Regulation of Seasonal Mating Behavior in *Thamnophis sirtalis parietalis*

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At latitudes of about 50°–55° N in Manitoba, Canada, the red-sided garter snake (*Thamnophis sirtalis parietalis*) hibernates in concentrated aggregations of several thousand individuals and mates shortly following emergence in late April or early May. Mating is most intense when air temperatures are above 15 C, and lasts about 4 weeks.

Mating activity of about 10 days duration can be induced in the laboratory by: 1) collecting snakes at the hibernaculum site in September, subjecting them to 5 C, 0L24D for at least 4 months and then transferring them to 25 C, 12L12D; and 2) collecting snakes at the hibernaculum site in late April or early May, holding them at 5 C, 0L24D, and transferring them to 25 C, 12L12D at any time until August. Food intake is completely inhibited for 3 days following the transfer, and then increases progressively in an inverse relationship to declining mating activity. A transfer from 5 C, 0L24D to 5 C, 12L12D does not result in mating. On the basis of these experiments we hypothesize that the increase in body temperature experienced by the red-sided garter snake during emergence from hibernation induces the intense mating activity observed shortly following emergence.

The evolution of precisely-timed seasonal reproductive cycles is a fundamental aspect of the adaptation of animal populations to northern environments. The timing of events in such cycles is usually regulated by environmental control factors that act as "Zeitgebers" or "time-givers" for the reproductive system (Bullough, 1965; Farner, 1964; Licht, 1971; van Tienhoven, 1968). The elucidation of seasonal organization in reproductive cycles, and the factors that regulate it, is essential to an understanding of how reproduction is successfully accomplished at northern latitudes.

The red-sided garter snake (*Thamnophis sirtalis parietalis*) is the most northerly occurring reptile in North America (Logier and Toner, 1961). In terms of numbers and distribution, it is the most successful reptile existing under the extreme climatic conditions (bordering on subarctic) of central Canada. At these latitudes, extreme seasonal changes in the environment undoubtedly represent a major evolutionary force moulding the characteristics of the population (Aleksiuk, 1970, 1971; Aleksiuk and Stewart, 1971). The entire life history of the population, including reproduction, is highly seasonal in nature. Mating activity occurs shortly after emergence from hibernation in late April or early May, and birth of young apparently occurs shortly prior to movement of snakes to over-wintering sites in late August (Gregory, 1971). Clearly, the timing of reproductive events is a critical factor in the success of the population. We have initiated a series of studies on aspects of seasonal reproduction, and the environmental regulation thereof, in this cold climate population of *Thamnophis sirtalis parietalis*. The purpose of this paper is to document the seasonal mating behavior characterizing the population, and to demonstrate experimentally that the increase in body temperature occurring during emergence from hibernation is the most probable factor that triggers mating behavior in the spring.

Methods

Field observations.—Observations of mating behavior in the field were made at a large hibernaculum (referred to as Den #1 by Gregory, 1971) during the spring and fall seasons of 1970, 1971 and 1972. The terms hibernaculum and den will be used interchangeably in this paper. Den #1 is located in the Interlake region of Manitoba (elevation 260 m), about 21.7 km northwest of Teulon and 19.3 km south of Narcisse. It consists of a large, oval-shaped limestone sink about 7.5 m in length by 4 m in width and is well fissured, providing the snakes with access to underground spaces. A more detailed description of the hibernacula used by this population, as well as details of the life history of the population, are provided by Aleksiuk and Stewart (1971). Several other dens are located in the vicinity of Den #1, and observations of mating activity were also occasionally made at these. The activity of snakes at Den #1 was recorded nearly every day, leading to observations of a qualitative nature. Similar records were kept for the den in the autumn of each of the three years. In addition, some preliminary dissections were made to determine the presence or absence of spermatozoa in female reproductive tracts during the field season of 1972.

Laboratory experiments.—Garter snakes used in most of the experiments were obtained from a hibernaculum near Narcisse, Manitoba on 8 May 1972. The weather at the time of collection was sunny and warm (about 22 C), and consequently the snakes had been exposed to relatively high temperatures for 1 or 2 hrs. The hibernaculum had been checked on 1 May 1972, at which time spring emergence was not yet in progress. Mating activities were fairly intense at the time of collection on 8 May. Five hundred garter snakes were collected in cotton bags (100 per bag) and placed in a controlled environment room at 5 C, 0L24D within 2 hours of collection.

