## Territorial Behavior in Snakes and the So-Called Courtship Dance

By Charles H. Lowe, Jr.

It is generally believed that territorial behavior does not occur among snakes although it is at the same time recognized in their close allies, the lizards. With regard to snakes, however, there is considerable evidence already in the literature to the contrary though at present much of it is hidden under the mise of a so called "courtchin dance"

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Davis (1936) first described the "courtship dance" of crotalids, as observed by R. Marlin Perkins, among captive Mexican west coast rattlesnakes (Crotalus basiliscus) and water moccasins (Agkistrodon piscivonous). This seems to be the only record of such crotalid behavior prior to 1942. During 1942, Carr and Carr reported "dance" behavior in A. picivorous, observed in the field in Florida. In the same year, Lowe reported such behavior in recently captured Crotalus atrox in California during the fall, and in C. ruber, as observed in the field by J. Duell of San Diego, California. Recently, Gloyd (1947) has called attention to its presence in the copperhead (Agkistrodon m. mokeson) as observed in the field in Virginia, by J. Ackroyd of Moorestown, New Jersey, and in the prairie rattlesnake (Crotalus v. viridis) as observed in the field in Montana by the late L. B. Gallaher of Harlowton, Montana. Cyrus B. Perkins of the San Diego Zoological Society has observed this behavior in captive copperheads. Others have infrequently seen it in our pit-vipers. Thus it is known to occur in the three groups of North American crotalids, having been observed in all three, both in the field and in captivity. It has been seen in the spring and in the fall of the year and in all reports to date has been considered courtship or mating behavior. It is my purpose to point out that this activity is apparently not courtship nor mating behavior at all; it is, in all probability, territorial display (intraspecific fighting response) among these vertebrates lacking limbs. Territoriality among snakes is, as with other animal groups, a fundamental and widespread pattern of behavior, either inherited by them from probable saurian ancestry or a parallel development with that reptilian group.

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When one critically studies the reports of such "dances" and notes exactly what was observed, it is found that they have the following fact (among others) in common: no copulation was definitely observed. In short, as far as is known, the "dance" pattern is neither followed nor preceded by copulation or an attempt at copulation. Further, many competent observers on numerous occasions have witnessed the actual mating of crotalids and other snakes. In no instance has the "courtship dance" been observed to precede or to follow copulation. The view that the "dance" is fighting between two individuals of one sex, and not courtship involving opposite sexes, eliminates this heretofore unexplained

<sup>&</sup>lt;sup>1</sup>The general statement by Davis (op. cit.) concerning the captive behavior observed by R. Marlin Perkins, that "dancing" crotalids copulated, is a case to the contrary. Unfortunately no details are presented.

inconsistency which has puzzled many herpetologists for years. Copulation and "dance" have so far been seen as separate, distinct, and mutually exclusive phenomena not occurring between the same pair of individuals.

For various reasons, observers have not always sexed the "dance" participants. In those cases where sex was definitely determined, the snakes were males. In no case have the members of a dancing pair been shown to be male and female. Failure to sex individuals and error in doing so have been factors contributing to the present misconception of the true nature of the behavior involved. In his report on the "dance" in crotalids, Lowe (op. cit.) stated that one pair of Crotalus atrox consisted of two males (hemipenes were definitely present in both), and another pair of a male and female (hemipenes in one, not found in the other). The case where two males were involved was considered an odd situation at that time. In the other instance, one was definitely a male and the other was considered a female. It is realized now that the method of sexing the one individual, the so-called female (a living individual), was inadequate for determining sex. I must confess that the attempt was made with a maximum of youthful enthusiasm and a minimum of good judgment. The sex of the individual in question must be considered as undetermined. With apparently less grounds for recording the sex of the individuals involved, Carr and Carr (op. cit.) state as a male and female the two moccasins they did not collect after observing the "dance" in the field. They were perhaps led to the old and unfounded conclusion that "dance" means courtship of male and female; therefore, the two individuals must be of opposite sex. Apparently such has been the reasoning that has led to reports in good faith which have perpetuated this unfounded conclusion, the most recent being that of Gloyd (op. cit.).

