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The Ecological Physiology of a Garter Snake

In order to survive in the harsh environment of western Canada the red-sided garter snake has evolved a precisely timed cycle of physiology and behavior with several spectacular features

by David Crews and William R. Garstka

The red-sided garter snake (*Thamnophis sirtalis parietalis*) is found farther north than any other reptile in the Western Hemisphere. It ranges into western Canada, where the winter temperature is often below −40 degrees Celsius and the snow cover is often continuous from late September through May. Throughout the long winter it takes refuge in sinks and caverns in the limestone that characterizes much of western Canada. Each such hibernaculum, or den, harbors as many as 10,000 snakes. In the den the overwintering garter snakes undergo a set of profound physiological changes. Their blood becomes as thick as mayonnaise. Occasionally they move, but only sluggishly.

Late in the spring the garter snakes emerge. Although males and females hibernate together in equal numbers, the males come out more or less en masse. Neither food nor water is available at the den. Nevertheless, the males stay nearby. Then the females come out. Some of them emerge as early as the males. Unlike the males, however, the females emerge singly or in small groups. The difference in the timing of their emergence means that at the opening of the den males may outnumber females by as many as 5,000 to one; each female is vigorously pursued and courted by a multitude of suitors.

The typical result is a writhing mass of snakes called a mating ball, consisting of as many as 100 males all trying simultaneously to align themselves with a single female. Within 30 minutes of the female's emergence she has mated, and the unsuccessful males are awaiting the appearance of another female. Meanwhile the mated female sets off on a migration to summer feeding grounds. Migrations of as much as 15 kilometers are known. The males will follow at the end of the mating season, which may last for only three days or for as long as three weeks. Early in the fall each female gives birth at the feeding ground to as many as 30 living young; then the adult snakes return to their den and reenter hibernation. (It is not known where the newborn spend their first winter.)

The question addressed in our research, first at Harvard University and now at the University of Texas at Austin and the University of Alabama, is how a species such as the red-sided garter snake, which lives in a region where the climate is extreme, comes to have its physiology and its behavior synchronized with the demands of its environment. In the case of the red-sided garter snake the young must be born before the adults reenter winter dormancy; hence the species must mate, migrate and feed, give birth to its young and return to hibernation on a precise schedule spanning three summer months. In trying to understand this cycle much of what is known about the physiology of other vertebrate animals that have a breeding season turns out not to be relevant. In advance of the breeding season the gonads of such an animal typically get bigger and the blood level of sex hormone rises. The gonads prepare gametes (sperm or eggs), and the rising concentration of circulating sex hormone acts on the brain to trigger mating behavior. The red-sided garter snake is different. When the snakes emerge from their den for their short, intense mating season, their gonads are at their smallest and their hormones are at an ebb.

The springtime increase in temperature that allows the red-sided garter snake to emerge from its den is known to trigger its mating behavior. Alexander Hawley and Michael Aleksiuk of the University of Manitoba have shown that the snakes will mate in the laboratory only if the dormant animals are exposed to a temperature of at least 25 degrees C., which simulates spring. Few males will try to mate at temperatures of less than 20 degrees. We ourselves have found that males must be exposed to a temperature of less than 10 degrees for at least seven weeks if they are to show mating behavior when they are exposed to warmth.

The mating behavior is unmistakable. Males first recognize females by means of a pheromone: a chemical released by some members of a species that controls the physiology and the behavior of other members. In this instance the female releases the chemical, a fact that G. Kingsley Noble of the American Museum of Natural History inferred more than 40 years ago by observing the snakes' behavior. Noble also found that males, which normally ignore other males, courted the males he had rubbed against sexually attractive females. The work of John Kubie and Mimi Halpern of the Downstate Medical Center of the State University of New York suggests how the pheromone acts. The male catches pheromone molecules on his tongue, which he repeatedly flicks as he nears the female, and the tongue delivers the molecules to the vomeronasal organs, which are in the roof of the mouth. The chemical-sensitive cells of the vomeronasal organs send signals along nerve fibers to the brain. (All other snakes and those lizards that have forked tongues detect chemical trails laid down by

CARPET OF MATING GARTER SNAKES covers the floor of a limestone sinkhole in Manitoba; the springtime increase in temperature has caused them to emerge through fissures from their den in a cavern under the sink. The snakes are red-sided garter snakes. The males are from 12 to 18 inches long, the females from 18 to 24 inches long; otherwise they look much the same. As many as 10,000 red-sided garter snakes may share a den through the winter. The photograph was made by Bianca Lavies. Copyright © 1975 National Geographic Society.

other members of their own species in the same way. Vomeronasal organs are found even in mammals. They are the principal means by which animals communicate chemically. In human beings they are vestigial but in the human fetus they are well developed.)

If the male red-sided garter snake finds the female sexually attractive, the tongue flicking becomes more frequent. Soon the male begins to rub his chin along the back and side of the female, rapidly and repeatedly traversing the length of her body. This chin rubbing is observed only as part of mating behavior. The male traverses the female with increasing rapidity, and then he comes to rest draped over her. The scales near the opening of his cloaca (in reptiles the combined end of the urogenital and intestinal passages) are sensitive to touch; hence the male has sensory guidance as he aligns his body with the female's.

When the male is properly aligned, he initiates muscular contractions that send waves up and down the length of his body. The waves are a prelude to further maneuvers that bring the tail of the male under the body of the female so that his cloaca is apposed with hers. The male then achieves intromission. He rolls the female's tail upward and everts one of his hemipenes slightly. (The hemipenes are two saclike copulatory organs in the cloaca.) Small hooks at the base of the hemipenis engage the cloacal scales of the female, so that the female's cloaca is drawn open. Finally the male fully everts the hemipenis into the female's cloaca. Sperm enters the female by flowing along a groove in the hemipenis wall.

The female's mating behavior is also characteristic. During the courtship that leads up to intromission the female breathes more deeply than usual but not more rapidly. If she is sexually receptive, she remains stationary. Indeed, she may cooperate with the male by lifting her tail and widening the opening of her cloaca. If she is not receptive, she retreats from the male's advances and may even vibrate her tail, making intromission impossible. At intromission itself the male stops moving and is dragged about by the female. The hooks at the base of the hemipenis keep the cloacas locked together.

Intromission marks the moment when the unsuccessful males in the mating ball stop trying to court the female and disperse from the copulating pair. The copulation usually lasts for some 15 minutes. In that time the male deposits a translucent gelatinous plug in the cloaca of the female. The plug acts as a mechanical obstruction to further mating. In addition the plug contains a pheromone that makes the female unattractive to other males. Thus the female and the male produce pheromones with opposite functions. The mated female quickly leaves the site of the den.