Each major experiment involved the transfer of 50 randomly selected garter snakes, plus 5 known males and 5 known females, from 5 C, 0L24D to a fiber-glass observation tank (75 cm deep and 130 cm in diameter) at 25 C, 12L12D. Wood shavings were placed in the tank to absorb excretions, and water was always made available. Food, in the form of ocean perch fillets diced into 1 cm cubes, was offered daily and the consumption measured. Observations of behavior were made continuously from 0830 to 1630 of each day, from the time of transfer until all evidence of mating behavior disappeared. In particular, the number of mating groups (Fig. 2) during the observation period of each day was noted. The temporal pattern of moulting was determined by recording the number of skins shed each day.

Repetitions of the above procedure using the 8 May 1972 sample of snakes, as well as similar transfers using other snakes, were performed and will be described in the results section.

Results

Emergence from hibernation and mating behavior under natural conditions.—Considerable variation existed among dens in the timing of first spring emergence, probably due to variations in the local topography of each den site. Dens in areas well exposed to the sun became active as early as mid-April, while more protected dens became active as late as mid-May. Individual dens, however, were fairly consistent from year to year. For example, snakes were first observed at Den #1 on 25 April in 1970, 15 April in 1971 and 18 April in 1972. Mating was first observed on 29 April, 22 April and 2 May in 1970, 1971 and 1972 respectively, while the periods of most intense mating activity in the 3 years were 7–28 May, 29 April–16 May, and 7–10 May. The dates of last observed mating were 2 June, 1 June and 26 May respectively. In all 3 years snakes were seen at the den for a few days after mating had apparently ceased.

The intensity of mating activity was quite variable. In both early and late spring, it was sporadic in nature, depending primarily on weather conditions. Even during the mid-spring period of intense activity, it ceased entirely in cold, cloudy weather. Mating activity was most intense on warm, sunny days, but courtship was observed twice at air temperatures as low as 4.5 C, albeit at an extremely low level. Early in spring, mating took place mostly in direct sunlight, but later on, as daily maximum temperatures increased, it occurred in the shade as well.

The major feature of mating activity was the formation of mating groups or "balls." Such groups consisted of close aggregations containing one female and varying numbers of males, possibly up to 100 on occasion but usually 30 or fewer. All the males in these groups were apparently attempting to mate with the single female. Fig. 1 shows one such aggregation, consisting of three males entwined around one female, suspended in the air by hand. The aggregations usually existed as individual entities for 5–10 min, dispersing after copulation had presumably occurred. In the early and late spring, isolated mating pairs were observed, but these were infrequent. Mating almost invariably occurred within the den

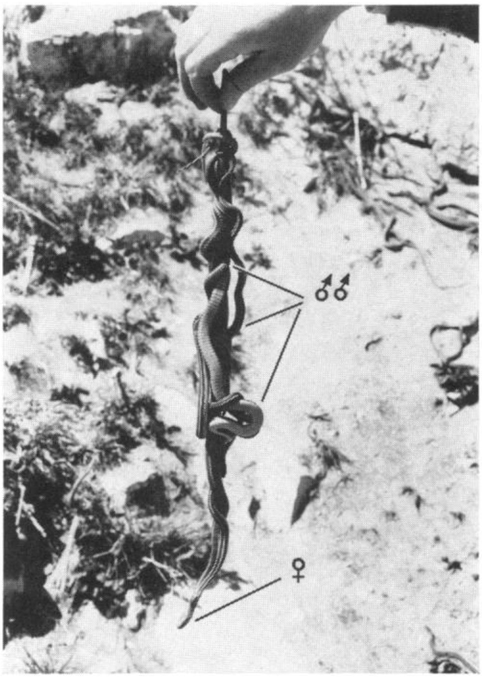

Fig. 1. An example of small mating group of red-sided garter snakes (*T. s. parietalis*) photographed at the site of a hibernaculum on 8 May 1972, less than one week after emergence from hibernation.

proper, but in two instances in late spring when snakes were dispersing, a mating "ball" was seen 10–15 m from the den. On warm days in mid-May most dens are strewn with large mating groups, constantly moving and changing in shape and size.

The mating response was observed to be very strong, especially in mid-spring. On one occasion, a group of males attempted to copulate with a dead female. Males also actively chased females, even up into small trees and bushes where mating balls were sometimes formed. Recently emerged and half-emerged females, still cold and torpid, were immediately courted. Active mating groups attracted males from all directions. Catching males was simplified by removing a female to the den margin, holding her there, and picking up all males attracted to the spot. In a few instances, males were seen to pursue other males that had recently been in proximity with a female, and mating balls lacking females were occasionally observed.

