THE BREEDING HABITS OF THE MOLE SALAMANDER, *AMBYSTOMA TALPOIDEUM* (HOLBROOK), IN SOUTHEASTERN LOUISIANA[1]

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Various aspects of the breeding habits of several ambystomatids[2] in the northern United States have been described. Knowledge of the reproductive activities of the species of *Ambystoma* endemic to the Southeast remains fragmentary. Only the eggs and time of breeding of *Ambystoma talpoideum* have been described. Much of the literature dealing with the mole salamander reports only the occurrence of the form in one or more localities.

In the region studied, freezing temperatures are infrequent, and seasonal variations of moisture limiting the activity of salamanders are less pronounced than those in most other parts of the country. Studies of the behavioral and ecological isolating mechanisms, of which courtship patterns may be a part, of the sympatric species of *Ambystoma* in the Southeast are needed to understand better their phylogenetic relationships. The purpose of this study was to obtain detailed information of the breeding behavior of *Ambystoma talpoideum* in southeastern Louisiana.

Studies of the breeding habits were conducted both in the field and in the laboratory from October, 1957, through March, 1959. Occasional visits were made to the field area during the winter of 1959-60.

Materials and Methods

Juvenile and adult *Ambystoma talpoideum* were collected by seining and dip-netting in ponds and ditches and random turning of sticks, logs, paper, and boards on land. Immediately before ponds filled with water, adults in breeding condition were captured by raking the moist floor of the pond depression by hand. During the breeding season of 1959-60 specimens were collected with the aid of a 230 V. AC electrical shocker. This was the most efficient method of collecting.

Two standard temperature readings were made during each visit to the breeding ponds: (1) air temperature 1 meter above the surface, and (2) water temperature (water 10 cm in depth). When specimens were found on land, ground surface temperatures were recorded at the exact location of capture.

A United States Weather Bureau Cooperative Observer Station, at Slidell, St. Tammany Parish, Louisiana, close to the study area, provided useful climactic and weather data.

Measurements of total length, body length, and tail length were made with the aid of vernier calipers. An ocular micrometer on a dissecting microscope was used for measurement of eggs and spermatophores.

The distance from the tip of the snout to the posterior end of the cloacal aperture constitutes the body length; tail length is the distance from the posterior end of the vent to the tip of the tail. Each measurement is estimated to be accurate within 1.5 mm.

Specimens collected during the 1957-58 breeding season were killed in ten percent formalin before hardening and preservation. Those collected and preserved during the 1958-59 and 1959-60 seasons were killed in ten percent isopropyl alcohol before preservation. All specimens were hardened and preserved in eight percent formalin. Representative series collected during this study have been placed in the Tulane Collections.

The ovaries of gravid females consist almost entirely of mature ova. Counts of ova were made in excised ovaries. The ova were carefully teased from the ovary, counted with the aid of a hand tabulator, and deposited in the Tulane Collections.

Night observations were made with the aid of bright and dim flashlight illumination, both in the field and in an outdoor concrete pit on the Tulane campus. The entire courtship activity was observed using a dim

[1] Awarded the Stoye prize as the best student paper in Herpetology at the 40th annual meeting of the American Society of Ichthyologists and Herpetologists.

[2] For usage of the emended Ambystomatidae rather than the conventional Ambystomidae, see Tihen (1958:1 footnote).

flashlight, the lens of which was covered by red cellophane simulating the photographer's red light used by many authors in observing the courtship dances of salamanders (*cf* Kumpf and Yeaton, 1932).

A single natural study area was utilized for this investigation. It is designated "Siren Ponds", and is in St. Tammany Parish, Louisiana, three and one-half miles west-northwest of Slidell, at about ten feet above sea level. The area consists of two separate ponds adjacent to a road. The larger pond, North Siren Pond, reaches a size of 30 by 25 meters and a depth of about 1.5 meters at full capacity. The smaller pond, located about 30 meters south of North Siren Pond is designated as South Siren Pond and is L-shaped, measuring approximately 15 meters in length and 10 meters on the shorter leg. South Siren Pond varies from one to four meters in width and up to one meter in depth during high water.

During the summer and fall of 1958 large portions of North Siren Pond were destroyed or disturbed by roadbuilding operations. Several mole salamanders collected during the 1959-60 breeding season exhibited body damage and regenerated limbs and tails indicating that the disturbance affected at least a portion of the population. The roadbed, composed primarily of clay, erodes during rains, and the water throughout most of this pond in early 1959 was extremely murky. Water samples kept undisturbed in the laboratory required over a month to settle.

Within and around North Siren Pond proper are live oak (*Quercus virginiana*), sweet gum (*Liquidambar styraciflua*), and southern hackberry (*Celtis mississippiensis*) trees. Within and around South Siren Pond are loblolly pine (*Pinus taeda*) and a few small sweet gum. The land surrounding the ponds is heavily forested with loblolly pine. Dead pine needles cover the floor of the forested area in some places to a depth of almost a meter. Few shrubs are present, although greenbrier (*Smilax* spp.) is present in large colonies. Grasses are present in the more open areas. Burrowing mammals and their extensive tunnels are found in the decaying pine needles. The small burrows are probably constructed by shrews, (*Blarina brevicauda* and *Cryptotis parva*) and cotton mice (*Peromyscus gossypinus*). Other mammals present in the area are skunks (*Mephitis mephitis*), opossums (*Didelphis marsupialis*), swamp rabbits (*Sylvilagus aquaticus*), and gray squirrels (*Sciurus carolinensis*).