Investigators trying to identify the nature and the source of the female's attractiveness pheromone have long been puzzled by the fact that the skin of garter snakes is devoid of any obvious glands that might produce, store or release such a chemical. An alternative possibility was suggested to us by two recent discoveries. The first was made by Josephine C. Rauch of the University of Manitoba. She described a network of capillaries along the back of garter snakes in the dermis, the deep layer of the skin. The second discovery, made by Lucas Landmann of the University of Basel and independently by Harvey Lillywhite of the University of Kansas, was that the skin of snakes is not an impermeable barrier. It allows lipids (fatty molecules) to pass through it. We reasoned that the female attractiveness pheromone might be a blood-borne substance that leaves the capillary network and percolates through the skin.

Taking advantage of the observation

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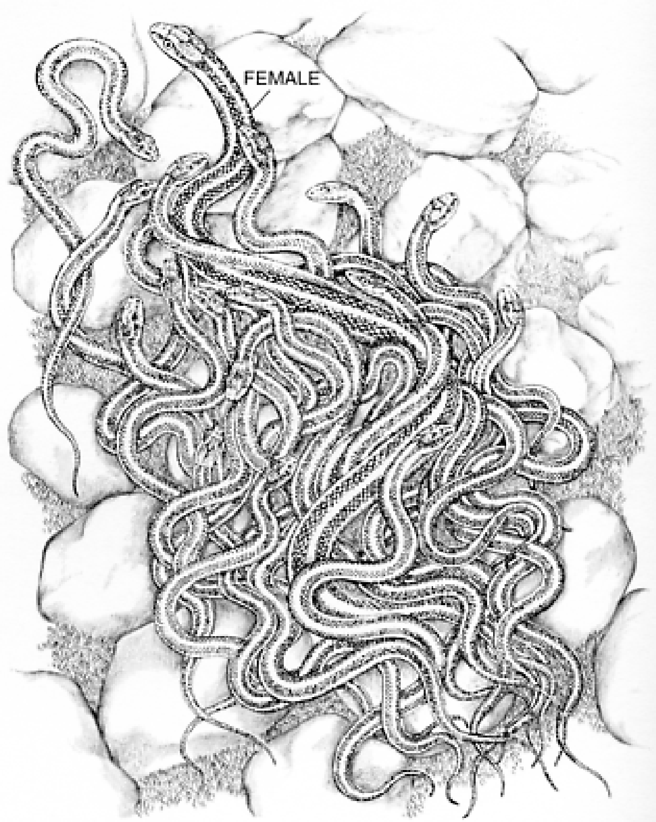

MATING BEHAVIOR of the red-sided garter snake is confined to a short, intense springtime breeding season. For a period of from three days to three weeks the males sun themselves near the den from which they emerge. Females emerge singly or in small groups (*1*). Attracted by a pheromone (a messenger substance) on the back of a female, as many as 100 males form a "mating ball" (*2*). One male

by Noble that males court males that have been rubbed against attractive females, we employed a simple behavioral assay to test for the pheromone. We spread various substances on the back of males and observed the response of other males. Since chin rubbing is seen only in sexual behavior, it would be an unequivocal indication that the attractiveness pheromone was present. In our initial experiments we spread the blood serum of males on the back of other males; it had no effect. We tried estrogen, the female sex hormone; it too had no effect. Then we tried the blood serum of females that had been injected with estrogen. Estrogen is known to induce sexual attractiveness in a variety of vertebrate animals, including female garter snakes, and earlier work had established that the injection of estrogen into female garter snakes makes them attractive to males; hence the injected estrogen stimulates the production of the female attractiveness pheromone.

The new result was clear-cut: the blood serum of the females we had injected with estrogen elicited courtship behavior; thus the pheromone was present in the blood. Remarkably, the blood serum of males injected with estrogen also elicited courtship behavior, and yet the estrogen-treated males themselves were not attractive to other males. Perhaps the attractiveness pheromone, which normally is not present in the male, cannot percolate through the skin of the male.

In order to identify the pheromone we prepared extracts from the skin of the females we had treated with estrogen. Since the pheromone acts only on males that are in physical contact with an attractive female, we suspected it was not an airborne substance. Instead it might be a protein, which does not evaporate readily. Our behavioral assay showed that it was not a protein. Specifically, male snakes did not court the males whose back we had rubbed with the protein fraction extracted from the skin of estrogen-treated females. A further assay revealed, however, that the pheromone was in the lipids we had extracted from the skin. Certain lipids do not evaporate readily either.

We therefore turned our attention to the lipids that circulate in the blood of the garter snake. The lipids in the blood of any vertebrate animal other than a mammal contribute to the manufacture of yolk in the follicles (developing egg cells) of the female's ovary. The lipids are stored as phospholipids in organs called abdominal fat bodies; they are released into the blood when estrogen acts on the fat bodies. The estrogen is secreted by the ovaries. In the liver the phospholipids are incorporated into a lipophosphoprotein known as vitellogenin. This step too is governed by estrogen. Vitellogenin is the blood-borne precursor of yolk, and under the control of hormones from the pituitary gland it becomes yolk as it enters a growing follicle in the ovary. Although the gene that encodes the structure of the protein part of vitellogenin is in the DNA of both males and females, it is normally expressed only in the female. Nevertheless, the injection of estrogen into a male will increase the level of lipids in the blood and bring on the synthesis of vitellogenin.

With the help of Francis J. Schwende and Milos V. Novotny of Indiana University we analyzed garter snake blood by electrophoresis, the technique in which the various substances in a mixture separate from one another because they migrate at different rates through a medium (in this case cellulose acetate) to which an electric field has been applied. The blood of both male and female garter snakes we had treated with estrogen turned out to contain abundant vitellogenin. This finding meshed well with behavioral assays indicating that the liver of a female attractive to males and the liver of a female injected with

