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COURTSHIP AND MATING BEHAVIOR IN SNAKES

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Darwin, in the *Descent of Man and Selection in Relation to Sex* was the first to give point to study of the courtship and mating behavior of animals. Since his time much of the investigation in this field has been devoted to critical consideration of his evidence and conclusions. Recent widespread interest in manifestations of sex has opened up aspects of the subject that were unknown to Darwin. Most important among these are the genetic relations of sex, the role of the endocrines in the physiology of sex, as well as of sexual behavior, and, of still broader interest, the fundamental relation between sexual behavior and the general social behavior of animals.

Snakes as a group were mentioned briefly in the *Descent of Man*, but two subsequent extensive reviewers (Cunningham, 1900; Pycraft, 1913) ignored them completely. The absence of striking secondary sexual characters and the extraordinary dearth of published observations on sexual behavior in snakes are probably largely responsible for the general lack of interest in this subject. The recent appearance of an excellent and comprehensive account of the mating behavior of their nearest living relatives, the lizards (Noble and Bradley, 1933), makes the meagerness of our knowledge with respect to the snakes particularly apparent.

The most satisfactory approach to a study of the courtship behavior of animals is direct observation, preferably of undisturbed individuals in the field. Serious misinterpretations have not infrequently arisen from observation or experimentation on captive material, where unnatural associations almost inevitably alter behavior. Unfortunately one student, no matter how much time he may spend in the field, can not hope to witness mating behavior under natural conditions in more than an extremely small number

of animals. This results in the necessity of trying to collate the scattered, fragmentary observations of many individuals, with the attendant possibility of error.

In attempting to work up an unusual series of observations on the mating of *Thamnophis radix* made by Mr. A. C. Weed, of the Field Museum staff, it became increasingly apparent that the sexual behavior of snakes merits more attention than it has received. Existing knowledge is not only comparatively limited, but it is also widely scattered through literature, largely in the form of brief notes. Many important observations are buried in the midst of unrelated material, where their presence would be unsuspected. No one has tried to correlate his work with that of others, and consequently few have realized what constitute the significant features of courtship in this group. In order to stimulate and direct further work in this subject, the following summary of the literature has been drawn up. This is followed by a brief consideration of sexual dimorphism in snakes, with particular reference to secondary sexual characters. I have tried also to draw a few tentative conclusions as to the broader implications of mating behavior in snakes. These cannot be regarded as final, since they rest on data that are inadequate for indicating more than probabilities.

Many individuals have assisted in the preparation of this paper. I am particularly grateful to Mr. A. C. Weed for making careful observations and extensive notes on *Thamnophis radix* over a period of several months when circumstances prevented me from witnessing its activities myself. Mr. R. M. Perkins, of the Zoological Society of St. Louis, has supplied data from personal observations without which the summary would have been much less complete. My colleague and mentor, Mr. Karl P. Schmidt, has continued to give unselfishly of his time and thought and I am under great obligation to him. Mr. John J. Janecek devoted painstaking care to the preparation of the illustrations.

SUMMARY OF LITERATURE

Naturally a major part of published observations deal with the most common members of the cosmopolitan family Colubridae. Indeed, this is true to an unfortunate degree, and disappointing gaps are left at important points, notably among the Elapidae, Viperidae, and Crotalidae. Since these include the most highly specialized of all snakes, they are important in the present connection. Through the generosity of various individuals, particularly Mr. R. M.

Perkins, it has been possible to fill some of these gaps by drawing on unpublished notes and observations. The information supplied has been included in the summary given below, and has helped to make possible a reasonably well-rounded picture.

Some of the observations cited are of doubtful importance, but have been included both for the sake of completeness and because the present state of knowledge does not permit intelligent elimination of extraneous material.

Boidae.—The members of this and the succeeding family differ from the more familiar snakes in possessing remnants of the posterior limbs. In the males these structures appear externally in the form of stout spurs or claws. They are present in both sexes, but are extremely small in females. The extraordinary part they play in the courtship of *Constrictor constrictor* is vividly described by Mole and Urich (1894) as follows:

"These claws, however, are capable of being slightly protruded and are endowed with considerable mobility. When about to couple, the male extends these hooks at right angles to the body and vibrates them in an extremely rapid manner, scratching, as he does so, the back and sides of his companion. The claws scratching the scales of his mate make a noise which can be distinctly heard two yards off. This habit has also been observed in *Epicrates cenchris.*"

At a later date Mole (1924) observed a similar use of the spurs in the anaconda, *Eunectes murinus.* He states that the male "throws a coil or two around the female, which is usually the larger of the pair, and his claws are moved quickly and scratch the scaly sides of his mate, inducing her to crawl forward slowly until union is established. One pair was thus engaged from December 24 until January 13."

Pythonidae.—Mr. Perkins has observed the use of the spurs in the blood python, *Python curtus.* The male lies close beside the female, with the anterior part of his body frequently lying over her. He then extends his spurs at right angles to his body and moves them *slowly* and rhythmically from side to side, stroking the body of the female with them directly over her cloaca. This behavior, which has been observed to continue uninterruptedly for more than two hours, does not produce a scratching sound, as described by Mole and Urich for *Constrictor.* Under the stimulation of this "tickling" the female gradually twists her cloacal region laterally and the male works his tail under hers. When her cloaca is nearly in a vertical position the female suddenly gapes it, the male inserts a hemipenis, and copulation takes place.

Colubridae.—The recent observations of Stemmler-Morath make it obvious that at least two widely different types of courtship behavior are found among the members of this family. Further work will unquestionably reveal additional behavior patterns in this enormous assemblage of forms. Matings have been observed in a number of colubrid genera, but unfortunately the meager notes that have been published on most of them reveal nothing that bears on the problem under consideration here.

What may be designated the *Natrix type of mating behavior* has been more frequently and more completely described than any other. Indeed, until recently it was the only type of snake-mating of which there was any but the most fragmentary knowledge, and it has frequently been assumed to characterize snakes in general. Many of the important features of this type of mating were accurately described more than fifty years ago by Franke (1881), who apparently was a careful observer. His account of the mating of *Coronella austriaca* is as follows (translation):

"Pairing begins about the middle of April. For several years I kept from forty to fifty individuals in the terrarium; the males at pairing time exhibited much jealousy and not infrequently engaged in fighting, in which they bit each other. The not always willing female also protected herself from unwelcome attentions by biting. The act of copulation is like that of the common [European] water snake. The male crawls slowly onto the back of the female, in which it takes exactly the same curves in which the female happens to lie, and also adapts itself to any changes of position which the female may make. Only the anal region of the male hangs down toward that of the female, who recognizes the intention of the male by a lateral turning of the anus. During these preparations, but still more so during the two to three hour duration of the act itself, both individuals exhibit uninterrupted contractions of irregular strength attended by motions of the tails, which are not infrequently mutually intertwined. The female, in the lower position, frequently changes her position during this time, and may crawl some distance away, but not without the male, who immediately imitates every motion of the female. I have never observed interference on the part of other companions, which, in fact, crawl over or beneath the pair without taking any notice of them. I must emphasize that I have never observed a 'close intertwining' that has been described by other authors either in the present species or in the common water snake, although I have witnessed copulation more than a

hundred times. Nor is a 'suitable soft substratum' sought out, for rough, uneven places, heaps of stones, etc., are preferred. Copulation takes place only on warm days, and most frequently during the mid-day sun of April or May."

Additional features of the mating process have been noted by others. Truitt (1927) records an instance of a female *Thamnophis sirtalis* being followed by two males. When imprisoned in a wire enclosure and transported some distance, the female attracted three snakes of the same species to her. One of these was captured and found to be a male. Truitt suggests that the females, of certain species at least, probably attract mates by means of odors. Stemmler-Morath, on the basis of observations made in the large open-air terrarium at the Basel Zoological Garden, reports that he has observed competition among males for the possession of a female only in the species of the genus *Natrix* among European colubrids. He states (translation):

"Only in the species of the genus *Natrix* does there appear to be in nature a kind of competition for the female. As many as twenty males besiege a female lying under them for hours, all lying in the same direction and constantly attempting to gain the back of the female, which is as regularly prevented by a competitor. But this takes place quietly, without one biting the other. As soon as one of the males has attained his goal, he is pulled out of the wriggling mass, tail foremost, by the female. The competitors who have been left behind, as soon as they notice the disappearance of the female, dash around excitedly and attempt copulation with any snake encountered, whether it be of the same sex or of a different species. The escaped pair meanwhile lies somewhere in a quiet place, and only the frequent convulsive movement of the tail of the male shows that they are alive."