Within the two ponds is a variety of poikilothermic vertebrates including siren (*Siren intermedia*), newts (*Diemictylus viridescens*), green frogs (*Rana clamitans*), leopard frogs, (*Rana pipiens*), cricket frogs (*Acris gryllus*), chorus frogs (*Pseudacris triseriata*), mud turtles (*Kinosternon subrubrum*), pigmy sunfish, (*Elassoma zonatum*), and mosquito fish (*Gambusia affinis*). At times of overflow, black bullheads (*Ictalurus melas*) and very small largemouth bass (*Micropterus salmoides*) are present. Fairy shrimp, crawfish, back swimmers, diving beetles, leeches, and other invertebrates are common.

Many observations were conducted in a rectangular concrete pit 2.32 by 1.52 meters and 0.68 meters deep on the Tulane campus. Water depth was varied to suit the particular experiment. The sides were vertical and the floor sloped slightly to a drain. An overflow drain prevented the water level from rising above 0.53 m. A certain amount of debris (sticks, twigs, catkins, and leaves) continually fell into the pit.

Aquaria of several sizes were utilized for laboratory studies. Water in the aquaria was filtered and aerated. Fine gravel was used as a substrate with *Anacharis* sp. as the only vegetation. The room in which the aquaria were kept was 20° C. ± 2°.

Results and Discussion

Breeding Season

The breeding period.—Professor F. R. Cagle (personal communication) recorded breeding of *Ambystoma talpoideum* from early December until the middle of February for the years 1949 through 1955 at the Siren Ponds. Gentry (1955) remarked that *A. talpoideum* deposits eggs during January or February in Tennessee. Allen (1932) witnessed *A. talpoideum* "breeding" in Henderson County, Mississippi on February 12, 1930. Carr (1940) collected breeding adults in Alachua County, Florida on February 14, 1933. Mosimann and Uzzell (1952) found breeding adults in Dorchester County, South Carolina on December 31, 1951. Apparently throughout the greater portion of its

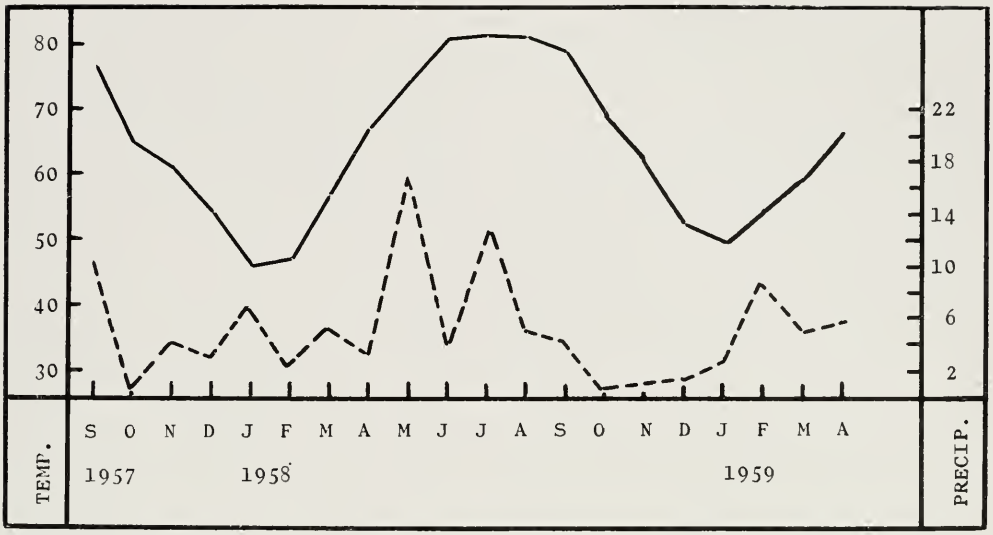

Figure 1. Average monthly temperature in degrees Fahrenheit (solid line) and total monthly precipitation in inches (dashed line) from September, 1957 to April, 1959 as recorded by the U. S. Weather Bureau at Slidell, Louisiana.