A total of 10 instances of apparent mating or pre-mating behavior were recorded at Den #1 in the autumn seasons of 1970, 1971 and 1972. These varied in degree from 1 occurrence of a male pursuing a female, to five instances of actual mating. Of the latter, four were isolated pairs and one was a small group. The earliest instance of fall mating behavior was noted on 30 August in 1971 and the latest on 24 September, also in 1971. Most of these observations were made in sunny and/or warm weather.

Evidence of late summer or fall mating was derived from 2 other sources. On 18 and 26 August 1971 and 4 August 1972, single females possessing copulatory plugs were found, indicating recent mating. All were found away from dens. In addition, 27 out of 111 females (24.3%) collected between 30 July and 8 October inclusive in 1972, had spermatozoa in at least one oviduct. All of these females were beginning at least their second year of life, based on age-size categories as defined in Gregory (1971). A sample of 33 similar females collected away from dens between 28 April and 6 June inclusive yielded 21 individuals (63.6%) with sperm in at least one oviduct. No females in a similar sample of 33 non-gravid specimens collected away from dens between 6 June and 30 July 1972 contained sperm.

Experimental induction of mating behavior by an increase in temperature.—In the course of conducting related studies in the laboratory, we observed that the transfer of garter snakes from 5 C, 0L24D to conditions of room temperature and 8L16D was followed by several days of copulatory behavior. These observations led to the hypothesis that a change in environmental conditions from cold and dark (hibernating conditions) to warm and light (immediate post-hibernating conditions) triggers the sequence of mating activities observed at den sites immediately upon emergence of garter snakes from hibernation.

The first major experiment designed to test this hypothesis was initiated on 15 May 1972, using garter snakes that had been collected in the field on 8 May 1972 (see Methods) and held at 5° C, 0L24D continuously. A group of 60 individuals, consisting of 5 known males, 5 known females, and 50 randomly selected snakes, were used. Observations were made continuously from 0830 to 1630 daily, during which the number of mating groups (Fig. 2), was determined. Transfer from 5 C, 0L24D to 25 C, 12L12D

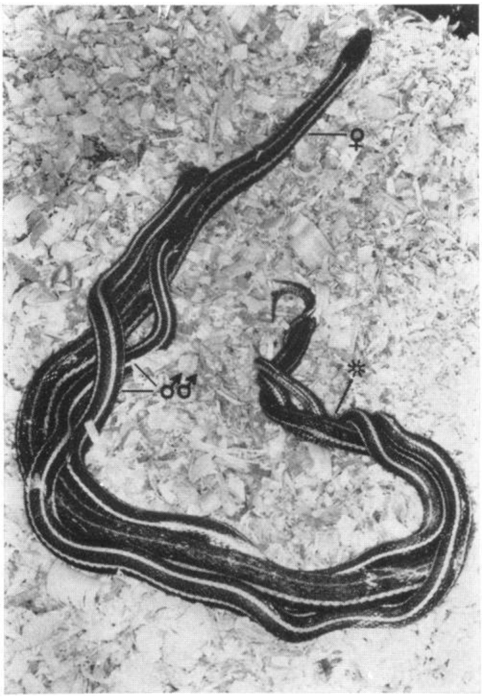

Fig. 2. A typical example of a mating group of red-sided garter snakes (*T. s. parietalis*) following experimental induction of mating behavior in the laboratory by transfer from 5 C, 0L24D to 25 C, 12L12D. The asterisk points to the placement of each male's vent in juxtaposition to the vent of the female.

was followed by immediate dispersal of snakes in the observation tank. Males began pursuing females within about 10 minutes of the transfer, and the first discrete mating groups, of the type depicted in Fig. 2, were noted within 20 minutes. The first copulation occurred within one hour. The temporal pattern of mating activity, as reflected by the number of mating groups observed per day, is depicted in Fig. 3. Mating activity remained at a high and fairly constant level for 3 days following the transfer, and then decreased steadily to day 10, when it ceased. Food intake first occurred on day 4, increased in an inverse relationship to the declining mating activity, and plateaued on about day 10 (Fig. 3). Moulting began on day 15 following the transfer and was complete on day 19. The entire experiment was repeated on June 12 and on July 17, again using garter snakes that had been collected on 8 May 1972 and held continuously at 5 C, 0L24D. In each case, results similar to those of the 15 May experiment (Fig. 3) were obtained.

