle as a manifestation of sexual rivalry. Under natural conditions two snakes may, on rare occasions, find themselves pursuing the same prey. It is improbable, nevertheless, that combats observed in the field often arise from competition for food. More often, at least when the observer has been noting the behavior of colubrids and elapids, it seems likely that he has failed to note the quiescent, perhaps protectively colored female, which may be resting several meters away from the males in combat.

Viperids and crotalids seldom move far from the site where combat begins. Anyone suddenly and unexpectedly confronted by the spectacle of the upraised trunks of the males is unlikely to devote much effort to searching for the female. Prior admitted that he watched two encounters between male adders before he discovered that "the leafy area" to which one male repeatedly returned was in reality "the coiled body of a great golden female adder," with dusky brown blotches that blended with the coppery-yellow ground colors.

Combats under natural conditions may not invariably be manifestations of sexual rivalry, but negative evidence is inconclusive. It should also be noted that many persons who report combats in the field have entertained the belief that what they saw was courtship. Aside from the presence of food, other stimuli evidently elicit combat behavior in captive males. Klauber (1956) reported that after three rattlesnakes, *Crotalus viridis viridis*, had been caged together for six years they suddenly engaged in combat. It might be assumed that the onset of combat behavior marked the attainment of sexual maturity. The possibility remains, for precise information is unavailable for males of this subspecies, although

female rattlesnakes adapted to warmer climates reproduce within three years of their birth. Klauber cited another instance, however, in which two males were observed in combat shortly after a third male had been placed in the cage. Sexual discrimination in most snakes is largely dependent on chemoreceptors. The complex interplay of hormone levels and sensory mechanisms that regulates their behavior in the field, however, often seems to be disrupted in the abnormal conditions of captivity. Had the third male been in contact with a female immediately prior to being added to the cage, traces of her odor may have precipitated the combat that ensued between the other males.

It is conjectural whether errors in discrimination are attributable entirely to olfactory cues, but no doubt exists that combats arise when one captive male attempts to court or to copulate with another. Shaw (1951) cited several accounts that describe homosexual behavior in captives. It is noteworthy that conclusive evidence of such behavior under natural conditions is lacking. Information derived from lizards, particularly species in which vision seems to be the dominant sense, may not be applicable to snakes. Nevertheless, it is pertinent to note that investigators (Noble and Bradley, 1933), whose studies of the courtship behavior of lizards were based largely on individuals perhaps overly crowded in laboratory cages, reported that "males frequently copulate with other males." In his critique of this earlier investigation, Evans (1938), who had studied the courtship of two species of *Anolis* in their natural habitats, stated that "no single case of homosexual behavior was observed . . . in all of the 1,133 separate observations made in connection with this paper or in the field."

It may be added that the prevalence of abnormal behavior in captive snakes is manifest, not only in their failure to discriminate between the sexes, but in their inability to discriminate between species. Leloup's (1964) account of interspecific courtships, matings, and combats in mambas is mentioned above. Both Shaw and Klauber reported combats between males belonging to different species, and Wagner (1962), for example, stated that males belonging to different genera, *Crotalus* and *Agkistrodon*, were observed in combat. Wagner also reported that a male rattlesnake, *Crotalus adamanteus*, mated with a female water moccasin, *Agkistrodon piscivorus*. In every instance these reports deal with captive snakes. Most hybrids on record are the result of matings in captivity, but hybrids are occasionally encountered in the field. Hence matings between snakes of separate species, or more rarely between snakes of different genera, occur under natural conditions. Combats between males belonging to different species, as well as homosexual behavior, may also occur

in nature, but owing to their rarity there is little likelihood of their being seen and reported. All information available suggests that the incidence of abnormal behavior is considerably greater among captive individuals.

Neither Shaw (1951) nor Klauber (1956) found sufficient evidence to substantiate assumptions that male combat was either a manifestation of social dominance or territorial behavior. Shaw, who carefully avoids dogmatic statements, nevertheless tended to stress homosexual behavior in his discussion of the functional aspects of combat. In view of the information supplied by Leloup, however, it is reasonable to assume that snakes interrupted during courtship in their natural habitat rarely become confused and attempt to court intruders. Certainly nothing contained in Prior's account of combat in the European adder suggests any manifestation of homosexual behavior. Male adders in their natural environment, like the male mambas in the "semi-free" state that Leloup described, behaved as though they readily distinguished males from females. The limbless, elongate bodies of snakes impose limitations on the diversity of maneuvers they can perform. It is not astonishing, therefore, that snakes react in much the same way, whether the stimulus that actually arouses combat happens to be a female, food, or a manifestation of homosexual behavior by another male.