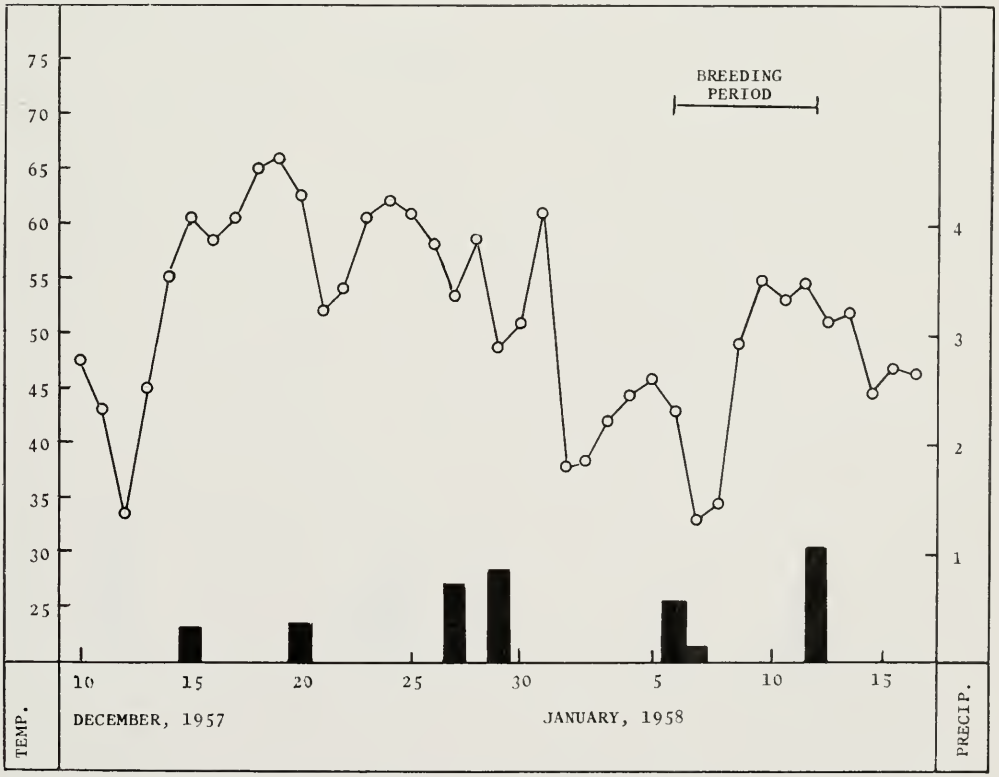

Figure 2. Average daily temperature in degrees Fahrenheit (solid line) and total precipitation in inches (darkened columns) recorded at Slidell, Louisiana, for the period December 10, 1957, through January 17, 1958. The breeding period of *Ambystoma talpoideum* is indicated.

range, the mole salamander is a winter breeder, although the length of an individual breeding period has not yet been reported.

In 1958, breeding activity in the Siren Ponds began on or about January 6, as judged by the appearance of eggs found on January 8. This breeding period ended by January 12, when intensive efforts to collect mole salamanders in the ponds were fruitless. Thus the reproductive activity apparently covered a span of seven days. The breeding period of 1959 lasted for eight days, January 30 to February 6. Breeding adults were found in North Siren Pond on January 8, 1960. On January 23, 1960, two adult mole salamanders in breeding condition were located by the electrical shocker in the same pond, indicating a possible breeding period of 15 days.

Climatic factors influencing the breeding period.—Weather conditions during the two breeding seasons of this study varied considerably. A relatively large amount of precipitation throughout the late summer and fall of 1957 filled the ponds by November 1957. Precipitation was relatively sparse in the late summer and fall of 1958 (fig. 1); no water was present in the ponds until January 30, 1959. The average air temperatures during the first fall and winter of this study were lower than those a year later (fig. 1).

On December 30, 1957, there were no salamanders in the pond or under logs surrounding the pond. Rains had occurred one and three days previously, and temperatures were relatively warm during those rains (fig. 2). Precipitation occurred on January 6 and 7, 1958 with accompanying cold temperatures; breeding activities began at this time.

As soon as the ponds began to fill in 1959, and lower temperatures and rains coincided, breeding took place (fig. 3). Water and air temperatures in 1959 were higher