Snakes were collected in the field in early September, 1971 and maintained in the laboratory at 5 C, 0L24D throughout the winter. Individuals from that sample were transferred to 25 C, 12L12D in February, 1972 and April, 1972. In both cases, the transfer resulted in the onset of intense mating activity. Individuals collected in early September, 1972 and held at 5 C, 0L24D did not exhibit mating behavior when transferred at 25 C, 12L12D on 11 October 1972. However, similar transfers on 14 November 1972 and 10 January 1973 did induce mating behavior, although it was not as pronounced as that observed in spring transfers. A transfer in late January, 1973, resulted in intense mating activities. Other snakes collected in September, 1971, and held at 25 C, 12L12D throughout the following winter and spring, were not observed to mate at any time.

Two consecutive experiments were performed on one group of snakes to explore the possible role of light in the induction of mating behavior. The first experiment involved the transfer of 20 males and 10 females (collected on 8 May 1972) from 5 C, 0L24D to 5 C, 12L12D on 17 May 1972. Although snakes are capable of only slow movements at this low temperature, at least a partial response might be expected if light plays a role in triggering copulatory behavior. No evidence of pre-copulatory or copulatory behavior was observed during 2 weeks of exposure to 5 C, 12L12D. This group of snakes was transferred from 5 C, 12L12D to 25 C, 12L12D on 1 June 1972. Copulation occurred within one hour of this transfer. Copulatory behavior followed a temporal pattern similar to that depicted in Fig. 3. These 2 experiments were repeated in late June, 1972, with identical results.

The strength of the copulatory response under natural field conditions is evident in Fig. 1. In spite of the fact that the female in the photograph was picked up by hand, the mating group consisting of the female and 3 males remained intact. The strength of the response was further demonstrated by the following experiment in the laboratory. Six females from the group collected on 8 May 1972 were killed by freezing at –20 C, warmed to 25 C, and presented respectively to 6 different males freshly transferred from 5 C, 0L24D to 25 C, 12L12D. All 6 males

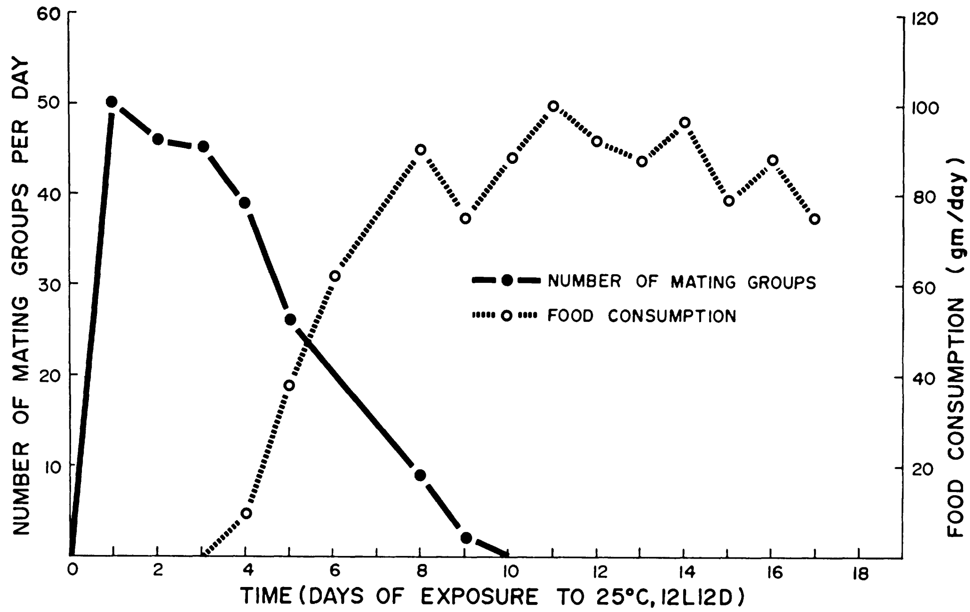

Fig. 3. Temporal patterns of mating activity and food intake following transfer of 60 red-sided garter snakes (*T. s. parietalis*) (5 known males, 5 known females, plus 50 randomly selected individuals) from 5 C, 0L24D to 25 C, 12L12D on 15 May 1972 (day 1). The snakes used in the experiment were collected at a natural hibernaculum on 8 May 1972, and held at 5 C, 0L24D until 15 May.

immediately (within 15 min) entwined themselves around the respective females, as illustrated in Fig. 2, and in 2 of the 6 cases copulation occurred between the live male and the dead female. As well as demonstrating the strength of the copulatory response, this experiment suggests that the behavioral role of the female during copulation is minor. This passive role of the female is supported by the observations of Blanchard and Blanchard (1941b).