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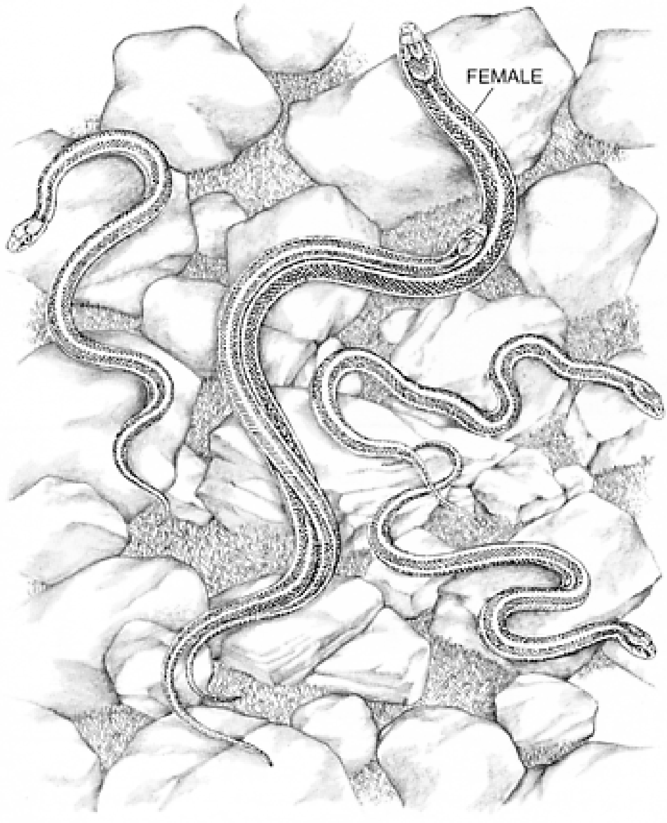

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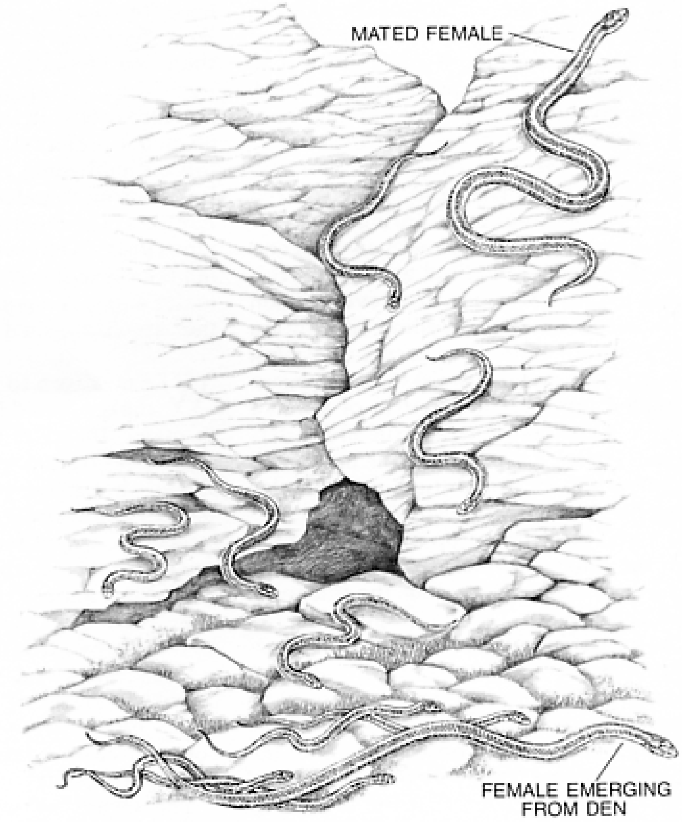


in the ball succeeds in mating with the female by inserting one of his two hemipenes into her cloaca (her urogenital opening). The other males immediately disperse (*3*). The mated female, rendered unattractive to males by a pheromone her mating partner conveys into her cloaca, immediately leaves the vicinity of the den. The males stay near the den to await the emergence of another unmated female (*4*).

estrogen both contained the attractiveness pheromone, whereas the fat bodies did not. Finally, the finding meshed with a behavioral assay in which male courtship was elicited when vitellogenin that had been extracted from the blood of estrogen-treated females was spread on the back of males.

Michael C. Devine, who was then at the University of Michigan, and Neil B. Ford of the University of Texas at Austin have each shown that male garter snakes follow females of their own species and ignore females of other species; hence the female attractiveness pheromone is specific to each species of garter snake. The molecular structure of egg yolk is also unique to each species. As vitellogenin enters the follicle it is broken down into lipovitellin and phosvitin, which are remade into yolk. The structure of lipovitellin is much the same among species; the structure of phosvitin varies among species. When egg yolk from three species of garter snake and from a lizard and a chick was made the subject of our behavioral assay, courtship by a male garter snake was elicited only by the yolk of a female of the same species.

At this point we had evidence that the female attractiveness pheromone is vitellogenin, thereby adding to its internal role as the precursor of yolk an external role as a messenger substance. We did not know how vitellogenin gets from the blood to the surface of the skin. In order to find out we froze the skin of the snake, sectioned it and stained it so that lipids would be preferentially dyed. Two distinct regions containing lipid were revealed. A dense layer of lipid appeared in the epidermis, the outer layer of the skin. The lipid is sequestered in the epidermal cells during the cycle by which the snake grows new skin and sheds old skin; the lipid aids in controlling the loss of water from evaporation and also facilitates shedding. In addition a wealth of lipid-filled sacs, or vesicles, was found deep in the skin of estrogen-treated females, in a matrix of striated muscle and connective tissue in the dermis. These sacs were absent in normal males, but we found them in the males we had treated with estrogen.

Lipid also turned up outside the skin in the hinge regions between neighboring scales. In such regions the thickness of keratin, the protein responsible for the hardening of the scales, is at a minimum. Since lipid is lost in the course of shedding, there must be a way for it to accumulate. Linking our examination of the skin with our observation that females breathe deeply as they are courted, we hypothesized that the breathing stretches the skin along the back of the female and moves the scales apart, so that lipid is exposed and (perhaps) pheromone is ejected.