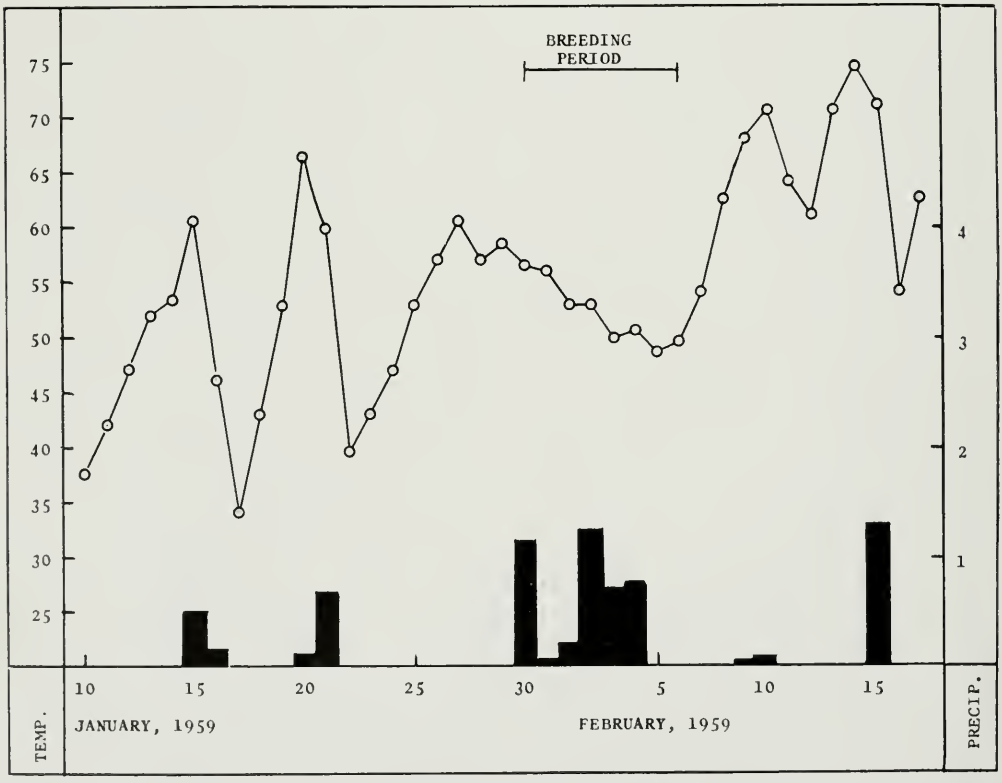

Figure 3. Average daily temperature in degrees Fahrenheit (solid line) and total daily precipitation in inches (darkened columns) recorded at Slidell, Louisiana, for the period January 10, 1959, through February 17, 1959. The breeding period of *Ambystoma talpoideum* is indicated.

TABLE 1.

Summary of collections at the Siren Ponds during the breeding seasons of 1957-58 and 1958-59

Date	Number of Males Collected	Number of Females Collected	Total Adults Collected	Time (PM)	Temperature °C Water	Temperature °C Air	Water Depth (in cm)
Dec. 30, 1957	0	0	0	8:15-9:00	16.0	14.0	30
Jan. 8, 1958	2	1	3	8:30-9:30	4.5	—1.1	58
Jan. 9, 1958	2	1	3	8:00-9:30	6.0	2.5	58
Jan. 10, 1958	12	11	23	7:30-8:30	7.0	6.5	60
Jan. 11, 1958	6	4	10	5:30-7:15	10.0	11.0	60
Jan. 12, 1958	0	0	0	8:30-9:30	11.0	15.0	73
Jan. 13, 1958	0	0	0	8:30-9:30	12.0	15.5	79
Total 1957-58	22	17	39				
Jan. 30, 1959	11	5	16	8:00-9:20	15.5	12.5	15
Jan. 31, 1959	2	1	3	3:00-4:30	15.5	15.0	15
Feb. 2, 1959	2	6	8	8:30-9:30	10.5	11.5	22
Feb. 4, 1959	25	11	36	8:20-9:20	9.0	7.0	25
Feb. 6, 1959	2	1	3	8:30-9:20	11.0	11.0	26
Feb. 8, 1959	0	0	0	5:45-7:00	18.5	22.0	15
Total 1959	42	24	66				

than those during breeding activities in 1958. The largest collection of individuals during one evening in 1959 occurred when the water temperatures were the coldest of the year and approached those of the previous year (Table 1).

The factors constituting a stimulus to breeding in southeastern Louisiana are complex. Heavy rains and lower temperatures apparently interplay in stimulating the breeding of *A. talpoideum* (figs. 2, 3). During the breeding season of the years 1957 through 1960, moderate to heavy rains were associated with breeding activity. If low temperature is unimportant, the heavy rains of December 27 and 29, 1957, should have been sufficient stimulus for breeding to occur. At that time, temperatures were seasonally normal and the ponds contained water. No breeding activity resulted, but when rains and relatively cold temperatures coincided (January 6, 7, 1958), breeding commenced (fig. 2). During the winter of 1958-59, when the ponds were unseasonably dry, breeding was delayed until water was present. When breeding occurred, the temperatures were not as low as those of the previous year. This observation would seem to indicate that only cool temperatures are needed, or that the lack of water in the ponds forced the adults to utilize conditions which were not optimum.

Breeding Adults

Males.—The cloacal region of the male swells and becomes protuberant (figs. 4, 5) during the breeding season. The tail becomes finned (as in other ambystomatids), and the tip of the tail is oar-shaped. A rough, glandular appearing area located dorso-laterally on the tail is prominent. Salamanders kept in the concrete pit after breeding lost the pronounced tail fin within one to two weeks. The cloacal swelling recedes after one to three weeks.

Of 88 males from the breeding pond, the largest specimen (T.U. 13589.5) collected in North Siren pond during the breeding season, was 122 mm in total length (body 66).[3] The smallest breeding male was 83 mm in total length (body 48). The body lengths of 88 breeding males varied from 48 to 68 mm (mean, 57.2 mm). The tail lengths of 83 males made up 38 to 47 per cent of the total length (range, 33 to

[3] The tail is somewhat fragile and was broken or injured in several individuals. In starved animals or adults collected in seasons other than winter, and having no fin, the tail is proportionately smaller than in breeding adults. For these reasons, I consider body length a more valid measurement than total length. However, total lengths and tail lengths are presented for comparisons with measurements given by other authors.

Figure 4. Dorsal view of two *Ambystoma talpoideum* in breeding condition. Left, female; right, male.

Figure 5. Ventral view of two *Ambystoma talpoideum* in breeding condition. Left, female; right, male.

56 mm; mean 42.7 mm) (fig. 6).

Females.—A slight swelling of the cloacal region is evident in the breeding female, although the amount of protuberance is much less than that of the male (figs. 4, 5). The tail fin is somewhat pointed at the distal end. A dorso-lateral glandular area on the tail, such as found on males, is much reduced. If the adult is kept in water the fin is lost within one to two weeks after courtship.