Leloup's interpretation of male combat, as a normal activity that permits males to dispense with rivals during courtship, seemingly affords the most satisfactory explanation offered thus far for most combats observed under natural conditions. Until we know more about male combat, it is preferably construed as a manifestation of sexual rivalry than as a reaction to the homosexual behavior of another male.

#### RECORDS OF MALE COMBAT AMONG SNAKES

Much of the confusion in the literature dealing with male combat is indirectly traceable to the secretive habits of snakes. Competent students of animal behavior, biologists with the training and interest needed to record and interpret the activities of animals on a meaningful basis, would encounter numerous difficulties but very few snakes if they restricted their investigations to the field. Understandably, therefore, students of ophidian behavior turn to the laboratory where they may control conditions but rarely manage to simulate natural environments. The laboratory investigator may never see snakes in combat, but the odds in favor of his seeing a combat are appreciably greater than they would be were he a field naturalist. Professional biologists so rarely see males in combat in their natural environments that those who discuss

these aggressive displays depend heavily on the information supplied by casual observers or amateur naturalists.

Such informants, whether they have watched snakes in the field or in their home terrarium, virtually always interpret combat as mating behavior. Reuss (1926), a notable exception, was aware that the adders he photographed while in combat were both males, but a photograph in the series published by Reuss was reproduced a few years later with a caption that identified it as that of a "mating dance." Vipers and pit vipers are normally prone throughout their courtship and mating, but, as shown by Reuss for adders and by Shaw (1948) and Klauber (1956) for crotalids, they elevate their trunks at frequent intervals during combat. Among elapids and colubrids, the trunk of the male is usually resting on that of the female, although, while endeavoring to insert its copulatory organ, the male may have its tail and the posterior portion of its body partly interlaced with corresponding portions of the female. Tightly entwined bodies characteristic of males in combat are unlikely to be observed during courtship. During their combats, however, male colubrids and elapids occasionally disentwine their bodies and momentarily assume postures that closely resemble those seen when the male is courting a female.

The illustrations accompanying Oliver's (1956) account of the courtship of king cobras, *Ophiophagus hannah*, reveal that both members of the pair occasionally distend the hood and elevate the anterior portion of the body. The postures assumed at times by the male and female during their courtship (as may be noted in figs. 2 and 3 accompanying Oliver's account) are much like those of the male elapids, *Demansia* and *Pseudechis*, that Fleay (1937, 1951, 1957) depicted in combat. A single photograph of two snakes, unless it depicts them in the posture most characteristic of the activity in progress, may not reveal whether it is courtship or male combat. Fortunately authors convinced that they were observing mating behavior usually supply notes along with their photographic evidence that make it possible to decide whether it was courtship or male combat. Curry-Lindahl (1956) had ample evidence to point out that the behavior Grant (1956) described as the mating activity of mambas represented male combat rather than courtship.

Not all authors have distinguished male combat from other forms of aggressive behavior displayed by snakes. Wagner (1962) reported male combat in *Crotalus adamanteus* and mentioned similar combats between males of *C. adamanteus* and those of *C. atrox*, as well as between males of *C. adamanteus* and those of *Agkistrodon piscivorus*. He prefaced his account, however, with a list of the snakes in which comparable behavior

purportedly occurs. Male combat has been reported for several of the genera that Wagner listed, but not for *Thamnophis*, a genus assigned to the colubrid subfamily Natricinae. Shaw (*supra cit.*) has commented on the lack of evidence that males of this subfamily engage in ritualistic struggles. Wagner's list also included *Ophiophagus*. The snakes of this genus are undoubtedly aggressive in the sense that they attack intruders and they aggressively pursue their prey, which consists of other snakes and monitor lizards. Nevertheless, combats between king cobra males remain to be reported. The larger mambas, *Dendroaspis polylepis* and *D. angusticeps*, perhaps defend territories by attacking intruders, as suggested by people who have reported encounters with these large elapids in parts of Africa. Such behavior is undoubtedly aggressive, but, unless it is directed against members of the same species, it is neither territorial nor associated with male combat, which has, of course, been described for some mambas.

The few species for which male combat has been recorded since the reviews of Shaw (1951) and Klauber (1956) were published are listed below, along with those previously cited or documented by Shaw or Klauber. The recent accounts that, in some instances, are mentioned or discussed in preceding sections of this review require no further comment. Others do, however, and portions of one account are quoted in order to explain why it is interpreted as male combat for the species. The combats reported may have been attributed to rivalry over mates or food, or to the homosexual behavior of the opponent. Other struggles were in progress when first observed, and in some instances the behavior was misconstrued and described originally as mating or courtship. Some combats were in the field; others were observed in captives. For convenience the species are arranged alphabetically following the names of the respective families.