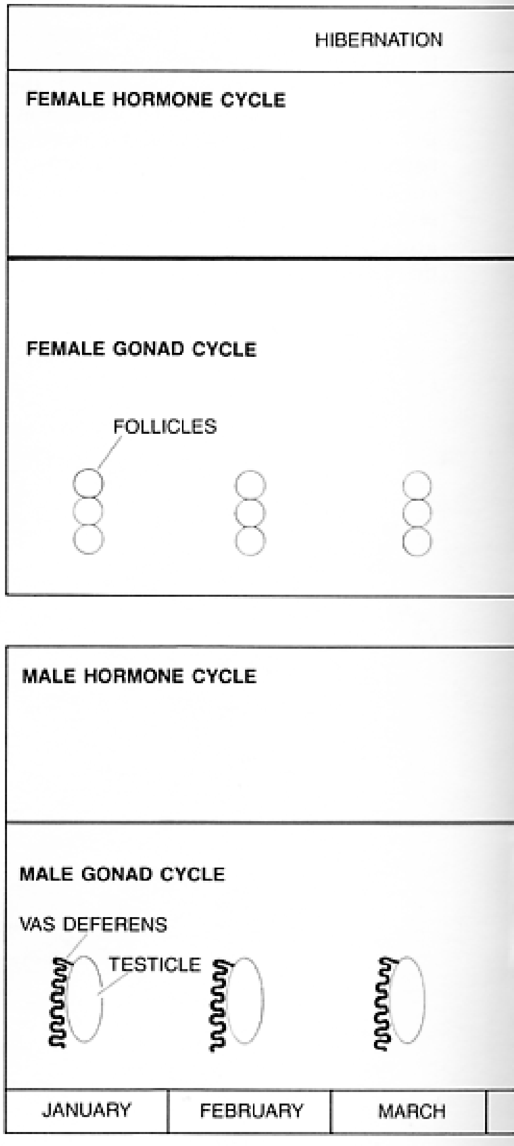
One problem persisted. Gauged by the behavior they elicit in males, female garter snakes are at their most attractive over the period of from three days to three weeks in the spring when the snakes come out of hibernation. Yet at that time the ovaries of female garter snakes are small (a fact we shall discuss more fully below). The ovaries do not begin to grow until the snakes have mated, and they are not at their largest until they have grown for about eight weeks. Since the estrogen produced by follicles growing in the ovaries promotes the synthesis of vitellogenin, the mismatch between the onset of mating behavior and the size of the ovaries is paradoxical.

A possible explanation of the paradox is that the female appears to be capable of storing in her skin the vitellogenin left over from previous reproductive seasons. As in other vertebrate animals, mating stimulates in the female the release of gonadotropin, the pituitary hormone that promotes the growth of the ovaries. In response to the gonadotropin the ovaries grow follicles and the follicles secrete increasing quantities of estrogen. This change in the hormonal balance, which rapidly follows mating, causes the vitellogenin stored in the skin to be shunted to the ovaries for deposition in the growing follicles as yolk. Mating therefore triggers the synthesis of yolk with little delay.

In this regard it should be noted that male garter snakes show a strong preference for courting large females and that large females, which are usually older than small females because snakes grow throughout life, tend to have more eggs and also more vitellogenin. Hence males attracted preferentially to females with more vitellogenin on their back would be choosing females on the basis of the female's reproductive output of the previous year. In effect the males are assessing the reproductive potential of the females and seeking to mate with the ones that are established as being fecund.

We now turn to the pheromone that makes mated females unattractive to males. Its effect is pronounced; Patrick Ross, Jr., working at Harvard, has shown that male garter snakes of the species *Thamnophis radix* will not court a recently mated female even if she receives continued injections of estrogen. Moreover, males exposed to a mated female often stop courting females for a day or longer. It is truly a male-inhibiting pheromone: it not only advertises the mated status of the female to other males but also renders the males that come in close contact with the mated female impotent.

The means by which the successful male applies the repellent pheromone to the female is well established. If the plug the male deposits in the female's cloaca is removed soon after the snakes have copulated, the female remains attractive to males. Conversely, if the material of the mating plug is spread along the back of an unmated female treated with estrogen, she is rendered unattractive. The source of the pheromone is also known: it is manufactured by the part of the kidney called the renal sex segment, which also manufactures the secretions from which the mating plug is formed. The significance of the pheromone becomes clear when one recalls the natural history of the snakes. Since mated females are unattractive to males, they are not subjected to repeated attempts at mating as they leave the vicinity of the den. Therefore the time the female is exposed to predators is reduced. The predators include crows and ravens, which prey at the dens in the



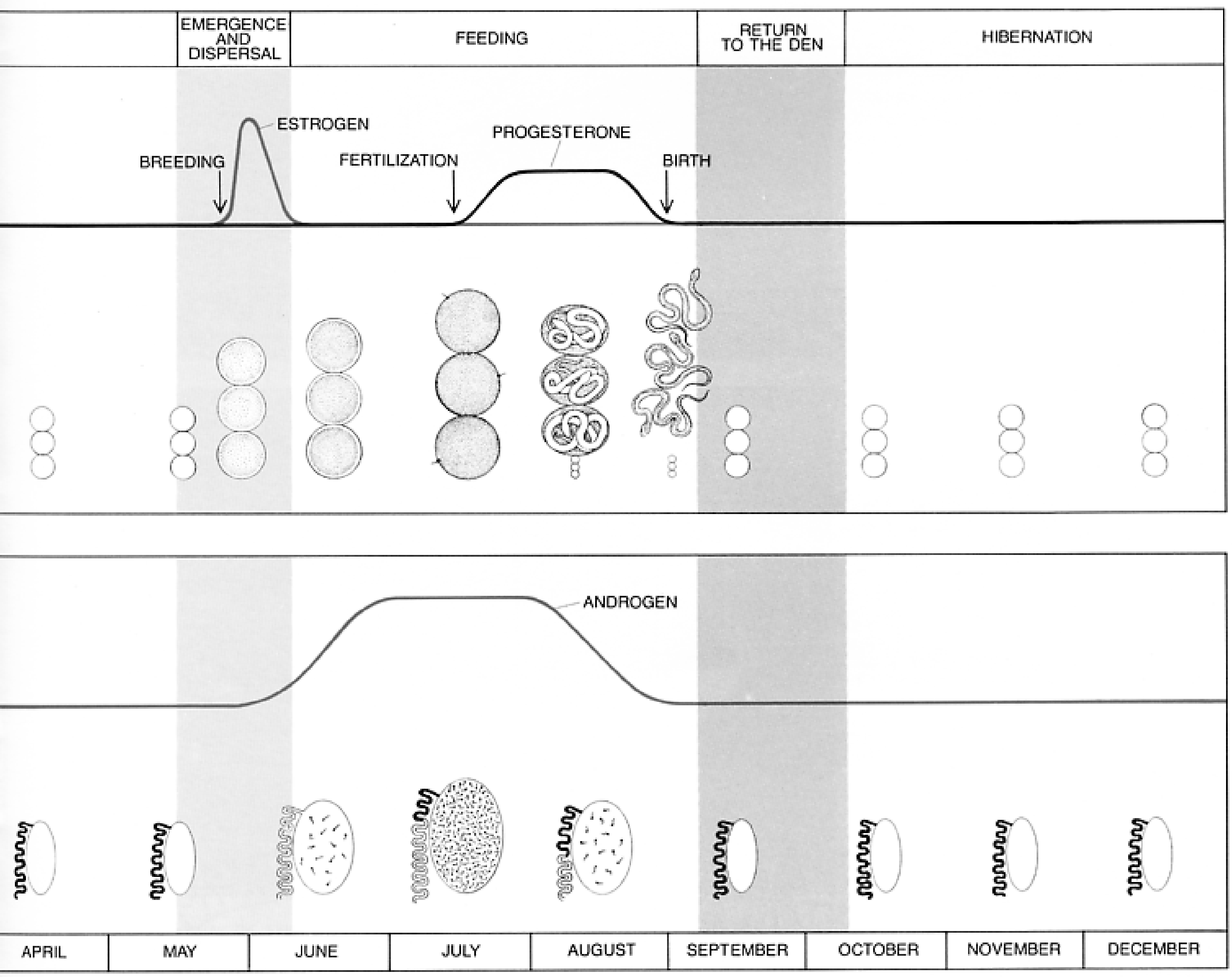
MISMATCH of physiology and behavior characterizes the reproductive behavior of the red-sided garter snake. From January through early May the snakes are in their den. In the female the blood level of the sex hormone estrogen is low, and the gonads (the ovaries) contain only small egg cells (follicles) lacking a