Of 52 females from breeding aggregations in the Siren Ponds, four had a total length of 111 mm, the maximum for this series (mean, 96.6 mm). The smallest total length was 81 mm (body 46). Body lengths of the females ranged from 46 to 67 mm (mean, 59.5), and tail lengths ranged from 33 to 48 mm (mean, 41.0 mm) constituting 37 to 46 per cent of the total lengths.

Sizes of males and females combined.—The mean total length of 135 breeding adults (83 males and 52 females) was 99.5 mm and the mean tail length was 42.0; the average body length of 140 breeding individuals (88 males and 52 females) was 58.0 mm. The maximum total length of adults according to Bishop (1947) is 97 mm; Conant (1958) noted "3 to 4 inches." Many individual *A. talpoideum* measured during this study were considerably larger. The male measuring 122 mm in total length represents a record size for the species. The size range of both males and females is great (fig. 6), perhaps indicating that breeding populations may be composed of several age groups.

Coloration.—Coloration of any individual may change during a given period of time. When the adults are removed from the breeding pond, a color pattern is barely discernible. The back and sides are liver color with light flecks, fading into blue-gray on the ventrum. If kept in captivity for some time, the animal becomes blue-gray dorsally and lichen-like markings develop on the dorsum. Except on very young specimens, a light brown or tan area is present on the dorsum of the tail and occasionally on the back of the head. Young specimens invariably have a dark median stripe on the belly.

The Breeding Aggregation

Composition of the breeding aggregate.—All specimens collected within the ponds during the breeding season were sexually mature. One sexually immature individual was collected near the ponds during the breeding season.

No distinct size groups can be seen in this sample, although the smallest individuals are probably young adults breeding for the first time. Many of these young adults possess vestiges of the larval belly pattern (*i.e.* a dark median belly stripe). The finding of a single immature specimen during breeding season indicates that at least some of these salamanders do not breed during the first breeding season following metamorphosis.

Males are more common in the breeding ponds at the onset of reproductive activities. They may continue to be more numerous than females throughout most of the breeding period (Table 1). Spent females were observed leaving the pond during the breeding period, showing that females leave the breeding pond soon after laying their eggs. Males apparently remain for the entire period. Undoubtedly, both males and females continue to enter the pond throughout this time. Non-continuous sampling of the breeding population might give erroneous indications of the sex ratio. Blanchard (1935) emphasized that in the determination of the relative numbers of the sexes, exclusion of adults is necessary because of differences in habits, and only juveniles should be used for the determination.

Behavior of individuals in the breeding aggregation.—Twenty days prior to the breeding activities of 1959, one male was collected under a board near North Siren Pond. There had been rain two days earlier, but no water was present in the pond. During a light rain ten days later three males and two females were found in the moist floor of South Siren Pond. Evidently the adults are near the ponds before reproductive activities commence, and during unusually dry winters, they presumably may burrow in the pond floor prior to the breeding period.

Individuals in the breeding pond often burrow in the debris covering the floor during daylight hours. At night, they may be found in every part of the pond; no dis-

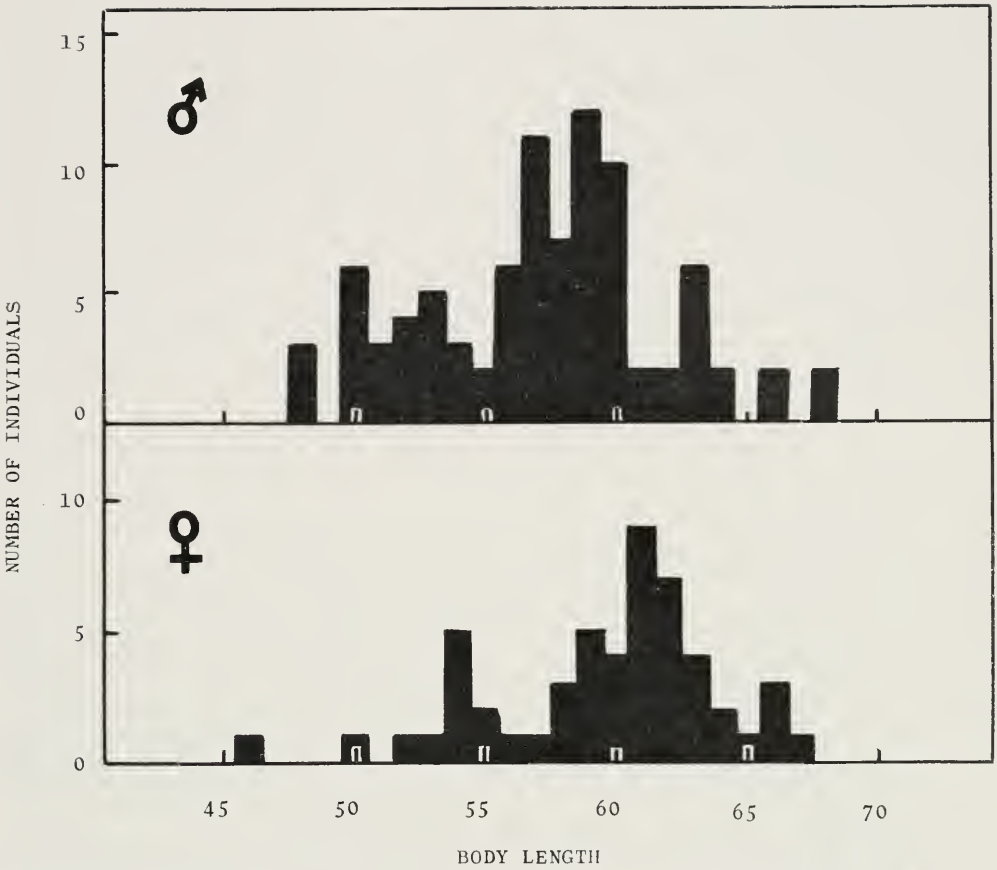

Figure 6. Body lengths of 88 males and 52 females in breeding condition. Measurements are in mm.