Discussion

According to Fitch (1970), mating in *Thamnophis sirtalis* ". . . may occur in the fall or in spring but is especially concentrated in the first few warm days after spring emergence. . . ." His statement is based on studies in the United States, in regions where the climate is warm temperate. In the population of *Thamnophis sirtalis parietalis* examined in the present study, which is subjected to a cool temperate climate, the major period of mating clearly occurs in the spring during the first 4 to 5 weeks following emergence from hibernation. Indeed, mating is by far the most dominant feature of spring activity in this population.

Blanchard and Blanchard (1941b) have outlined the courtship and mating behavior of *T. s. sirtalis* in Michigan, and Munro (1948) has briefly noted that of *T. s. parietalis* from Arkansas. Blanchard and Blanchard alluded to mating aggregations similar to those described in this paper, and mating groups or "balls" have also been described for other forms of *Thamnophis* (Finneran, 1949; Fox, 1955; Gardner, 1955, 1957). In courtship, males apparently recognize females by odor (Fitch, 1965; Noble, 1937). The observations reported in this paper strongly suggest that odor is important. The odor of receptive females probably plays a major role in the formation of mating groups consisting of one female and several to 100 males.

Blanchard and Blanchard (1941b) found that copulation in *T. s. sirtalis* occurs in sunny weather when the air temperature is above 15.5 C. They also state that in early spring, unconsummated courtship is common at lower temperatures. In this study, courtship was observed at least twice when air temperatures were between 4.5 and 7 C and the sky was partly cloudy, although actual copulation was not observed. According to

Vincent (1971) the garter snakes under study are capable of maintaining a body temperature of at least 25 C when the air temperature is 12 C and the sky is partly cloudy. Therefore, rare instances of mating activity at air temperatures of 4.5 to 7 C are not unexpected. However, mating activity in this population does normally take place only when air temperatures are above about 10–15 C.

Evidence based mainly on mark-recapture studies (Gregory, 1971) suggests there is differential behavior between the two sexes with respect to spring breeding activities in this population. After mating, the females apparently leave the dens for their summer habitat, while the males remain at the den for a variable number of days and copulate with unmated emerging females. This is consistent with the observation of Blanchard and Blanchard (1941b) that males of *T. s. sirtalis* generally mate several times, whereas females become intolerant of courtship after mating.

The importance of the relatively few instances of late summer and autumnal mating behavior observed in this study (a total of 10 in 3 years) is not clear. Fall mating, however, was recorded frequently by Blanchard and Blanchard (1941a, b) and is common in *T. s. tetrataenia* (Fox, 1954). Although we have observed spermatozoa in the reproductive tracts of females in August, September and October, we are uncertain when such spermatozoa fertilize eggs or indeed if they do at all. The absence of sperm in females in early summer indicates that matings in these instances did occur in late summer or fall. Blanchard and Blanchard (1941a, b) suggest that in such cases the sperm "hibernate" with the female and fertilize eggs the following spring. This is apparently fairly common in snakes (Rahn, 1940, 1942; Trapido, 1940). The significance of the difference between the figures of 63.6% (spring) and 24.3% (late summer and fall) for females containing sperm cannot be assessed at present because the reproductive status of most of the specimens examined and its effect on mating behavior are unknown.