spring. When they catch a snake, they peck out its liver.

Although Wade Fox of the University of California at Berkeley reported nearly 30 years ago that garter snakes breed at a time when their gonads are collapsed, little has been made of the significance of the discovery. This is odd, because the discovery is startling. Almost all seasonally breeding vertebrate animals exhibit what is called a prenuptial pattern of gametogenesis: the sex cells are produced either during the mating season or just before it. In either case the sex cells are produced when the gonads are large and the sex hormones they manufacture are circulating in the blood at their highest level of the year. The sex hormones activate mating behavior. It has long been known, for example, that removal of the gonads typically causes a decline of reproductive behavior in both males and females, and that the administration of the appropriate sex hormone induces sexual behavior in sexually inactive animals and in animals from which the gonads have been removed.

Several studies of Temperate Zone lizards have revealed a similar prenuptial pattern. One might therefore assume that the control of mating behavior in garter snakes would also fit the pattern. This, it soon became clear, is not the case. Garter snakes (along with many other snakes and some species of turtles, fishes and bats) exhibit a postnuptial pattern of gametogenesis, that is, the gametes are produced only when breeding is over. In the male red-sided garter snake the testicles do not begin to grow until the end of the mating season. Over a period of six weeks the testicles attain their greatest size and the sperm they produce move into the duct called the vas deferens. There the sperm are stored until they are needed for mating the following spring. By the time the males enter the hibernaculum in the fall their testicles are fully regressed. When the males emerge in the spring, their testicles are still regressed, and their level of androgen, the male sex hormone, is low. If a male does not mate, the sperm he has stored disintegrate but his testicles begin to grow at the same time as those of males that have mated.

The female garter snake also follows a postnuptial pattern. When the female mates in the spring, her ovaries contain

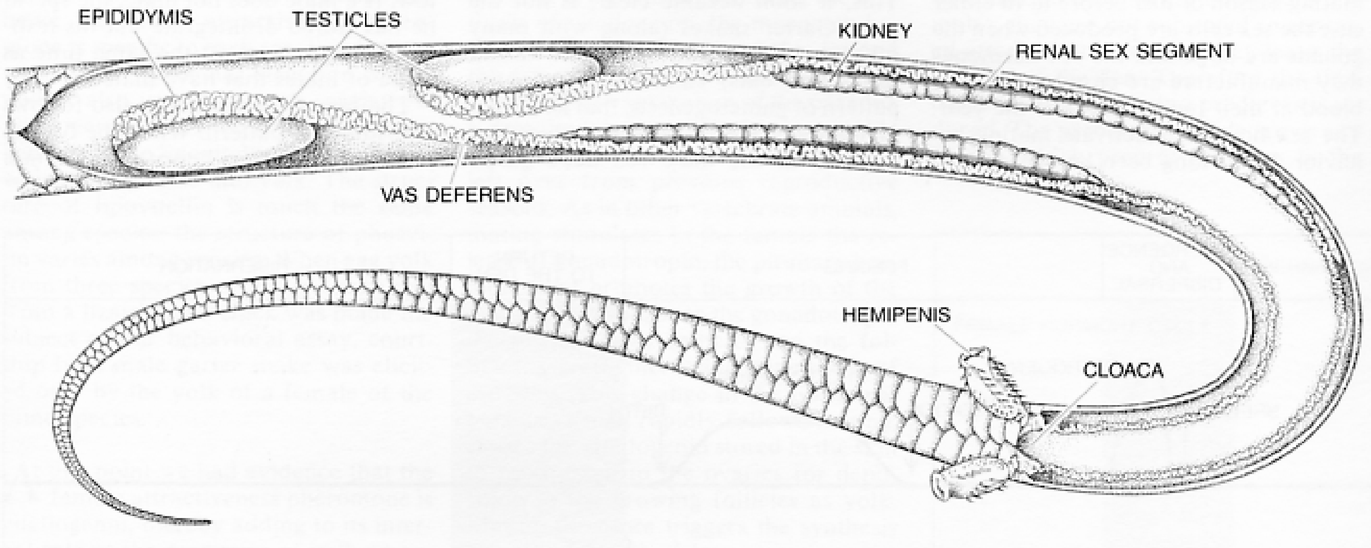


yolk. In the male the blood level of the sex hormone androgen is low, and the gonads (the testicles) are small. The male's vas deferens, or sperm duct, is packed with stored sperm. The snakes emerge and mate late in May. Thefr gonads are still small and their sex hormones are still at an ebb. Only after mating are changes observed. In the female the mating causes the level of estrogen to rise. In response the eggs grow large and are filled with yolk. In the middle of July the eggs are fertilized by sperm the female has stored for six weeks. Then the level of progesterone, the pregnancy hormone, rises. In the male the level of androgen starts to rise at a time when the females have left the vicinity of the den. During the summer the testicles grow large and produce the sperm the male will need the following spring. In August or early September the female gives birth, and by about the end of September both the male and the female have returned to their den.