Mr. Perkins has noted a similar behavior in captive *Natrix* and *Thamnophis*. When a female is placed in a cage containing a number of males, the males are at once thrown into a state of frenzied excitement. They crawl excitedly over and among one another, and attempt to mate with any individual encountered, regardless of sex. There is no evidence of courtship in such cases.

This striking behavior probably does not normally take place in nature, but is to be regarded as a result of confining a number of individuals in a small space under artificial conditions. Thus, Perry (1920) described a suggestive incident in *Natrix sipedon*. A copulating pair was encountered on a bush overhanging a stream.

Below this pair was a "confused mass" of "at least six" other individuals. "Presently the convulsions of the pair on the outer end of the bush ceased. The smaller snake slowly disengaged himself and joined the bunch below. His place was taken quickly by another and the convulsions began again. One after another, the smaller males paid their respects to the largest one, which I believe was a female." Nevertheless, as pointed out below, the probable relation between this aggregation reaction and the formation of snake "balls" cannot be overlooked.

Dymond and Fry (1932) observed two mated pairs of the green snake, *Liopeltis vernalis*. One pair was found in shrubbery, about a foot above the ground. They noted that in neither pair was the male in contact with the female except in the cloacal region.

Blanchard (1931) has briefly described the *Natrix* type of mating, drawing attention to two highly important features previously overlooked: "Before the act of copulation the male snake slides forward along the upper surface of the female, his chin pressed close to her back and his body lying along hers in sinuous curves. He then sets his body into rhythmic undulations. The chin tubercles are thus particularly well placed to serve as rubbing organs during the maneuver." In addition to these comments on the chin tubercles, he also draws attention to the fact that the supracloacal keels or tubercles characteristic of the males of many snakes are brought into contact with the body of the female during copulation.

The behavior of other colubrids differs strikingly from that of *Natrix* and may be called the *Coluber type of behavior*. Stemmler-Morath (op. cit.) has observed a complex courtship "dance" in *Coluber gemonensis*, *Elaphe longissima*, and the species of *Malpolon* among European snakes. The behavior is stated to be essentially the same for all these species, and is described as follows for the European whip-snake, *Coluber gemonensis* (translation):

"A pair of splendid aesculapian snakes crawl quietly one behind the other. The rear animal, obviously the male, tongues the body of the crawling female almost continually. She gradually begins to move more rapidly, but the more rapidly the female glides along, the more actively the male follows. Finally the two long bodies of both snakes dash along one behind the other, almost completely extended. There is no longer any of the close application of the body to the terrain in crawling which we are accustomed to see in these snakes. The two animals hasten with uncanny speed through the area, over rocks and ponds, often up into the bushes and down

again over the outermost twigs. This chase lasts until the male succeeds in reaching the side of the female. He at once throws his neck around the body of the female with lightning speed and draws up his body, coiling around her in several turns while crawling forward on the body of the female. The entwined pair continues to move about the area, and for a quarter of an hour or more they crawl through each other's coils uninterruptedly, so that first one and

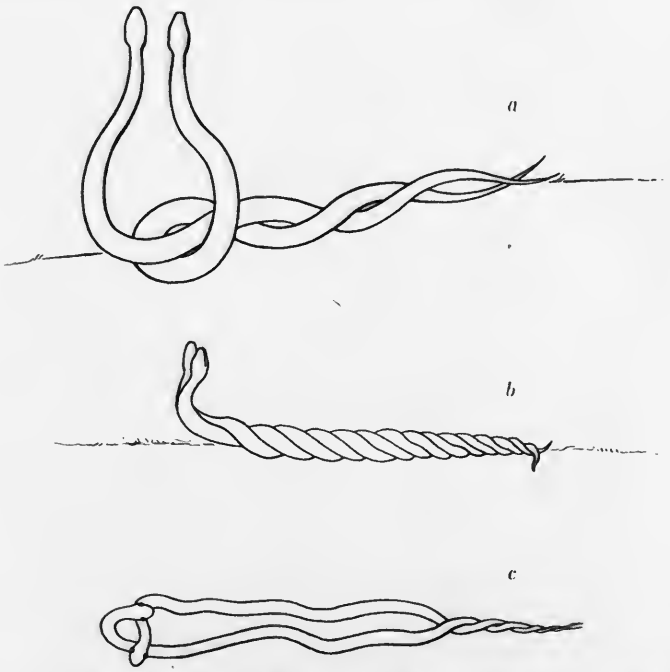

FIG. 28. Courtship behavior in various colubrid snakes. *a*, Mating dance of *Coluber gemonensis* (after Stemmler-Morath). *b*, Mating pair of Indian ratsnakes (*Ptyas mucosus*) (after Prater). *c*, Mating pair of *Coluber v. carbonarius* showing the neck grip characteristic of certain colubrids (after Schreiber).

then the other is above. The heads are now carried always at the same height. Suddenly one of the animals raises its front end until the anterior third of the body, freed from its partner, stands almost vertically. The other animal does likewise, and now the heads are placed quite near each other and obliquely depressed forward. The upraised anterior parts of the body, well separated from each other, with only the posterior two-thirds of the bodies twined together like wire, resemble a lyre (fig. 28, *a*). But not only do they exhibit this handsome shape when at rest; they often dash through the terrarium

in this attitude. In spite of the fact that they continually change their relative positions by their constant crawling around each other, they carefully preserve the character of the figure. Although these dances often last more than an hour, I was never successful in photographing it. The final union then usually takes place under a bush, a rock or a tree, so that one rarely is able to see it. The male always bites fast on the neck of the female."

Schreiber (1912) likewise states that the male often grasps the neck of the female in his mouth. He also describes a unique courtship behavior in *Coluber v. carbonarius*. He states (translation) that "they had *mutually* taken hold of each other's necks with their mouths, while their tails were twisted together in a spiral." When picked up by their tails, "their union persisted and they only let go from time to time with their heads, only to attempt to seize each other immediately, making twitching and pendulum-like back and forth motions with the neck."

On the other hand, Stemmler-Morath claims that this behavior does not take place in *Elaphe q. quatuorlineatus*. In this species the male merely crawls quietly after the female for some time until copulation takes place. The male, however, often seizes the neck of the female in his jaws for a short time.

The mating behavior of the Indian ratsnake, *Ptyas mucosus*, as described in a number of notes by various observers, apparently is similar to that described by Stemmler-Morath for the European colubrids. Wall (1921) quotes a letter from a Major Frere. "Their bodies," he says, "were twined together and writhing, except for the anterior quarter. Their heads were raised from the ground for one foot to eighteen inches and appeared to be sparring at each other like two young cockerels. Their movements were active and vigorous." Millett (1909) described the same procedure as follows: "The smaller snake was slowly working his coils throughout up and down the other, and both snakes were keeping their heads and free part of their length erect and alternately twining their free part round each other and approaching each other's heads in a 'billing and cooing' manner. At the same time they were travelling very slowly in a forward direction." Beadon (1910) speaks of coming upon mating ratsnakes "with heads and free parts of the body [i.e. those not mutually intertwined] slightly off the ground, facing each other." A striking photograph of a pair of these snakes in copulation, unfortunately without comment in the text, accompanies a paper by Prater (1933). This illustration, from which figure 28, *b* has been drawn, shows

both individuals fully extended, their bodies twisted spirally around each other from a point a short distance behind the head almost to the tip of the tail. It is impossible to determine from the photograph whether or not the male has taken the female in his jaws.