tinct preference is shown for a certain depth of water. A congregation of females was detected during the breeding period of 1958 in a region of the pond where large numbers of twigs and sticks were located. These females were probably laying eggs in this region.

All individuals invariably shy from the light of a flashlight if they are not courting. Adults in captivity attempt to hide during the day.

Lower temperatures are apparently preferred for breeding purposes (figs. 2, 3). The largest concentration of adults was found when water temperatures were lowest. No breeding adults were found in the ponds in water warmer than 16° C (Table 1), although warmer water was utilized for breeding in captivity. Two spent females were collected from water with a thin ice coat near Hickory, Louisiana, on January 8, 1958.

Courtship Pattern

Courtship was not observed in the field. On January 30, 1959, two pairs were found following each other about the edge of the pond. Subsequently, four males and four females collected on this date and kept refrigerated until February 3, were placed in the concrete pit on the Tulane campus. Water depth ranged from 4 to 22 cm due to the slanting floor. The water temperature was 17° C. A small amount of debris consisting of leaves, twigs, larger sticks, a concrete block, and a brick was scattered about on the floor of the pit. Observations from 7:00 PM to 9:30 PM using a dim flashlight showed no courting activity. The individuals seemed to shy from the light. At 8:00 AM the following morning, two

clusters of eggs, containing 11 and 13 eggs, respectively, were found on a small twig in the deepest water. By 3:30 PM, 18 more eggs were found on leaves and on the bottom of the pit. Occasionally the adults would move about and swim to the surface to gulp air. At 8:00 AM on February 5, the debris on the floor, and the walls were covered with small clusters of from 2 to 22 eggs. Spermatophores were common on the floor; ten spermatophores were collected, measured, and preserved. This was the first indication that captive specimens would court. During the evening of February 6, the egg laying of several females was observed.

At noon on February 7, all eight salamanders were removed from the pit. At this time two females collected on January 30 and 31, and kept in a refrigerator at 6° C., were placed in the pool. Two males, which had been kept in the pit previously and two males collected January 30 and kept at 6° C. since capture, were released in the pit at 6:15 PM. A dim flashlight covered with red cellophane was used to observe these salamanders continuously from 6:15 until 10:00 PM. No unusual movements were observed until 7:15 PM. At this time a male began bumping the head of a female with his snout. Air temperature at this time was 17° C while the water temperature was 14° C. From this time until observations ceased at 10:00 PM, courtship activity occurred almost continuously. Nine separate courtship dances were observed during the evening of February 7. Only two dances resulted in sperm transfer.

All spermatophores were removed from the pit the morning following observations of the dances. No subsequent spermatophores were found in the pit, indicating that courtship, at least of the females in the pit, had ended.

On February 20, ten pairs of adults collected on February 4, and kept refrigerated, were placed in the pit to verify previous observations and to provide eggs for future studies of larvae. On removal February 27, only 14 individuals were in the pit. The tail fin was reduced in all of them and the cloacal swelling of males was lessened. All six missing individuals were females.

Courtship. — After bumping the female for about 10 seconds (fig. 7A), the male runs his head along the sides of the female to her cloacal region. The female begins nosing the cloacal region of the male and both of them push with their heads. This results in a circular movement or "waltz" of one or two revolutions (fig. 7B). The male here breaks contact with the female's cloacal region and begins to straighten his body. The female slides her head down to the tip of the male's tail. Thereupon the male begins a peculiar wagging of the pelvic region and proximal portion of his tail while keeping the posterior part of the tail undulating and often touching the female's head (fig. 7C).

At this time his cloacal aperture opens and the spermatophore stalk may begin forming. Using the front feet for propulsion the male moves forward slowly continuing the wagging motion. The female follows, keeping her head in contact or in close proximity to the male's tail. After one to eleven minutes of following, the female pushes her head along the male's tail until she reaches his cloacal region or hind legs. At this time she bumps the male (fig. 7D) on the cloacal region one or two times and the male ceases the pelvic movement. With the hind legs directed outward and posteriorly, the male deposits a spermatophore (fig. 8A). If he does not stop his movements, the female returns to the distal end of his tail. Immediately after deposition the pelvic motion is resumed. The female noses the spermatophore and slowly begins to crawl over it (fig. 8B), the male keeping his tail near the female. If the female is led by the male to a position in which her cloaca is directly over the spermatophore, she will assume the same posture taken by the male in depositing the spermatophore and, using her cloacal lips, pick up the entire spermatophore or clip off the sperm cap (fig. 8C). Rarely does the male so lead the female. If the female successfully picks up a spermatophore or cap, immediately after or within a minute or so, she loses interest in the male and wanders away from him (fig. 8D). The male continues his wagging movements for several minutes. If a successful pickup is not made, the female continues to follow the male until such occurs or until the dance is terminated, usually when the pair becomes separated. One female was ob-