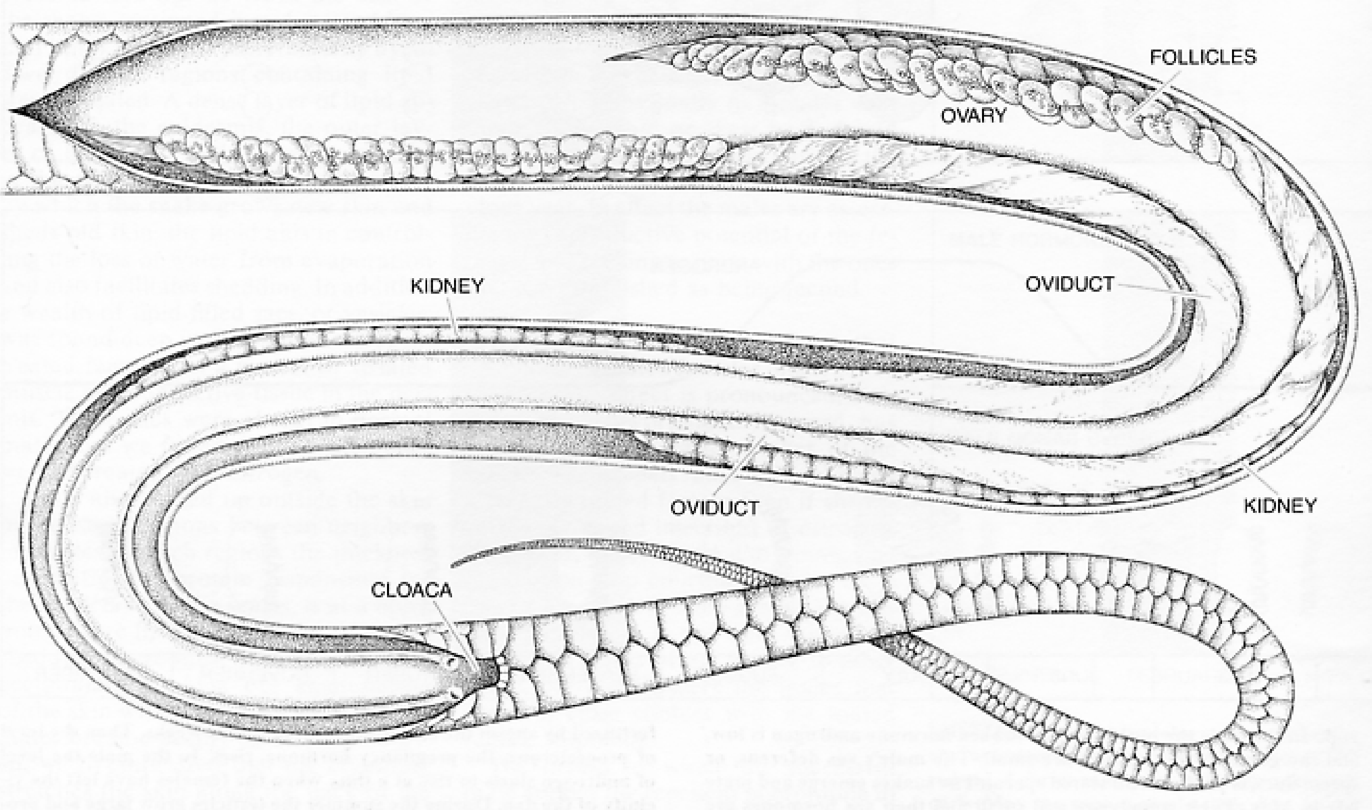
small follicles lacking yolk. It is the act of mating that induces the follicles to grow and fill with yolk. (In this we have confirmed a finding first made by Antonella Bona-Gallo and Paul Licht at Berkeley.) Working at Harvard, Andrew P. Halpert has discovered that the female stores sperm in specialized regions of the oviduct, the passage from the cloaca to the ovaries. After a period of from six to eight weeks the follicles are ready to be fertilized. Halpert also discovered that the spring mating initiates the degeneration and expulsion of all sperm remaining in the oviduct from the mating of the previous year. A similar displacement of old sperm by new has been reported in a variety of insects and rodents.

The organisms that exhibit postnuptial gametogenesis present intriguing questions. For example, how are the sexual activities of male and female garter snakes controlled without the hormonal changes that characterize prenuptial gametogenesis? The control cannot be exercised by the pheromones alone. If it were, the attractiveness pheromone could always elicit courtship behavior on the part of the male. Yet a male will not court females after the spring mating season until he has hibernated again.

In initial studies of the control of sexual behavior in garter snakes five males



REPRODUCTIVE ANATOMY OF THE MALE red-sided garter snake includes the epididymis, the segment of the vas deferens in which sperm is stored over the winter. It also includes the renal sex segment, the part of the kidney that makes the pheromone by which a mated female is rendered unattractive to males. Each hemipenis is a saclike organ the male everts to transfer sperm to the female.