This behavior has not been reported in any North American snake, although it may be looked for in *Coluber* and possibly in some species of *Elaphe*. Meade (1932) in describing mating in a captive pair of *Lampropeltis getulus holbrooki* notes that the male "seized the body of the female in his jaws" and that "from time to time during the preliminaries of the mating, which continued for over half an hour, he would release his hold momentarily, grasping the body at a new place after a few seconds."

Mr. A. S. Windsor, of the General Biological Supply House in Chicago, recently described to me a curious series of observations on the fox snake, *Elaphe vulpina*. Two individuals, from two to three feet in length, were encountered in June, 1936, during field work in a forest preserve area southwest of Chicago. When first found, one snake apparently had swallowed some four inches of the anterior end of the second, as evidenced by the bulge produced in the neck of the one by the head of the other. The bodies of both were undergoing continuous rhythmic and practically synchronous undulations. The snakes were kept under observation for about twenty minutes, and during all this time the undulations continued uninterruptedly. The first snake made no effort to continue engulfing the second, nor did the second seem to be alarmed by its extraordinary position. The snakes were definitely not in copulation.

The observer left the scene and returned about fifteen minutes later. At this time the first snake no longer had its partner's head in its mouth, but had grasped it immediately behind the head. The strong muscular contractions of the first individual indicated that it was trying to regain the head of the second. The second snake did not seem to resent this aggressiveness in the least. The undulations of the bodies of both individuals continued without interruption during this time. Observation was continued for about five minutes, when the observer again left the scene. When he returned a few minutes later both snakes had disappeared.

Elapidae.—Wall (op. cit.) has recorded a few fragmentary notes on the mating of the cobra, *Naja naja*. "In Mr. Hampton's vivarium coitus lasted intermittently for three days. He observed that the pair nodded their heads continually, and their bodies quivered. They did not take the slightest notice of anybody in front of their

cage. They did not expand their hoods, neither did they enwrap themselves around one another. Each turned the vent upwards and sideways to effect engagement."

Poyntz (1927) took a copulating pair of the related sea snakes (species not identified) from the water in the Persian Gulf, but gave

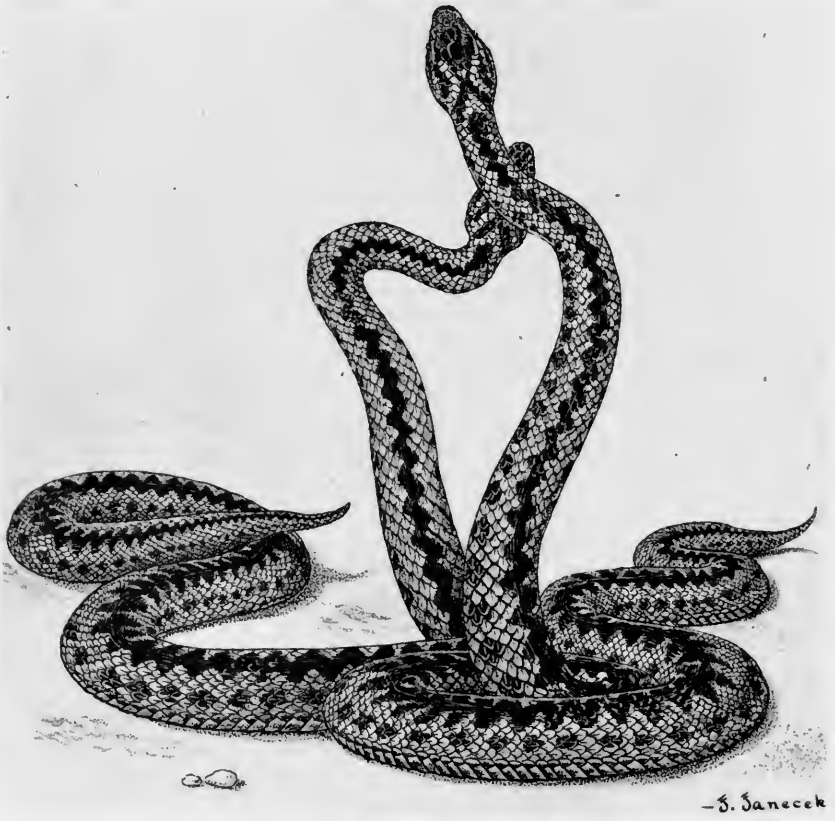

FIG. 29. Mating dance of *Vipera berus*. Crotalids assume a similar position during courtship (from photograph by Reuss).

no details on their behavior. It is highly interesting, however, that copulation takes place in the water in these extremely aquatic snakes.

Viperidae.—It is extraordinary that nothing has appeared on the courtship behavior of members of this family, since the genus *Vipera* is widely distributed over Europe. A photograph by T. Reuss (in Heilborn, 1930) shows a pair of *Vipera berus* reared up in an attitude similar to that described below for the pit vipers (fig. 29).

It is probable that the mating behavior of the Viperidae is similar to that of the Crotalidae, at least in its essential features, and consists of a form of courtship dance, possibly associated with movements by the male directed toward arousing the female. Should this prove to be true, the courtship dance of the extremely heavy-bodied vipers, such as *Bitis gabonica*, would be a curiously grotesque affair.

Crotalidae.—Little has appeared on the mating behavior of the pit vipers. It is regrettable that this highly specialized group of snakes should have escaped observation, since they might throw considerable light on the phylogeny of this behavior in the Serpentes. Fortunately, Mr. Perkins has been able to supply some extremely valuable information from observations made on captive specimens at the St. Louis zoo. It is possible that the mating activities of both the vipers and pit vipers normally take place at night, which would explain the lack of field observations. However, Wood (1933), who observed a pair of rattlesnakes courting in daylight, is inclined to doubt this.

Guthrie (1927) observed several incomplete matings in a captive pair of *Sistrurus catenatus*. He records that the male was seen trying to copulate with the female three different times during one day, the female seeming "entirely passive. The tail of the male was wrapped entirely around the other, with the vents near together but not in contact. The male showed a sort of spasmodic twitching, mainly of the posterior half but sometimes of the entire body. At one time his head exhibited excitement, the tongue frequently darting far out and the head being thrust about above the body of the female, who paid not the slightest attention."

Wiley (1929) observed several matings in a captive pair of *Crotalus atrox*. She records that the male showed particular attention to the female "by rubbing his head and the anterior part of his body over her. He followed her about whenever she moved around in the cage and caressed her all the while. The next day the same thing happened. It was not until a month later that the mating occurred."

Mr. Perkins has repeatedly witnessed courtship in the water moccasin, *Agkistrodon piscivorus*. Under the artificial conditions of captivity matings take place at all seasons of the year. Individual pairs in captivity seem to consort together for months. Under the stimulus of artificial warmth and sunlight they frequently engage in a characteristic courtship dance, which is highly spectacular because of the extreme vigor with which it is carried on by these powerful,

heavy-bodied snakes. Both individuals erect the anterior half of their bodies into the air. These elevated parts of the body are then waved and lashed about erratically. Frequently the upraised parts of the pair are placed together and each snake pushes and rubs vigorously against its mate. The force with which these pushing movements are carried on is occasionally evidenced when one individual slips past the other. The sudden release of resistance under these circumstances may throw the other snake several feet across the cage. This extraordinary behavior may continue for hours at a time, and is usually followed by copulation. The posterior ends of the bodies are not usually twined together, although this may occasionally take place accidentally. Other snakes in the same cage do not seem to be affected by the activity of the courting pair.

Mr. Perkins has also observed the mating behavior of captive specimens of the Mexican west coast rattlesnake, *Crotalus basiliscus*. The courtship of this snake is essentially the same as that of the water moccasin, although it is neither so violent nor so prolonged. The male nudges the female and rubs the side of his head against her body during courtship, which is a feature that has not been noted in *Agkistrodon*.

Wood (op. cit.) momentarily observed a pair of courting *Crotalus confluentus* in the field. She states that the female was "crawling along the ground, and the smaller male, newly moulted, weaving along her back." Unfortunately this courtship was neither observed long enough nor described clearly enough to reveal anything of the normal mating behavior of rattlesnakes in the wild.