On the basis of our field observations and laboratory experiments, we conclude that a change in environmental conditions from cold and dark to warm and light during emergence from hibernation triggers mating behavior and copulation immediately following emergence. Furthermore, we hypothesize that the change in temperature is the primary environmental factor involved in the regulatory process. Deep ground temperatures at the sites of hibernacula are near freezing at the time of emergence, as evidenced by ice and snow in crevices and fissures. Air temperatures, on the other hand, are often as high as 22–24 C. During the first few minutes after appearance on the ground surface, snakes are cold and torpid. However, body temperatures of up to 25 C and higher are attained rapidly, particularly if the sun is shining. This, in turn, is followed by intense mating activity. A similar transition in body temperature under controlled laboratory conditions results in pursuit of females by males within 10 min, and copulation within an hour. The similarity of mating groups artificially induced in the laboratory (Fig. 2) to those occurring naturally in the field (Fig. 1) is striking. Fitch (1965) removed cold, torpid garter snakes from an artificial hibernaculum in March and observed intense copulatory activities one hour after the snakes had reached a body temperature of about 20 C. In the present study, transfer of garter snakes from 5 C, 0L24D to 5 C, 12L12D did not result in mating behavior, although it was followed by considerable locomotory activity. This suggests alteration of light conditions alone does not trigger mating behavior, but extensive experimentation will be necessary to test this hypothesis.

The population of *T. sirtalis parietalis* under study is characterized by inherent seasonal changes in metabolism (Hoskins and Aleksiuk, 1973). This inherent rhythmicity raises the possibility that the timing of mating activities in the spring may also result from an inherent seasonal rhythm. That is, perhaps high temperature results in mating only because it permits intense muscular activity (although movement occurs at low temperatures, garter snakes become "torpid" below about 3 C). However, the laboratory experiments demonstrate that the role of a possible inherent seasonal rhythm is negligible, if indeed it exists at all. The normal time of mating in the population is May. In the laboratory, we have been able to artificially induce mating behavior from mid-November (late autumn) to early August (late summer) of a given biological year.

A factor that imposes a temporal limit on the environmental induction of mating is the apparent prerequisite "cold conditioning" period. According to our studies, snakes collected in early September must be subjected to 5 C, 0L24D for up to 8 weeks before a transfer to 25 C, 12L12D will induce mating behavior, and for up to 14 weeks before intense mating can be induced. Apparently, important preparative physiological changes occur during that "conditioning" period. Alternatively, the autumn may represent an inherent refractory period. In either case, the effect may represent a mechanism of preventing extensive autumnal mating and promoting early spring mating.

In view of the results of our experimental studies, the occurrence of some fall mating in the population is perplexing. The fall mating behavior actually observed was extremely minor in comparison to the spring mating. In a study of *Thamnophis sirtalis sirtalis* in southern Michigan, Blanchard and Blanchard (1941b) noted that fall mating occurred particularly on warm days following periods of cold weather. Their results are suggestive of a thermal induction of mating following a "cold conditioning" process, similar to the situation in *Thamnophis sirtalis parietalis*. Although we have no weather data for our study area, the occurrence of some late summer and fall mating in our population may be owing to similar weather patterns. Alternatively, some or all of the fall matings we observed may be the result of genetic or physiological variation in the population.

Food intake does not occur during the first three days following a transfer from 5 C, 0L24D to 25 C, 12L12D in the laboratory. The observed temporal pattern of food intake (Fig. 3) is not related to a possible initial rejection and subsequent gradual acceptance of a new food item. Ocean perch, the food material used, is consumed within minutes by non-mating garter snakes that have never been in contact with the item previously. In agreement with the laboratory results, food intake does not occur during the spring mating period under natural field conditions (Gregory, 1973). This suggests that appetite is inhibited during intense mating activities. This inhibition of appetite may play a role in keeping male snakes at the hibernaculum site during the mating period. Individuals are in poor nutritional condition following the extended period of hibernation (Aleksiuk and Stewart, 1971) and theoretically would be expected to search for food upon emergence. An inhibition of appetite may function to prevent that, and thus to focus activities exclusively on mating. The inverse relationship between mating activity and food intake suggests the factor responsible for the inhibition of mating is also the factor that stimulates food intake. That factor may be an environmental one, such as continued exposure to high temperature or light, or an intrinsic one, such as a change in testosterone levels.

The duration of the mating period following a cold-warm transfer in the laboratory was about 10 days, while under natural field conditions the mating period at any particular hibernaculum may last up to 4 weeks or more. In the laboratory, garter snakes were subjected to 25 C continuously following transfer, and to 12 hrs of light during each day. In the field, on the other hand, individuals are subjected to such conditions only intermittently. Garter snakes are usually observed to be active above ground during periods of sunshine and relatively high temperatures; during periods of cool, cloudy weather they presumably return underground into the hibernaculum. Therefore, although it varies from year to year, garter snakes are subjected to high temperatures and light for an average of perhaps 4–6 hrs per day during the 4–5 week mating period. If continued exposure to high temperatures or light, or both, regulates the duration of the mating period, the disparity between the laboratory and field observations can be readily explained on the basis of different exposures to the hypothesized regulatory factors.