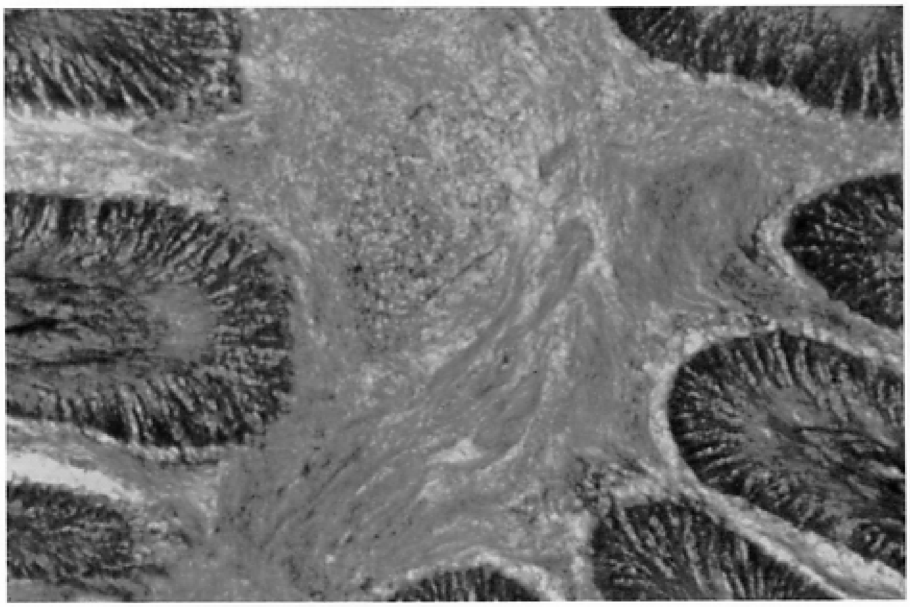


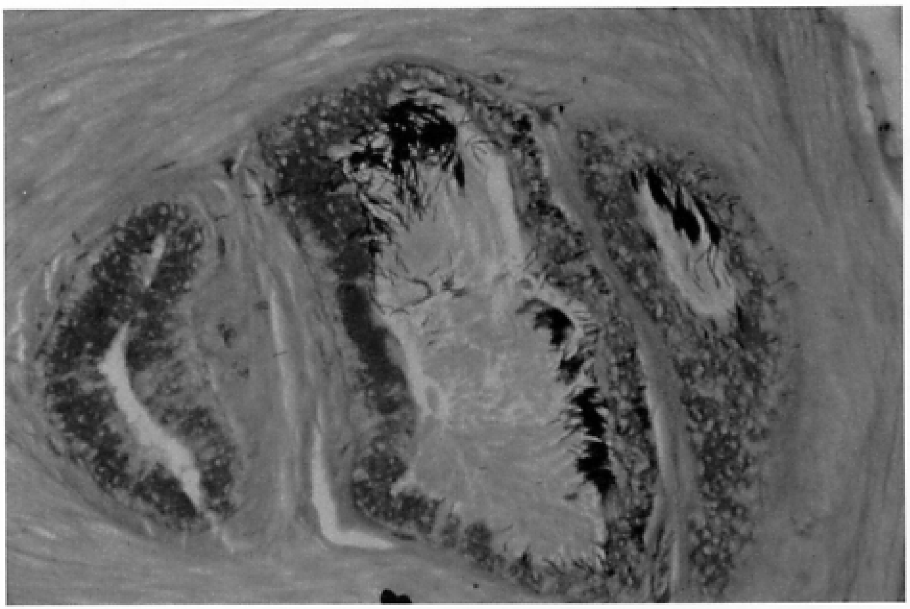
REPRODUCTIVE ANATOMY OF THE FEMALE red-sided garter snake includes the ovaries, which in the streamlined body of the snake are long files of follicles. The sperm the female gets by mating in the spring take some six weeks to travel the length of the oviduct and reach the developing eggs. Both the male and the female snake are shown approximately 1.5 times life size in these drawings.

were removed from hibernation and in each of them a slow-release capsule containing the androgen testosterone was implanted. Within four days all five of the males began to court estrogen-treated females. For seven days the males exhibited courtship behavior; then the capsules were removed and the courting stopped. The close correlation between the treatment and the behavior seemed highly suggestive. Correlation, however, is not causation. For one thing, working at Harvard, Brian Camazine discovered that males castrated soon after their emergence from hibernation, so that the testicles were no longer present and producing androgen, court females as actively as normal males do.

Then too it turned out that the administration of androgen does not induce courtship behavior in sexually inactive male red-sided garter snakes. At the time of the initial studies the snakes were in short supply, and so a control experiment in which males were simply removed from hibernation was not done. When the work was repeated with the proper controls, the untreated males showed courtship behavior. Apparently the testosterone capsules in the initial studies had been implanted at a time when the courtship behavior was about to begin and then the capsules had been removed at a time when the courtship behavior was ending.

The most conservative possibility that accords with these findings is that the brain mechanisms underlying male sexual behavior in the red-sided garter snake might be activated by androgen while the snake is hibernating. In favor of this hypothesis (or at least the possibility that something happening during hibernation promotes sexual behavior) we and Camazine have found that the longer the dormancy period, the more active the courting of the males. In order to test the hypothesis some males about to enter hibernation were castrated. Other males were castrated and a testosterone capsule was implanted; still others were merely opened surgically without being castrated. On emergence from hibernation all three groups exhibited intense courtship activity. In other words, the hypothesis was wrong.





SPERM STORED IN THE OVIDUCT of a female red-sided garter snake can be seen in stained sections of oviduct tissue. The oviduct in the micrograph at the top was removed from a female 10 days after she had mated in the spring. Purple dye marks the epithelial cells that line the oviduct; blue dye marks a mass of sperm that fills the central hollow of the duct. The oviduct in the micrograph at the bottom was removed from a female that was caught as she returned to her den in the fall. Here the heads of individual sperm are evident. The sperm are sequestered in side chambers of the duct. Mating the following spring would have caused them to degenerate and then to be expelled. The sperm embedded in the oviduct wall presumably were swept there by the microtome that sectioned the tissue. The micrographs were made at a magnification of 200 diameters by Andrew P. Halpert, working at Harvard University.

Is it possible that male mating behavior in the spring is primed by the elevated level of circulating androgen when the gonads are growing the previous year? To test this second hypothesis males were castrated when they were sexually active and thus before the postnuptial gametogenesis had begun. The males were then allowed to complete the breeding season and spend the summer feeding before they entered hibernation. Much to our surprise, these males too exhibited intense courtship activity when they emerged from the den the following spring.

The gonads of the male are not, however, the only source of androgen; the adrenal gland secretes it as well. Nevertheless, males that have had their adrenal glands and gonads removed when they emerge from hibernation continue to court females. By the same token males treated during hibernation with cyproterone acetate, a potent antiandrogen agent, court females when they emerge. It seems inescapable that male sexual behavior in the red-sided garter snake begins and then declines whether or not the glands that produce the male sex hormone are present.

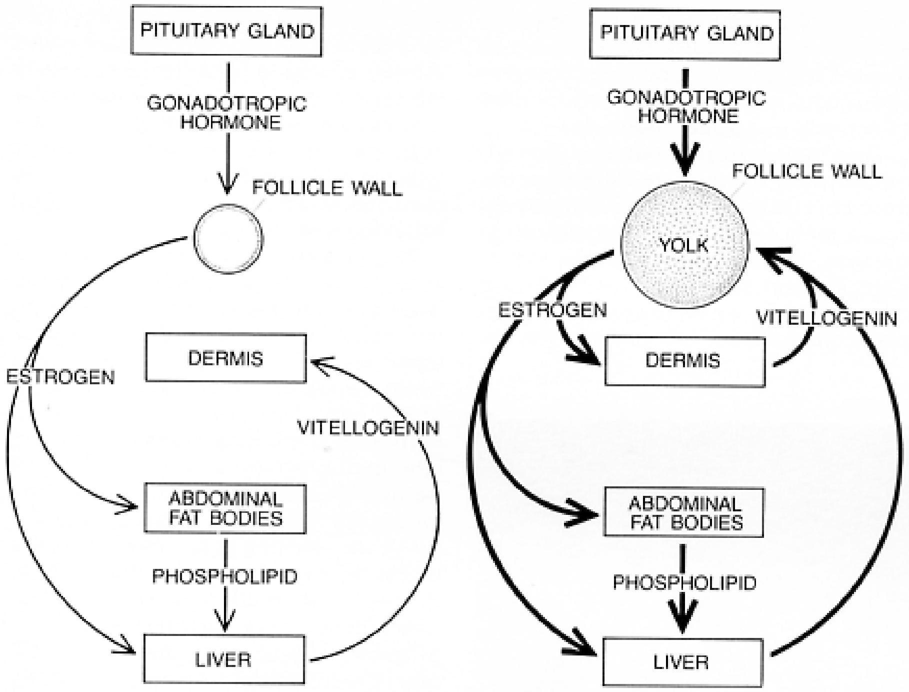
It was hypothesized next that in the red-sided garter snake the hormones secreted by the pituitary gland might control sexual activity by acting on the brain, in effect usurping the role of the hormones secreted by the gonads. Again the hypothesis was wrong. Males from which the pituitary gland had been removed before or during hibernation exhibited courtship behavior when they emerged. Conversely, males that were sexually inactive did not become active when they were treated with arginine-vasotocin, a pituitary hormone important in the regulation of sexual behavior in the rough-skinned newt.