Abnormal Mating Behavior.—Several brief notes on abnormal matings have appeared. These are instructive in the interpretation of certain phases of mating behavior, and may profitably be considered. Simultaneous copulation of one female with two males has been observed on a few occasions, although nothing is known of the frequency of its occurrence in nature. Thus, Brennan (1924) records an instance of two male garter snakes copulating simultaneously with a single large female, and Medsger (1927) observed a similar case involving two males of *Heterodon* and the badly mutilated carcass of a female of the same species. Truitt (op. cit.) has also observed a male garter snake copulating with the carcass of a dead female.

Dr. R. T. Hatt has loaned me several photographs of a captive mating between a male *Crotalus molossus* and a female *Crotalus atrox*. Nothing is known of the incidence of interspecific matings in nature.

Snake "Balls."—A regular and recurrent feature of herpetological literature is the description of tight aggregations or "balls" of snakes. This subject has recently been reviewed by Wood (op. cit.), who doubts that the phenomenon is related to mating: "It should give survival value for an animal possessing internal fertilization to mate efficiently, and not promiscuously in hampering aggregations. An instinct among snakes to procreate in large numbers seems improbable in animals whose physiological and anatomical development is well above the amphibian level." If sex recognition in snakes is accomplished by means of an olfactory stimulus, however, there is no apparent reason why an unlimited number of males should not be attracted to the same female. According to the observations of Stemmler-Morath and Perkins given above, proximity of a number of males to a single female may result in a mass frenzy on the part of the males. The phenomenon of a tight aggregation of males around one female might well follow without involving an "instinct to procreate in large numbers." Obviously the snake ball question can be answered definitely only by careful examination and sexing of the individuals making up a "ball."

SECONDARY SEXUAL CHARACTERS IN SNAKES

Snakes exhibit little sexual dimorphism. This is perhaps in keeping with the singular simplicity and uniformity of their entire habitus, since lizards display a wide variety of sexual differences in both form and color. Nevertheless, since secondary sexual differences frequently play a highly important part in sexual behavior, those that are present in the Serpentes must be regarded as important.

True secondary sexual characters do not appear until puberty and frequently are concerned in some way with sexual behavior. The term "sexual dimorphism," on the other hand, pertains to all differences between the sexes, and thus includes many differences that are not known to be functional, or that are present from birth. Since the nature and origin of many of these characters are obscure, all known conspicuous sex differences have been included in the following summary.

The total lack of striking sexual dimorphism among members of this group has doubtless contributed to the general lack of interest in the topic. Taxonomists, who have aided so much with other groups by cataloguing and describing sexual differences, have little to offer with respect to the Serpentes. Nevertheless, certain of the secondary sexual characters that do exist are of great interest, and

deserve much more attention than they have received. Only twice has anything like a broad survey of the sexual characters of this group been undertaken, and both instances are of recent date. Blanchard (op. cit.) considered a number of North American species from this standpoint, and Pope (1935) has reviewed them briefly in Chinese snakes.

Proportions.—As in most poikilothermous vertebrates, females tend to exceed males of the same age in size. This is by no means invariably true, however, and species in which males attain the greater size are very erratically distributed. The functional significance, if any, of this disparity is not at all clear, although Pope (op. cit.) remarks that "since it is a well-known fact that the large individual females usually produce more young than small ones of the same species, one may safely consider body length of more importance to females than to males." Klauber (1936) has verified this correlation in the prairie rattlesnake, *Crotalus c. confluentus*. He gives a coefficient of correlation of +0.7.

Apparently males of all species tend to have longer tails than females, but there is considerable overlap between the sexes in this respect. Thus, Burt (1928) measured 85 male and 115 female specimens of *Thamnophis sirtalis* and found that 56 per cent of the total fell in the overlapping group, although males exceeded females in the modal index as well as in the greatest absolute proportionate tail length. It is highly probable that the longer tail in males is correlated with the presence of the hemipenes and their elongated retractor muscles. The pronounced widening of the base of the tail in males is well known because of its general use as a means of sexing individuals in systematic work. It is obviously due to the presence of the retracted hemipenes.

Scutellation.—Sex-correlated variations occur in the scutellation of most snakes. This is conspicuously true of the gastrosteges. The summary of seventy-five Chinese species given by Pope (op. cit.) shows that males of these forms almost invariably have a higher subcaudal count. A few erratically distributed species show no variation in this respect, but in no case does the female exceed the male. While females tend to exceed males in number of ventrals, in some species there is no difference in this respect, while in others the males even exceed the females.

Sexual dimorphism in the number of dorsal scale rows is much less common. Ruthven (1908) showed that the number of scale rows in any region of the body is closely correlated with body girth,

and consequently he believed that females would tend to have a higher formula than males. Apparently this condition is seldom realized. Ruthven himself was unable to demonstrate any significant sexual difference in the enormous series of garter snakes examined by him. Procter (1919) likewise failed to find any sharply defined dimorphism in three British snakes, *Natrix natrix*, *Coronella austriaca*, and *Vipera berus*. While statistical studies of large series would doubtless reveal that females of many species tend to exceed males in numbers of scale rows, instances of complete and consistent dimorphism in this respect are singularly rare. In fact, the only snake known where this is invariably exhibited is the African colubrid *Bothrolycus ater*, where the males have 17 rows and the female 19 on the anterior part of the body. It is significant that in this species, as Schmidt (1923) has remarked, "the difference between the sexes is unusually pronounced, the difference in size being quite exceptional."

Dimorphism in the scutellation of the head appears not to have been demonstrated, although a statistical study of large series of individuals would probably reveal its presence, at least in some species.

Coloration.—Sexual dimorphism in color is certainly not general. Intensive work on large series, however, has revealed relatively slight differences in color or intensity of color, or even differences in the pattern, in a few species. Thus Pope (op. cit.) was able to distinguish sexual differences of this character in *Natrix annularis*, *Pseudoxenodon bambusicola*, *Psammodynastes pulverulentus*, *Trimeresurus monticola*, and *T. stejnegeri*, among seventy-five Chinese snakes. Of these, only *Trimeresurus stejnegeri* showed any marked dimorphism, the others exhibiting only increased intensity of color in one or the other sex. Among European snakes, *Coronella austriaca* and *Vipera berus* have long been known to present a more or less constant sex dichromatism (Franke, Schreiber, Durigen, Boulenger). Nevertheless, a hue or pattern characteristic of one sex is decidedly the exception rather than the rule among snakes. Whether any of those that do occur make their appearance only with the attainment of sexual maturity, and would thus be associated directly with the hormones of the gonads, is unknown.

Assumption of a nuptial coloration by the male is wholly unknown. In this respect snakes stand in striking contrast to lizards, among which nuptial livery is widely distributed.

Chin Tubercles and Anal Keels.—The sexual differences described above are instances of sexual dimorphism, but can hardly lay claim to recognition as true secondary sexual characters, since there is no evidence that they have any functional significance or that they are correlated with the onset of puberty. In some snakes, however, there are structures which play a definite role in courtship. In sexually mature males of certain species a cluster of tubercles is present on the symphysial region of the chin (fig. 30). The presence in males of ridges or knobbed keels on the dorsal scales surrounding the cloacal region is even more widely distributed. Blanchard (1931)