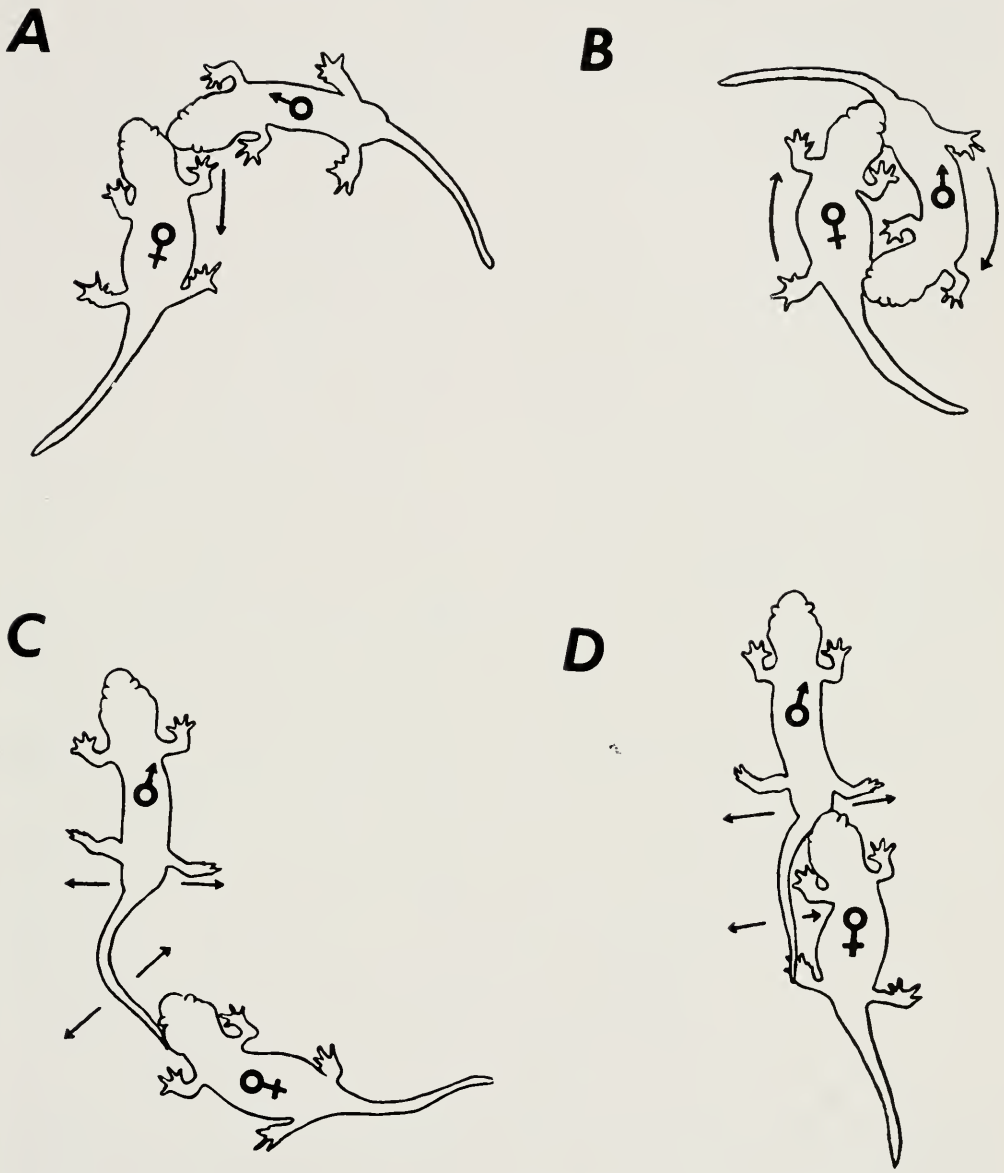

Figure 7. Courtship pattern of the mole salamander. **A**, male noses female; **B**, the "waltz"; **C**, female follows male; **D**, female bumps the cloaca of the male.

served to be unsuccessful in seven attempts to pick up a spermatophore, finally leaving the male courting her. The pair moved a distance of over seven feet during this courtship dance. A female may be courted by many males and offered many spermatophores before she picks one up. Females will pay no attention to spermatophores unless they are offered during courtship.