Thus far we observe the following facts: (1) Dancing pairs have (2) Copulating pairs have never been never been seen to copulate. observed to "dance." (3) Participants, when adequately checked for sex, have always been males. Another fact becomes apparent: There exists a fundamental difference between a true mating pattern exhibited by crotalids and other snakes, and a distinct territorial pattern exhibited by them. Both of these patterns are more or less stereotyped and seem to consistently follow the same basic sequence of events whatever species or genus of the group is observed. Mating has been observed both in the field and in captivity. Essentials of the mating pattern are the following: Participants remain relatively passive upon the ground, not raising the anterior portions of their bodies vertically above the surface. The male crawls over the female for some time until copulation takes place. Certain colubrid males have been observed to seize the females in their jaws for variable but usually short periods of time. This pattern involves a male and a female, its ultimate sequel normally being copulation. The territorial pattern (the so-called "courtship dance"), however, is distinctly different. Its general essentials follow: Participants do not remain passive upon the ground. They raise the anterior one third to possibly two thirds of their bodies vertically above the ground, face each other a few

inches apart with necks curved and heads generally held horizontally or slightly vertically, and sway their bodies slightly, keeping their eyes upon each other. Thrusts of the head and neck are usually made at one another; the snakes usually entwine their necks (nearly entire bodies in some) and may then "flop" to the ground. The entire procedure may be repeated several times. Such twisting and "flopping" is often severe and may discourage one of the participants from the bout. In some forms considerable forward movement of both may take place. This pattern involves, in so far as is accurately known, two males. It does not normally involve copulation, although conceivably should a female be involved, what may start as a territorial display might end in copulation. Such an interpretation might be placed on the behavior of male and female fox snakes (Elaphe v. vulpina) briefly observed in the field by Carpenter (1947). Territorial responses in some snakes may be involved, as in lizards, in sex recognition.

The prevailing interpretation (courtship) of the biological meaning of the "dance," which may, in my opinion, properly be termed a territorial fight, is partly due to the infrequency of its observation and the consequent paucity of reliable data concerning it. Two things have been instrumental in obscuring the significance of the "dance." First, herpetologists in general have only in recent years realized that territorial behavior exists commonly among lizards and many believe that as such it is, among reptiles, a peculiarity of the lizards and not to be found in the other groups. The second stumbling block has been certain of the statements and conclusions of Davis (op. cit.) in his well-known summary. Apparently these have strongly affected the thinking of many herpetologists even though he stated that his conclusions were tentative since they rested upon data that was inadequate for indicating more than probabilities. The reason for much misunderstanding dates to several early reports, the apparent errors of which have been accentuated by repetition with additional false conclusion resulting. Interpretation of certain observations by Millet (1909), Beadon (1910), Wall (1921), Prater (1933), Stemmler-Morath (1935), and others, upon which Davis rested much of his conclusion, has never been actually demonstrated, or "proven," to be correct. Briefly, it appears that the "Coluber type of [mating] behavior" of Davis, as opposed to the "Natrix type of mating behavior," is not mating or courtship behavior at all; that he is incorrect in stating that males do not fight among themselves during the breeding season, etc.

Perhaps one of the most critical reports cited by Davis (op. cit.), was that of Franke (1881), "who apparently was a careful observer." Franke stated clearly that the males of Coronella austriaca ". . . at pairing time exhibited much jealousy and not infrequently engaged in fighting, in which they bit each other." This was unemphasized by Davis, and perhaps logically so, for it failed to fit a "general picture" and as such was apparently a single exception. Unfortunately, the valuable report of McCann (1935) was not included in the summary by Davis. This is one of the earlier clear-cut cases of male fighting, involving the "Coluber

type of behavior." It is one of the infrequent cases where the reporter did not make assumptions but demonstrated the sexes of the individuals involved. McCann states:

"During the months of June and July this year, my neighbours, at Andheri [Envs. Bombay, India], sent me two couples of Dhamans or Rat-Snakes (Zamenis mucosus) [=Ptyas mucosus] which they had shot. The snakes when shot were entwined round one another like a twisted rope, which naturally suggested that they were in copula. Examination, by dissection, showed that in both cases the snakes were males. This goes to suggest that the respective couples must have been fighting at the time they were shot. There are many records of snakes seen in the manner described and in most cases, if not all, that attitude has been ascribed and in most cases, if not all, that attitude has been ascribed computation. However, as is well known snakes usually exhibit no obvious to copulation. However, as is well known, snakes usually exhibit no obvious external sexual differences and only a careful examination aided by dissection will

reveal the sex definitely.
"The combatants in these two instances were of almost equal size. What the fights were over it is difficult to say; but, as the breeding season was over these

snakes may have been fighting for territorial supremacy."