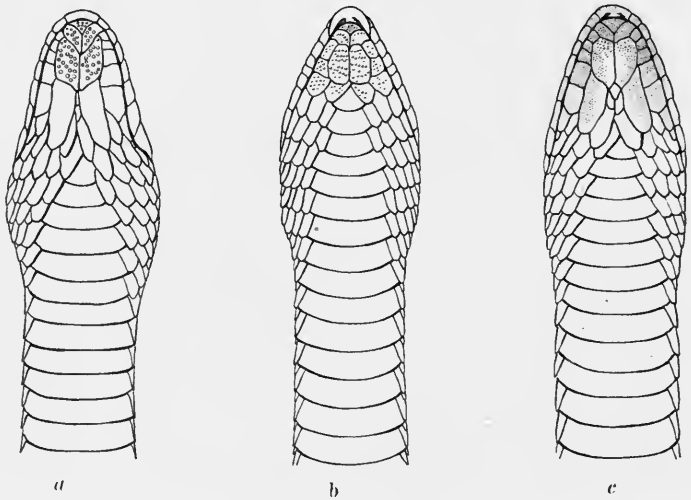

FIG. 30. Chin region in male snakes, showing the distribution of tubercles and pustules. The pustules in *Thamnophis* are not as prominent as indicated in the figure. *a, Natrix rhombifera. b, Ninia sebae. c, Thamnophis radix.*

has recently examined a variety of North American snakes with reference to these structures. He found that they are developed in *Carphophis, Diadophis,* and *Natrix* after sexual maturity is attained. An insignificant number of females also possessed anal keels, but whether or not their presence was correlated with abnormalities in the gonads was not determined. Harrison (1933) obtained similar results with *Thamnophis.*

Blanchard found chin tubercles only in *Natrix rhombifera* among North American snakes. From an examination of nearly two hundred male specimens of this species, of various ages and collected at various seasons, he was able to determine that these structures

make their appearance only with the attainment of sexual maturity, and that they are not subject to seasonal hypertrophy. Pope (op. cit.) identified them in eight species of Chinese snakes of the genera *Natrix, Ophisthotropis, Enhydris,* and *Amblycephalus.* They are well developed in the Central American snake *Ninia sebae* (fig. 30, *b*), and further work will doubtless reveal their presence in other species. These facts show that the distribution of these structures is erratic in the extreme. Their sporadic occurrence bears no relation to natural affinities. It seems likely, therefore, that they have evolved independently on several occasions. Observations on the courtship behavior of species bearing these structures are lacking, so that suggestions as to their functional significance must be tentative and inferential.

Chin tubercles are not present in *Thamnophis.* Comparison of the region in the two sexes, however, shows that the small sensory

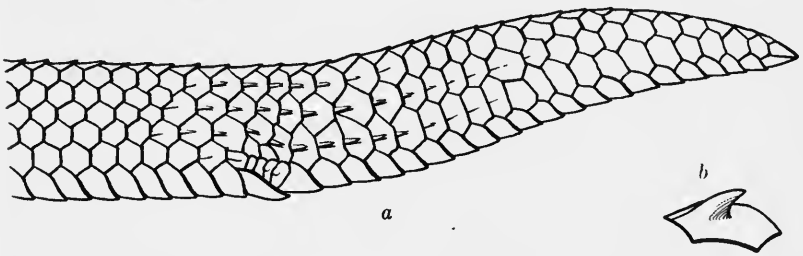

FIG. 31. Modification of the anal keels in male *Aspidura trachyprocta.* *a*, Posterior end of body, showing distribution of hooks. *b*, A single scale, enlarged, seen from the side.

pustules characteristic of many snakes are considerably hypertrophied in male garter snakes (fig. 30, *c*).

This is also true of some other North American colubrids (*Natrix, Storeria*). In others (*Coluber, Elaphe, Pituophis*), however, pustules are present but are equally developed in both sexes. There can be little doubt that the slightly hypertrophied sensory pustules in the male *Thamnophis* correspond to an early stage in the phylogenetic history of the tubercles in other snakes.

Noble (1934a) has recently examined both the chin tubercles and the anal knobs histologically. He states that "each organ consists of a capsule of irregularly arranged tactile cells and many nerve fibers. The organs of the chin differ radically from those above the cloaca in having one or more narrow extensions piercing the overlying epidermis to near the horny layer."

Spurs in Boas and Pythons.—There is considerable sexual dimorphism in the size of the claw or spur which is the only external vestige of the hind limbs in boas and pythons (Beddard, 1905). In the males of many species this structure is a comparatively large, curved hook, whereas in the female it is often reduced to a tiny horny projection (fig. 32). It is not known whether the hypertrophy of this structure in males is correlated with the onset of puberty, and the material at hand is not extensive enough to de-

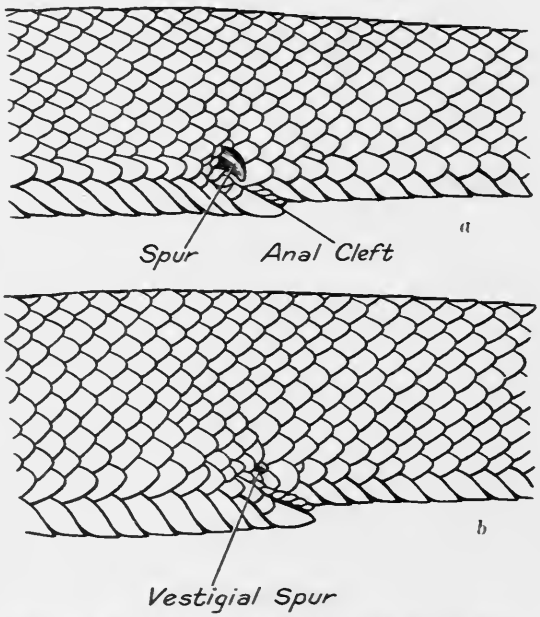

FIG. 32. Sexual dimorphism in the spurs of a boa, *Epicrates striatus*. *a*, Male. *b*, Female.

termine this by an examination of series of immature and adult specimens of both sexes. These claws deserve considerable attention, since they are among the few structures in snakes which function actively in courtship.

Anal Scent Glands.—Both sexes of snakes are provided with a pair of glands buried in the musculature of the tail. These glands pour into the cloaca a pungent secretion, the odor and color of which vary considerably from species to species. This secretion has often been associated with the sexual behavior of snakes, but since the glands are present and equally functional in both sexes, as well as in young individuals, its sexual significance is doubtful. The expul-

sion of this liquid is important in the defensive behavior of many species, and it is at least possible that it may function in recognition of species. Its true function, therefore, is obscure.

COURTSHIP AND MATING IN THAMNOPHIS RADIX

The plains garter snake, *Thamnophis radix*, is the commonest and most generally distributed snake in the Chicago region. It is a hardy species, varying its staple diet of earthworms with a wide assortment of foods, and thriving in a variety of habitats. It is not uncommon in well-populated suburban areas, where "rock gardens" constructed by amateur horticulturists offer it a congenial retreat. If unmolested, one or more individuals usually take up their abode in these loose piles of rock, where they seem to remain from year to year.

The observations forming the basis of the following discussion were made by Mr. A. C. Weed, of the Field Museum staff. Mr. Weed, an observer of long and wide experience, made voluminous notes on each of the three days when mating activities were observed. He has generously placed these notes in my hands and they have been amplified by personal discussions the day following the actual observations.

The observations were made in the yard of Mr. Weed's home at Morgan Park, Illinois. The arrangement of this area is shown in figure 34. The snakes had apparently been living in the rock garden for several years, retreating into it to hibernate in the fall and reappearing in the spring. They had not been seen in 1936 before the initial observations were made, on April 19. The individuals were not marked, but were readily identified on any given occasion through differences in size and coloration.

Observations of April 19, 1936.—The snakes concerned in the observations of April 19, two males and a female, were first seen in the rock garden shortly after 10:00 A.M. The day was bright and sunny, with a chilly southwest wind and an air temperature between 50° and 60° F. The larger of the two males, estimated to be about twenty-four inches in length, was brilliantly colored and had apparently shed recently; the colors of the smaller male, which was about six inches shorter, and of the female were comparatively dull. The female was approximately the same length as the larger of the two males.

The female and the smaller male were first seen together on top of the rock garden. They were then very alert and cautious and

disappeared quickly. A few minutes later they appeared together in a mass of dry leaves about three feet north of the rock garden, where they were sheltered from the wind and in the bright sun. They were still very alert and active, moving in and out among the stones. The male at this time showed no active interest in the female, although he remained near her. Within a few seconds the third snake, immediately recognizable by its brilliant colors, appeared for the first time and also entered the rock pile. A moment later the heads of all three snakes were in sight, protruding from crevices between the stones.