While we were at it we tested some further possibilities. The administration of a variety of hormones synthesized in the brain, including luteinizing-hormone-releasing hormone (LHRH) and melatonin, had no effect on male garter snakes that were sexually inactive. The administration of dopamine, epinephrine, norepinephrine and serotonin, all substances by which nerve cells transmit signals, had no effect. The administration of thyroxine, glucose and various types of ions, all of whose level differs markedly in dormant garter snakes from that in active ones, had no effect.

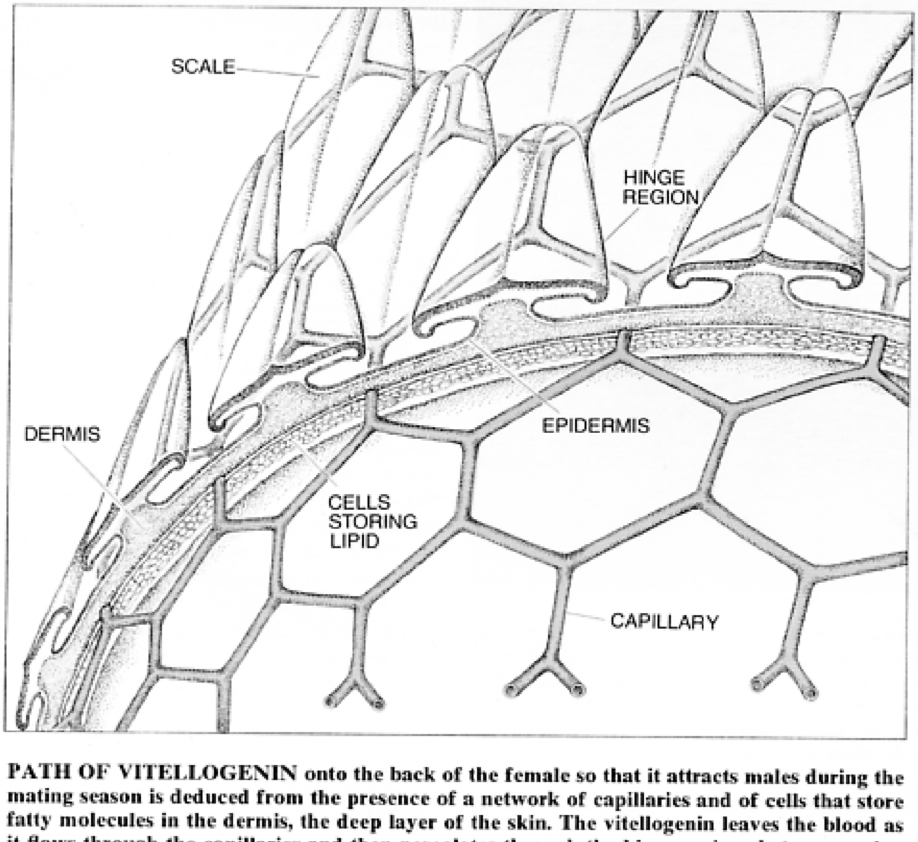
What, then, controls male sexual behavior in the red-sided garter snake? The answer is not yet known. Some recent studies, however, do provide a clue. It appears that if blood serum from a sexually active male is infused into a sexually inactive male, the inactive male will begin to court females within a few days. Serum from an inactive male, on the other hand, has no effect on another inactive male. Efforts are under way to find out exactly what it is in the blood that induces male courtship behavior.

The sexual behavior of the garter snake in the field and in the laboratory yields insight into the behavioral and physiological adaptations that suit an animal to its environment. In the case of the red-sided garter snake it is the springtime increase in temperature that makes the snakes emerge from their den and begin their precise yearly cycle of mating behavior and gonadal growth. Postnuptial gametogenesis allows them to mate as soon as they emerge from hibernation; at such times the population is concentrated and so mating is highly probable. Postnuptial gametogenesis also ensures that no energy is wasted by a female in growing eggs uselessly; she forms yolk only if she is inseminated.

In Mexico, where the range of temperatures throughout the year is not as great as it is in Canada and the indigenous garter snakes do not hibernate, we have found a somewhat different pattern. There the garter snake *Thamnophis melanogaster* has several mating seasons. Each pregnancy depletes the lipid stores of the female; at some point, however, the female regains enough weight so that her body redeploys on her skin substantial quantities of the attractiveness pheromone vitellogenin. In both the Canadian and the Mexican snakes a combination of behavior and physiology adapts the organism to its environment to promote the survival of the individual and the perpetuation of the species.



HORMONAL CHANGES induced in the female red-sided garter snake by mating in the spring may shunt the fatty substance vitellogenin from one role to another. Before mating (*left diagram*) gonadotropic hormone, which is secreted by the pituitary gland, causes the follicles in the ovary to secrete a modest flow of estrogen. In turn the estrogen causes the abdominal fat bodies of the female to release fatty molecules. It also causes the liver to incorporate the fatty molecules into vitellogenin. The vitellogenin is deposited (with other fatty molecules) deep in the skin. The authors propose that some of it gets onto the back of the female, where it serves as the pheromone that attracts males for mating. After mating (*diagram at right*) the pituitary gland responds to sensory signals to the brain that arise from the mating by secreting an increased quantity of gonadotropic hormone. In turn the ovaries secrete an increased flow of estrogen and the estrogen stimulates the liver to produce an increased flow of vitellogenin. The bloodstream carries vitellogenin from both the liver and the skin to the ovaries. There it becomes yolk of developing eggs, which will be fertilized by sperm the female has in her oviducts.



PATH OF VITELLOGENIN onto the back of the female so that it attracts males during the mating season is deduced from the presence of a network of capillaries and of cells that store fatty molecules in the dermis, the deep layer of the skin. The vitellogenin leaves the blood as it flows through the capillaries and then percolates through the hinge regions between scales.