It is interesting that in 1935, McCann was aware of the probable nature and purpose of the behavior observed, as well as the essential reasons for the misinterpretation of most other observers, even to the present day.

Another illuminating report is that of Fleay (1937) on an Australian elapid, the black snake (Pseudechis porphyriacus). As his report is perhaps not well known to naturalists in this country, it bears quotation

at some length.

"Early in September, 1936, I collected in the red gum (Eucalyptus rostrata) forest bordering the Murray River near Tocumwal, N.S.W., some very fine specimens of Pseudechis porphyriacus, the common black snake . . . it was not until the advent of the Tocumwal specimens . . . that truly spectacular revelations were made. Then it was proved beyond doubt that in the mating season there may be a very definite and exceedingly violent rivalry between the males of this species . . . On the morning of October 12, 1936, an air of excitement and irritability was noticeable for the first time among the black snakes. No sooner did one specimen come into accidental contact with another than both reptiles would shoot swiftly away to cover . . . As the day became warmer, two of the larger snakes approached one another and moved along side by side, with heads arched and raised about a foot from the ground. As they moved along their heads swayed slightly from side to side, and their mouths gaped open.

Though for a long time this curious alignment of the reptiles appeared to be a preliminary to copulation, this was definitely disproved, for the pairing of a male and female is an entirely different and more passive proceeding. Akin to a fencing bout, the 'on guard' position, with curved necks and raised heads, lasted just as long as it took one of the rival males to gain the advantage by placing its arched head above that of the other. Having seized the opportunity, the aggressor then twisted its neck about that of its enemy, and continued the twist, with furious writhing movements, until its whole body was entwined about that of its rival. The latter, though at a disadvantage, retaliated in similar fashion to the best of its

ability. The general effect was similar to that of a two-stranded rope.
"Writhing, hissing and struggling, with both reptiles exerting the greatest possible constriction on each other, and actually rolling slowly over and over en masse, the 'round,' if one may so term it, lasted for perhaps a minute. Then as if by mutual consent they suddenly disengaged completely, and separated, only to line up slowly, with gasping hisses, and repeat the whole 'on guard' position and bewildering twisting motions. And so many times on that first day and during those that followed providing the weather was sufficiently warm for action may those that followed, providing the weather was sufficiently warm for active movement, the two big snakes continued to struggle in terrific efforts to wear one another

down. Occasionally they glided slowly from one end of the 'pit' to the other with mouths gaping open, hissing and gasping, before one gained the coveted 'neck hold' and precipitated the twisting 'rope grip.' Not always did they fight with one another, for occasionally a different male was involved with one or the other of these deadly rivals. Smaller males were also observed in combat, and it was noteworthy that they appeared to struggle with snakes approximately their own size. However, the original large combatants persisted in their bitter feud. The scales on both dorsal and ventral surfaces had become frayed and worn painfully thin so that haemorrhages were visible along both bodies and a general reddish tint could be seen through the scales. So engrossed were the combatants that on several occasions they completely disregarded my presence and continued to struggle even when lifted from the ground!

"Doubtless in the wild during the pairing months the stronger male intimidates rivals and drives them away from his 'territory,' and in support of the fact that these battles are not mere 'stadium' events brought about by captive conditions I

have several observations to stress.

Firstly, during the two months of October and November, 1936, while rivals fought each other in the 'snake pit,' copulation also took place, being indulged in at times by the rival males with various females between competitive struggles. When acts of pairing ceased in November, so likewise did all inclination to fight,

and peace reigned once more.

"Secondly, in the month of November, 1936, Mr. Jack Clark, a keen bushman residing at the interesting Moira Lakes (Victoria), reported to me, quite independently of events in the Zoological Gardens, that he had chanced on two large black snakes in a swamp. They were tightly entwined, rolling about and struggling so furiously that they ignored his presence. He watched them for five minutes and then killed both reptiles. Mistakenly, but quite naturally, he considered that they were pairing.

"Thirdly, I have observed bitter struggles occurring among other male reptiles, particularly *Tiliqua nigrolutea* (the southern blue-tongued lizard), during the mating months of October and November (in south Victoria).