After half a minute of inactivity the female suddenly darted from the stone pile, with the smaller male in close pursuit. Moving north about three feet, she described a circle about two feet in diameter, finally stopping with her body nearly straight. The male was two or three inches behind. After a short pause he touched the female with his muzzle several inches from the tip of her tail, apparently directly over the vent. He hesitated momentarily, then started to glide along her back, following each curve of her body closely. During this movement the male's neck was arched slightly, thus bringing the symphysial region of his chin directly in contact with her dorsal midline. No flicking of the tongue on the part of the male was observed, and the female remained motionless.

When the tails of the pair were together the male stopped and began to bend the rear part of his body around hers. Contact was apparently established almost immediately. A few seconds later there was a gradual tensing and quivering of the entire body of the male. This movement brought the cloacal regions of the pair into very intimate contact. About five seconds later the body of the male suddenly relaxed slightly and became quiet. These actions, which were interpreted as indicating the actual orgasm, were repeated at intervals of less than a minute at first, with later contractions spaced somewhat farther apart. After a dozen or more contractions of his body, the male withdrew the hemipenis, turned his body, and seemed to make a new entry with the opposite hemipenis. The female was quiet during the first few orgasms, although during the later ones her body tensed and quivered in the same way as that of the male. After about a dozen orgasms in the new position the pair separated voluntarily and the male moved away.

During these activities the second male emerged from the rock pile. Moving up to the mated pair, he ran his chin along the back of the female exactly as described for the first male, but made no

attempt to copulate until the original male had withdrawn and reinserted, when he tried half-heartedly to maneuver his cloaca around to that of the female. At this time he emitted a small quantity of whitish, semi-liquid material, apparently the product of the scent glands, although its identity was not determined.

As soon as the first male started to move away the second renewed his attempt to copulate. The first returned quickly, however, and,

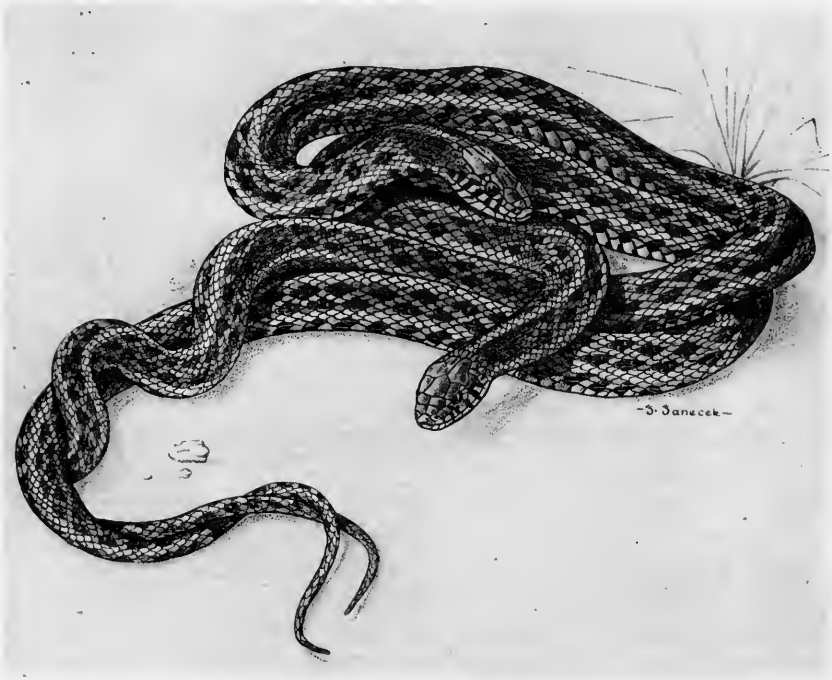

FIG. 33. Copulating pair of *Thamnophis radix*. Note the position of the head of the male (from photograph by Blanchard).

nosing his way under the other male, mated for the second time. Ten minutes later the three snakes were lying quietly near one another. At a slight disturbance the first male left. The second male immediately went through the courtship activities, running his chin along the back of the female from a point near the base of her tail until he had reached a position suitable for mating. Copulation took place at once, following the same pattern as that described for the first male. The hemipenes were employed successively as before. The first male returned and tried to effect an entry from the opposite side, but was unsuccessful.

Five minutes later all three snakes had moved so that their bodies were completely hidden in the leaves and grass, leaving only their tails visible. The tails were side by side, and were moving, in unison, quite rapidly from one side to the other, as if both males were trying unsuccessfully to copulate at the same time. A few minutes later the snakes were lying near one another and, contrary to their behavior a short time before, were very alert. When the observer approached they all beat a hasty retreat and hid in the rock pile.

These activities occupied approximately an hour. During the time of active courtship and mating, none of the snakes paid any attention to the observer's presence, allowing a cautious approach to within four or five feet without taking alarm. This behavior was in sharp contrast to their wariness immediately before and after mating activity. The dominance of the smaller of the two males over his larger companion of the same sex was striking and consistent. Although there was no evidence of active antagonism or pugnacity between them, the larger male seemed to recognize the dominance of his smaller rival and courted the female actively only when his companion was not present.

Observations of May 10.—A remarkable series of observations made on May 10 leaves little doubt that the sense of smell may play an important part in the mating of *Thamnophis radix*. They took place in the same spot as those of April 19, and under similar circumstances. The female was a smaller individual than the female of April 19.

May 10 was cloudy, with an air temperature of 76° F. The pair was first seen, *in copulo*, at 9:40 A.M. They were left undisturbed for ten minutes, during which time they remained in connection. Then the observer approached cautiously and the female left quickly when he had reached a distance of three feet. The pair apparently broke readily, for the male was not dragged by the female, as has frequently been described. When the observer approached to within six inches the male started to move, but stopped about the time his body was straightened out from the loosely coiled position it had occupied. He waited in this position for about twenty seconds, then obviously began to search for the trail of the female. He moved roughly in a circle, and made almost a complete circuit of the place where the pair had originally been before he struck her trail. During this circling he continually flicked the ground with his tongue, touching almost the whole upper surface of the forked

part, with the tips directed backward, to the ground each time. When he struck the trail of the female the tongue-flicking became noticeably more rapid. The subsequent movements of the snakes are shown somewhat diagrammatically in figure 34.

As soon as he found the trail, the male followed it very exactly into a clump of flowers, a distance of four feet. The snakes were lost to the observer for a moment, but were shortly seen to emerge from another clump of flowers four feet away. The female immediately started east toward a large clump of dense underbrush where

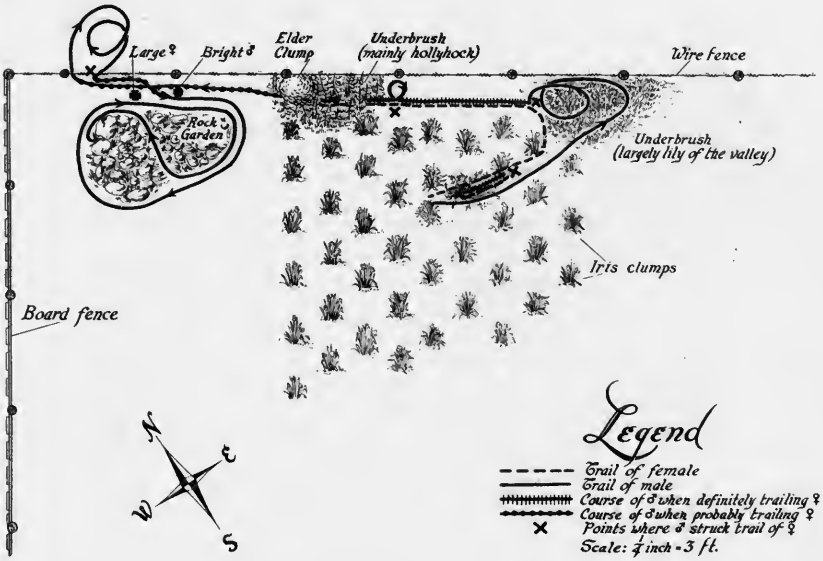

FIG. 34. Diagram showing movements of courting garter snakes (see text).

she could not have been followed by the observer. She was headed off, and turned northwest. She then moved rapidly into another large clump of underbrush along the fence, into which she disappeared. A few seconds later she was seen to emerge from the farther side of this clump. The female was lost permanently to the observer at this point, but from subsequent behavior of the male it is apparent that she continued moving along the fence, probably eventually taking refuge in the rock garden.