COLUBRIDAE: *Coluber constrictor*, *Coluber gemonensis*, *Drymarchon corais*, *Elaphe guttata*, *Elaphe longissima*, *Lampropeltis doliata*, *Malpolon monspessulanus*, *Pituophis melanoleucus*, and *Ptyas mucosus*. Some authors have mentioned *Coronella austriaca*, but it is questionable whether the behavior described is courtship or male combat. The *Malpolon* species listed is the only one that possesses rear fangs; the others lack fangs. Combats have been reported in four subspecies of *Pituophis melanoleucus*, and the combat of *Drymarchon* was between individuals of different subspecies.

ELAPIDAE: *Demansia textilis*, *Dendroaspis jamesoni*, *Dendroaspis polylepis*, *Naja naja*, and *Pseudechis porphyriacus*. Interspecific combats between the two species of *Dendroaspis* have been reported for captives.

VIPERIDAE: *Vipera aspis*, *Vipera berus*, and *Bitis arietans* (*B. lachesis* of

some authors). Curry-Lindahl (1956) stated that he had "seen a tendency to a combat dance between two *Causus resimus*." Harvey (1964) evidently believed that the *Bitis arietans* she observed were mating. It is virtually certain, as indicated by the upraised bodies of the snakes shown in the photograph she obtained, that the snakes were males in combat. Despite her reference to members of each sex, her description of the struggle corroborates this assumption. She stated: ". . . they were enormous puff adders, rearing high in what appeared to be a dramatic fight . . . then we observed that this was no fight.

"The female—if anything larger than the male—raised her head some two feet, hissing all the while; her mate moved rapidly along her back, attempting to pin her down. As his head reached the height of hers, they plunged backwards, taking him into a writhing snake mass. Emerging from these contortions, they began the same movements, again and again.

"Sometimes she managed to get her weight on him and, spreading her body to flatten him to the ground, she endeavored to pin his head under her. We could hear the scales rasping together in his efforts to drag his head free.

"We edged closer, yet so preoccupied were they that they didn't notice or care about us. . . . But it was getting dark and we couldn't stay to watch the finale. The following morning, when we returned to find the stage empty, we could guess that the dramatic 'dance' had lasted far into the night—for our tyre marks had been obliterated by the puff adders' writhing bodies."

These vipers were observed in Samburu Game Park in Kenya, and the snakes "were on an open patch of sand on the bank above the river." Vipers as large as puff adders, the stout bodies of which may exceed a length of 5 feet, would undoubtedly require more space during combat than *Vipera berus*. It would be inferred from this account that the puff adders' movements centered around the site where the combat was originally noted.

CROTALIDAE: *Agkistrodon contortrix*, *Agkistrodon piscivorus*, *Crotalus adamanteus*, *C. atrox*, *C. cerastes*, *C. horridus*, *C. mitchelli*, *C. ruber*, and *C. viridis*. Combats have been reported for more than one subspecies of several of the species listed. Interspecific combats have also been reported between *C. atrox* and *C. adamanteus*, and between *C. mitchelli* and *C. viridis*. Combats between *C. adamanteus* and *Agkistrodon piscivorus* have also been reported. Sutherland (1958) described combats between two male timber rattlesnakes, *Crotalus horridus*, that were aroused by the presence of food. Biased perhaps by his own observations, and apparently unwilling to accept the



evidence that combats stem also from sexual rivalry, Sutherland was inclined to believe that such struggles are associated largely if not entirely with competition for food.

In summary, if combats between males of different genera or species are not included, ritualistic struggles have been reported for nine species in the family Colubridae: one in Asia, three in Europe, and five in North America. For the family Elapidae the reports deal with five species: one in Asia, two in Africa, and two in Australia. Combats have definitely been reported for but three members of the family Viperidae: two in Europe, and one in Africa. All eight species belonging to the Crotalidae that have been observed in combat were in the United States, but a combat between two males of *Agkistrodon piscivorus* that allegedly terminated in a homosexual union took place in Europe. Six of the species seen in combats are rattlesnakes of the genus *Crotalus*; rattlesnakes of the other genus, *Sistrurus*, perhaps because they are less widely distributed and do not attain large size, have not been reported in combat. Combats have been mentioned or described for but 25 species of snakes, therefore, or for fewer than 1 per cent of the species currently recognized.

It will be noted that the only continent inhabited by snakes in which male combat remains unrecorded is South America. Two of the species in which combat has been noted in the United States, *Lampropeltis doliata* and *Drymarchon corais*, have distributions that extend well into South America. Combats between snakes of these or other genera may have been observed in South America, but, if so, they have gone unreported as far as we can determine.

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