In the population of *Thamnophis sirtalis* under study, development of mature spermatozoa and at least partial development of mature follicles occur in late summer, prior to entrance into hibernation (Gregory, 1973). A similar pattern of spermatogenesis characterizes other populations of *T. sirtalis* (Fox, 1954). In terms of their gametes, males are apparently prepared for mating at the onset of hibernation. Therefore, the induction of mating behavior by exposure to high temperature and light following a period of exposure to cold and dark represents an effective and adaptive mechanism of timing copulation to the early spring period. The change in environmental conditions that occurs during the actual process of emergence from hibernation triggers the onset of mating activity. By means of this mechanism, mating is precisely timed to a specific portion of the year. This is an important feature in the highly organized seasonal life histories of northern populations. A second adaptive quality of the mechanism relates to the fact that this population hibernates in aggregations of up to several thousand individuals. The timing of mating behavior to a portion of the year when the entire adult population is organized into immense and concentrated aggregations increases the probability that the majority of receptive females will be fertilized. Thirdly, if a considerable amount of mating occurred in the autumn, as it often does in more southerly populations, stored energy reserves remaining at the onset of hibernation might be insufficient for the extended hibernation period (up to 7 months in this population). Mating activities are extremely intense, particularly in males, and undoubtedly a great deal of stored energy is expended in the process. Even without fall mating, individuals are in very poor nutritional condition in the spring (Aleksiuk and Stewart, 1971). Individuals that mate in the fall may not survive the winter and thus may be selected against.

This paper demonstrates only that exposure to high temperatures and light during spring emergence induces mating behavior in *Thamnophis sirtalis parietalis* immediately following the prolonged hibernation period. A number of questions concerning the details of this regulatory process remain to be answered. We are continuing our research into this subject.

Acknowledgments

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Reproductive Ecology of the Florida Scrub Lizard, *Sceloporus woodi*

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Reproduction and growth of *Sceloporus woodi* in the Ocala National Forest, Florida, were studied. Females become sexually mature in their second warm season at 47 mm snout-vent length. Large females begin vitellogenesis in late February and deposit eggs by mid-April. Egg deposition continues thru August. Average clutch size is about four eggs. There are multiple clutches; and the first is larger than the second. Clutch weight averages 19% of total body weight.

Hatchlings appear from late June–early November and grow to adult size in 10–11 months. However, yearling females contribute less than half of the replacement rate of the population.

Population density is higher and frequency of regenerated tails is lower than in Texas *undulatus* studied by Tinkle and Ballinger. Since clutch size in *woodi* is smaller, both in number of eggs and % of female body weight, *woodi* appears less r-selected than Texas *undulatus*.

SCELOPORUS woodi, endemic to the sand-pine scrub of peninsular Florida, received scant attention until recently. Jackson (1973a), in treating the geographic distribution and variation, cites the early work. This paper reports on reproduction and growth in a northern population of *S. woodi*.

MATERIALS AND METHODS

Samples of varying size were collected at irregular intervals from 1968–1972 in the large continuous sand-pine scrub of the Ocala National Forest in Marion and Lake Counties, Florida. This is the northernmost population of the lizard. The calendar period covered by the collections was 27 February–6 November; individual *woodi* can be found active during the winter months, but large samples are not readily obtained.

One-hundred and fifty males and 170 females were autopsied after preservation to determine reproductive condition. Length and width of the right testis were measured by ocular micrometer, and testis volume was calculated as by Mayhew (1963). In females, the number and size of unyolked ovarian follicles, yolked ovarian follicles, oviducal eggs, corpora lutea and atretic follicles were recorded. All were measured by ocular micrometer except oviducal eggs, for which calipers were used.

Additionally, estimates of population density and predation pressure were made for *S. woodi* to allow comparison with *S. undulatus* studied by Tinkle and Ballinger (1972). Density was estimated by attempting to collect all the *woodi* in eleven separate 0.4 hectare plots during late April. The plots were chosen to be similar in plant cover to the areas that yielded *woodi* for reproductive examination. Areas densely shaded by sand-pine were avoided. Obviously this method provides only a minimum estimate because all resident lizards would not be encountered in a single search. Predation pressure was measured indirectly by the percentage of regenerated tails.