Meanwhile the male lay quietly in the open. A moment later he started to crawl toward the underbrush from which the female had been headed off. Circling through the vegetation several times,

he eventually struck the trail of the female again. The male was then crawling at a right angle to the trail. Turning abruptly, he followed it directly at full gliding speed until close to the second clump of underbrush. Here he apparently overran the "scent" on a slight turn. Circling about, he picked it up again on the first cast, and apparently followed it straight through.

Continuing along the fence for about ten feet, he came upon a large female *T. radix*, apparently the one of April 19. Just before this he must have passed unobserved very close to another snake, which was probably the "bright colored male" of April 19. His path brought him to the body of the female about at her vent. He stopped momentarily and seemed to press his chin down on her back, then passed on quickly. The observer at this time was about fifteen feet away, and the details of the behavior could not be seen. The male continued along the fence for about ten feet farther, and then seemed to lose the scent. He circled under the fence, and after casting about several times struck the trail he had just left and started to backtrack along it. He followed the trail until he again encountered the "large female." Again he stopped and pressed his chin along her back, moving toward her head for about an inch in the same way as described in the courtship of April 19. He did not continue courting this female, however, but left abruptly. Circling the rock garden several times, he finally entered it and disappeared at 10:10 A.M.

The "bright male" disappeared shortly after the male under observation had passed, but the "large female" remained in the same place for an hour longer. When the observer approached, she appeared nervous and disappeared.

The mating activities just described occupied approximately thirty minutes of elapsed time. On several occasions there was unmistakable evidence that the male was tracing the female wholly by means of some chemical sense, presumably smell. She was certainly invisible to him from the time the observations began. On three distinct occasions he was seen to search for her trail deliberately, and twice when he struck it he turned abruptly at a right angle to his former course. On a fourth occasion the male gave every evidence of picking up the trail of the female, although she was not seen by the observer to pass that point. Each of these points is marked by an x on the diagram (fig. 34). It has frequently been stated that the tongue in snakes serves to carry odorous par-

ticles to the olfactory organs, and in this connection the continuous flicking of the tongue by the searching male is particularly interesting.

The male's lack of interest in the "large female" is likewise noteworthy, indicating either that snakes are able to distinguish and identify individuals of their own species, or that the female during courtship gives some sign of acceptance or the opposite to the courting male.

Observations of May 24.—Observations were made on this date which supply further data on the mating behavior of this species. A close watch on subsequent week-ends failed to reveal further mating activity, although the snakes were seen regularly. The 1936 breeding season in *Thamnophis radix* therefore began about the middle of April and continued into the last week of May.

May 24 was warm and mostly cloudy, with an air temperature of about 80° F. The area around the rock garden was examined every half hour or oftener during the morning, but the snakes were not seen until 12:00 M. Three individuals, two males and a female, were observed. These were apparently the same snakes as those seen on April 19.

When first observed, one of the males was already in copulation with the female. The smaller male was trying vigorously to dispossess his rival by forcing his head and body between the mated pair. The movements of the unmated male agitated the copulating pair considerably, causing the copulating male to lose contact with the female several times. All three snakes were much more active than on previous occasions, and the female in particular seemed much more alert. The three snakes were so closely intertwined at all times that it was difficult to be certain, except two or three times, which male was actually in copulation with the female. The smaller male seemed to be unsuccessful at all times, however, in spite of his greater activity. During the entire time of certain contact, the larger male kept the whole lower surface of his head pressed against the back of the female, with its longitudinal axis parallel with her vertebral column. The smaller male also assumed this position a few times.

When the snakes were first seen, the smaller male was moving rather actively, and once was as much as three inches away from the other two. Later he twined in with the others and the three moved as a unit until they disappeared. The males seemed to pay no attention to the observer, but the female watched him very closely when he sat down within a distance of four feet. When he

returned after an absence of several minutes the three snakes had moved forward leaving no more than half their bodies exposed. The heads could be seen occasionally on the far side of one of the stones. They continued to move forward slowly, and within ten minutes had disappeared completely.

The behavior of these three snakes suggests a possible explanation of the formation of "snake balls." If two males will besiege a female simultaneously, what is to prevent this number from increasing, when additional males are present, until the writhing aggregations of snakes described in the literature are formed?

SEX RECOGNITION IN SNAKES

It has been realized only rather recently that sex recognition may have an important bearing on courtship behavior. In many animals, such as lizards and birds, striking secondary sexual characters and complicated "courtship" displays are now known to be used to intimidate other individuals, regardless of sex, rather than to court the female. Mating is attempted with any individual that can be forced to submit, and sex recognition as such appears to be absent. In other animals, as for example frogs, when a male attempts to mate with another male, the second individual gives a warning note which serves effectively to warn the aggressive male of his mistake. The female fails to make this warning cry, so sex recognition operates only between males. On the other hand, it has long been known that a female moth may attract hundreds of males by means of a chemical sense. In other words, the males recognize the female as distinguished from other males of the same species. In view of the voluminous literature on sex recognition in various other groups, it is strange that nothing has been written that bears directly on it in snakes. Experimental work aimed directly at this subject is much to be desired. Certain tentative conclusions may, however, be drawn from existing data.

The observations recorded above (p. 278) indicate that odor is an important factor in enabling the male to seek out and trail the female. From this it seems likely that the same factor is involved in enabling the male to distinguish between the sexes at the time of mating. If this is true, it is a method of sex identification that is unknown elsewhere among the lower vertebrates, and is strikingly similar to that employed by certain moths. Noble and Clausen (1936) have recently corroborated these observations experimentally. In studying the factors responsible for the aggregation behavior

of *Storeria*, they tested the ability of snakes to "trail" other individuals across the bottoms of glass-sided cages. The body integument or the cloacal region, respectively, were rubbed along marked trails, and the reactions of other individuals, when released in the cage, observed. They conclude that "it may be stated that normally, irrespective of the breeding season, there is some odorous substance given off by the integument of these snakes which attracts other members of the same species, and that during the breeding season this, or more probably another substance, is given off by the female which in turn attracts the male and enables the male to distinguish sex. The nature of this substance is as yet undetermined." Curiously enough, they state that snakes not only failed to follow a trail scented with the cloacal gland secretion, but even avoided it; they say "the body integument and not the cloacal glands leave a trail which aids snakes in seeking and identifying the opposite sex" (p. 308), and "in all cases the snakes failed to cross a trail scented with cloacal gland secretion" (p. 309). It is difficult to see how a snake crawling along the ground could fail to bring its cloaca into contact with the substratum, and in so doing leave a trail of scent from that part of the body, yet we have seen (p. 278) that a courting male *Thamnophis* will follow such a trail assiduously.

It is apparent, then, that snakes recognize sex directly, through an olfactory stimulus. In this they stand in very striking contrast to lizards, where sex is recognized by the trial and error method of attempting to mount any individual, regardless of sex, until a female is found with which mating can be accomplished.

DISCUSSION

The literature reveals a need for critical observation of the mating behavior of even the commonest species of snakes. Obviously there is not a simple, stereotyped pattern broadly characteristic of the entire group, as heretofore has been generally supposed. On the contrary, further investigation promises to reveal an extraordinarily rich variety of characteristic performances. Detailed knowledge is now available only for a few of the most common colubrids, although something is known of courtship behavior in nearly all the important families of snakes. Without attempting to theorize on the basis of a few genera which seem to supply favorable data, certain conclusions, some of them admittedly tentative, may be drawn.