"In the case of the main feud in the snake yard at the Zoo, following weeks of

prolonged struggling, one of the rivals eventually received the worst of the prolonged encounters and with scales torn and bleeding and evidentally totally exhausted it retired for several days to rest its battered body. Previous to this respite the encounters had been more than usually bitter, and several observations were made of the rivals actually biting one another savagely.

"However, in view of the strong immunity of Australian snakes to their own

venom, this was definitely a very futile proceeding and largely a display of temper.

"The actual mating process in Pseudechis porphyriacus is quite distinct from the furious 'rope-coil' competitive struggles of the male snakes. A male snake exhibits sexual excitement by quick nervous movements. The tongue flickers more rapidly than usual as the snake glides along in the keen alert fashion observed during the hunting of frogs. Occasionally the females are pursued for some distance. Actual copulation occurs with the male lying on—but not coiled about—the female, and heads are not raised above the ground.\(^1\) Curious spasmodic local twitchings and indicate of each root of the holy from head to tail are observed and these are head to tail are observed. jerkings of each part of the body, from head to tail, are observed, and these gradually attain a climax of excitement.

<sup>1</sup> Italics mine.

Fleay's description of elapid behavior parallels, in all its essentials, the behavior of many other snakes. Crotalids have not been observed to open their mouths, move along side by side entwining their bodies completely, etc. These, and others, are minor variations of the fundamental pattern that is present and they tend to vary somewhat in different groups of snakes. On the whole, the display of Pseudechis porphyriacus is more nearly like that of colubrids than of crotalids and viperids, as is to be expected on logical grounds.

Woodbury (1941) records fighting in male Pituophis catenifer deserticola as observed by Misses M. Berryman and L. Olson in the field at Great Salt Lake, Utah. They reported a pair of males in active combat near a passive female. When first observed, the males were bowing their necks and repeatedly striking at each other.

"The posterior parts of the [male] bodies were closely entwined like the strands of a rope, as if for copulation, but the anterior parts were free. During the quarter or half hour of watching, the larger of the two males, about 5½ feet long, appeared to be gradually constricting and crowding the smaller male out from his entwined position. The reaction of the smaller male to this crowding was to strike at the other's head, which recoiled when hit and immediately prepared a return strike. The female was entirely passive, evincing no interest or choice between the combatants, which occasionally rested between struggles.

"The snakes paid no attention when approached within 4 feet with the camera to take the picture; in fact they went on without showing concern of the human spectators until Mr. Barrie reached down and picked up the larger of the two males."

In this instance, as in several others, a female of the species was present. In general, the female is but one aspect of territory. Presence of the opposite sex is not requisite for elicitation of the territorial response.

In the majority of observations, territorial display in snakes has ensued with marked disregard for the persons observing. This, however, does not seem to be as often the case with mating behavior.

From the foregoing outline of observation, the following interpretation seems tenable. Like all conclusion drawn from data derived by observation, it can be stated only in terms of probability: The serpent "dance" as observed in certain colubrids, elapids, viperids and crotalids, is a fighting response elicited between males of the same species and may be termed a territorial fight. This behavior has been misinterpreted as courtship behavior. Two behavior patterns have been confused; the two are separate and observably distinct phenomena.

Detailed study of marked individuals in the field is highly desirable for better understanding of these phases of behavior. Such study awaits someone who has the enthusiasm and who will take the time needed to hurdle the difficulties of continuous field observation. Notwithstanding previous views to the contrary, territorial behavior does occur among snakes and has been observed both in the field and in captivity. In so far as I am aware, to the present time it has only been recognized and reported as such by McCann (1935) and Fleay (1937) who clarified the matter for a colubrid and elapid species respectively. For some reason their reports seem to have been overlooked or not recognized by herpetologists since then, a notable exception being Smith (1939).

Certain characteristic behavior of cobras indicates to me that the function of the hood mechanism of these snakes will, in all probability, eventually be shown to be involved in territorial display. Territorial behavior may eventually be found common to both sexes in some snake groups. With regard to snakes in general, several points related to the problem are in need of clarification. Future observation and experiment (eg. administration of sex hormone) is highly desirable, both in the field and

in the laboratory, to establish beyond reasonable doubt the true nature and evolutionary significance of the behavior involved.

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