It has long been known that certain definite courtship patterns characterize natural groups of species in some invertebrates, in salamanders, and in birds. Noble and Bradley (1933) have shown that this is also true to a certain extent among lizards. In the Serpentes, data for more than one or two genera of a family are available only in the Colubridae. There the courtship pattern of *Thamnophis*, which consists of rubbing movements by the male directed toward self-stimulation, with the female remaining entirely passive, is wholly different from the complicated "mating dance" of *Coluber*, *Elaphe*, *Malpolon*, and *Ptyas*, which is apparently an expression of mutual excitement. Whether the simpler procedure that has been described for *Lampropeltis* and certain species of *Elaphe*, in which the male merely grasps the female in his jaws, represents another modification of the behavior pattern or is merely incompletely observed or abnormal courtship, is uncertain. It seems likely that further observation will reveal that identical or closely similar performances tend to characterize natural groups. It is, of course, impossible to say to what extent this may be true. A simple courtship behavior perhaps is associated with more "primitive" species. In this connection it is suggestive that *Natrix* and closely related genera are regarded as more primitive than *Coluber* and its close relatives.

Data are extremely fragmentary for the non-colubrid families. The courtship behavior of boas and pythons is apparently unique. Indeed, because of the absence of well-developed external limb rudiments in other snakes, it could not be duplicated. Movements of the hind limbs form an essential part of the courtship pattern in many lizards. Although there is small probability of any correlation, this fact is interesting in view of the position the Boidae and Pythonidae occupy at the bottom of the evolutionary scale in snakes.

A mating dance takes place in all poisonous snakes upon which observations have been made. This dance is so strikingly similar to the *Coluber* type of dance as to suggest phylogenetic continuity, although in some respects the *Coluber* type is more complex than that of the morphologically more specialized poisonous snakes. In this connection, knowledge of the mating behavior of members of the annectant Boigidae might prove illuminating.

Extreme development of those secondary sexual characters not directly concerned with the act of copulation (horns and other appendages, hypertrophied or brilliantly colored parts of the body) is frequently associated with fighting or intimidating displays among

males. Such activities are directed either toward acquisition of a harem or defense of territory, or they are the means of sex recognition. Harem formation is highly characteristic of certain gregarious mammals, birds, and at least one lizard (*Amblyrhynchus*). Defense of territory during the breeding season occurs frequently among birds, and has been noted in several lizards. Sex recognition through intimidating displays is likewise characteristic of certain members of these two groups.

Fighting and development of weapons for conflict or intimidation are both conspicuously absent in snakes. Such sex-limited structures as are present function solely as stimulating organs. Aggregations of many individuals are known to take place during hibernation in *Coluber*, *Thamnophis*, *Storeria*, and *Crotalus*, and probably occur in many others, but snakes are in no sense gregarious. Mating normally takes place at the time of emergence from hibernation before the population has scattered, but in spite of the resulting close association of many individuals fighting does not seem to occur. Franke alone remarks that captive breeding males of *Coronella* "not infrequently engaged in fighting, during which they bit each other." Farther on he remarks, however, that he has never observed other individuals interfering with a mated pair. Other authors have been at pains to emphasize the absence of fighting.

This lack of fighting is probably correlated with the failure of males to defend territories or harems. The absence of armature or intimidating devices, in turn, is related to the failure of males to fight. The whole social life of snakes appears extremely simple in comparison with that of many other groups, yet the courtship behavior of these animals is curiously diversified, and in some respects rather complex.

In many respects the *Natrix-Thamnophis* group occupies a unique and anomalous position. The sexual behavior of these snakes is curious, even degenerate, compared with that of other snakes. Courtship is of a type unknown elsewhere. There is no indication that the female participates in it, except as a purely passive object of the attentions of the male, nor does the male behave in such a way as to stimulate her. There is no evidence that individuals recognize each other, whereas in other snakes pairs are known to consort together almost permanently. So-called polyandry has often been described in both *Natrix* and *Thamnophis*, and probably normally takes place when more than one male is in the vicinity of a breeding female. Strangely enough, this aberrant type of

mating behavior has generally been assumed to be typical of the snakes as a whole.

MATING OF SNAKES AND LIZARDS COMPARED

While the Serpentes and the Sauria form two sharply distinguished groups of reptiles, they are conceded to have had a common ancestry, and are far more closely related to one another than either is to any other reptilian line. It is therefore of more than ordinary interest to compare the mating behavior of members of these two groups.

The behavior of lizards has been studied in detail by Noble (1934b), Noble and Bradley (1933), and Evans (1935, 1936), mostly through observations on captive individuals. Noble and Bradley concluded that active sex recognition does not exist in lizards, but Noble (1934b) believed that sight might be a factor in *Sceloporus* after observing it in the field. Noble and Bradley concluded also that such sex discrimination as does exist is based on the fight reaction displayed by the males when approached by other individuals. In other words, copulation is attempted with any individual that can be forced to submit. Evans (1935) believed, on the other hand, that sight is an important factor in sex recognition in *Anolis*, and that homosexual matings are probably induced by captivity. The direct recognition of sex, through scent, which is found in snakes, stands in the sharpest possible contrast to that of lizards, whether it is indirect or by sight in the latter.

Noble and Bradley concluded that the courtship and mating of lizards is "a very stereotyped performance, which has changed slowly in phylogeny." The savage rape, with the female in active flight, which is practiced by male lizards, seems a very primitive type of behavior when compared with the mutual mating dance of many snakes, or the persistent, gentle persuasion indulged in by male boids and pythonids. The varied basic courtship patterns of snakes show that courtship in this group is by no means stereotyped, but has undergone radical and significant changes in the history of the group.

One of the most striking features of the behavior of lizards is the assuming and defending of territories by males. This practice, which is well known in birds, is probably closely correlated, or even identical, with the "despotism" or "dominance" noted by Evans (1935) in captive populations. In some lizards at least (*Anolis*, *Sceloporus*), it is in this connection that the secondary sexual characters of the male are brought into full play. Such sex-limited struc-

tures are invariably either true weapons or highly colored parts which are used in bluffing displays. There is no known structure in lizards which has a hedonic or stimulating function. It is noteworthy that snakes, on the other hand, are not known to define and defend territories, and fighting does not seem to be a normal accompaniment of their behavior. Secondary sexual characters are extremely limited among them. Highly ornamented parts, which are so common in male lizards, never occur. Both of the known secondary sexual characters in snakes (hypertrophied spurs in boas and pythons and chin tubercles in certain colubrids) function directly as stimulating organs. The same is probably true of the anal knobs or keels found in the males of many snakes.

As investigation progresses, it is increasingly apparent that the sexual behavior of lizards is strikingly similar to that of birds. This can readily be accounted for on the basis of the reptilian ancestry of birds, if the snakes are disregarded. Whether snakes have acquired unique behavior patterns along with their structural specializations is, of course, a question which cannot be answered. The indications are, however, that this may be true.

Under any circumstances, it is obvious that the mating behavior of snakes differs from that of lizards in every essential respect. The implications of this fact cannot be fully evaluated at this time, although they may well prove to be of great significance.

SUMMARY AND CONCLUSIONS

(1) Several distinct types of courtship are evident in snakes.

In boas and pythons, the male arouses the female by scratching her body, above the cloaca, with his spurs.

In the *Natrix* group of colubrids, the male rubs his chin along the back of the female, which results in self-stimulation of the male.

In the *Coluber* group of colubrids, there is a mutual mating "dance."

In the Crotalidae, and probably also in the Elapidae and Viperidae, there is a "dance" similar to that of *Coluber*.

(2) Available data indicate that given types of courtship behavior are common to related groups of species.

(3) Secondary sexual characters are almost unknown among snakes. The chin tubercles and anal keels or knobs found in a few species and the hypertrophied spurs in male boas and pythons are the only ones known to function in courtship.

(4) Sex recognition depends on the sense of smell. The males, of certain species at least, may trail the female for a considerable distance at the time of mating. Odor apparently emanates from the body integument, rather than from the scent glands (Noble and Clausen).

(5) Males do not fight among themselves during the breeding season. Correlated with this, there is no defense of territory or of mates.

(6) The courtship of lizards is in many respects similar to that of birds. On the other hand, the mating behavior of snakes is of a wholly different type. It does not closely resemble that of any other group of vertebrates.

(7) There is at present little evidence in favor of sexual selection in the mating behavior of snakes.

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