At times another male may join the dance and will push between the original male's tail and the female's head, thereby separating the pair engaged in the dance. The intruder then begins courtship by bumping the head of the female and following the above pattern. In this case, the rejected male continues the pelvic motion for some minutes. Use of a weighted sponge with

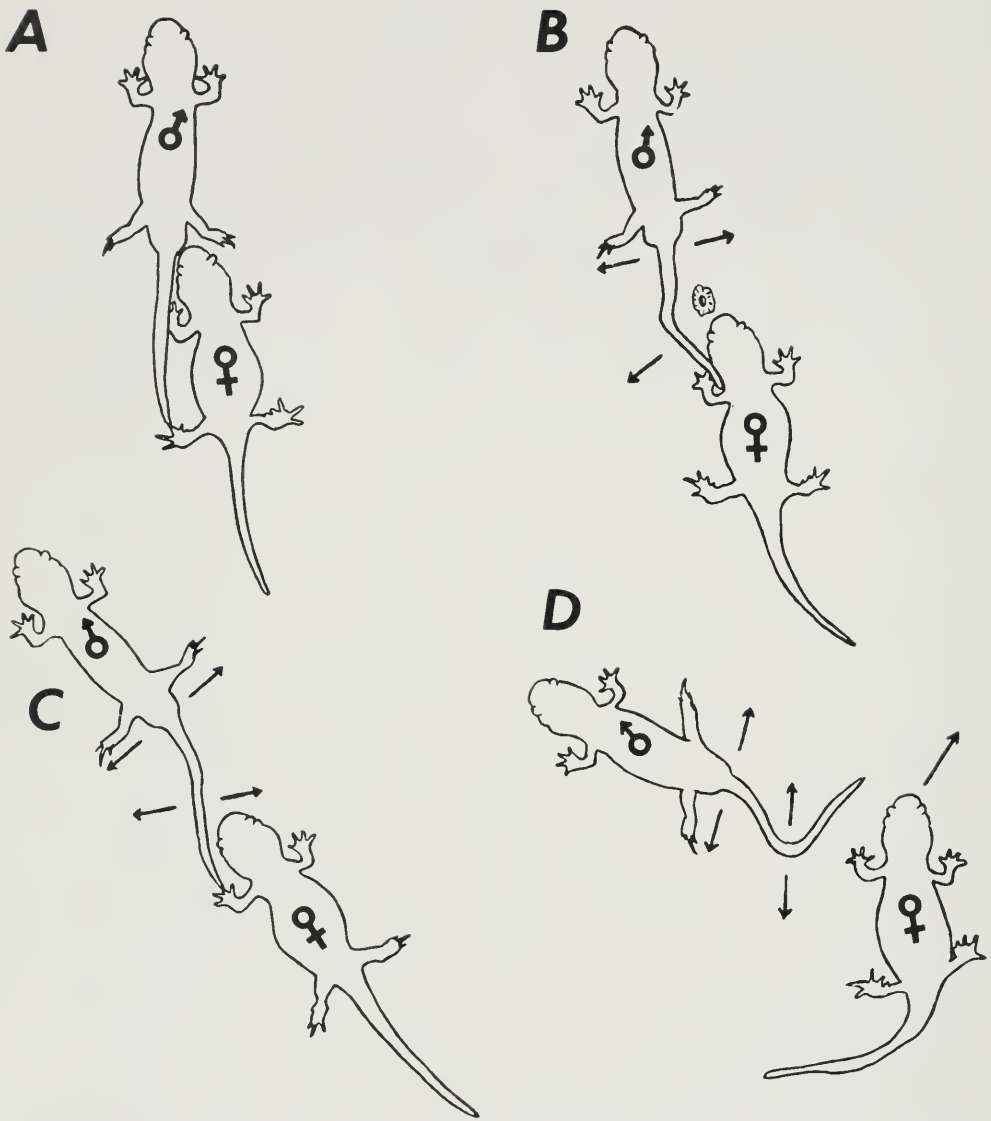

Figure 8. Courtship pattern of the mole salamander. **A**, male deposits a spermatophore; **B**, female noses spermatophore; **C**, female picks up spermatophore or spermatophore cap; **D**, female leaves male.

female secretions in the manner described by Twitty (1955) yielded no results. Apparently, meeting of the males and females is haphazard.

Total time for courtship dances ranged from seven to thirty-seven minutes. The shorter dances may have been terminated because of the use of flash bulbs in photographing the courtship.

Effect of light.—Dim light (red or white) has little effect on the courting individuals. Bright light will cause the participants to stop all movement. If the bright light is removed quickly, the courtship will continue. Any light, no matter how dim, may cause non-courting individuals to shy away.

Spermatophores

A male placed in an aquarium at 20° C without females deposited two spermatophores, indicating that courtship is not necessary for deposition. Males injected with

four female *Rana pipiens* pituitaries, as suggested by Noble and Richards (1932), began depositing spermatophores within 48 hours. The total observed number of spermatophores produced during courtship by an uninjected male was fifteen.

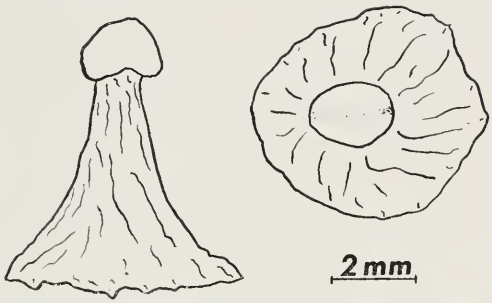

Figure 9. Spermatophore of *Ambystoma talpoideum*. Left, side view; right, top view.

The spermatophore has a wide circular base with a relatively thin stalk tipped by a sperm cap (fig. 9). All spermatophores were attached loosely to the pool or aquarium floor. The jelly-like base is clear and gelatinous, while the sperm cap is cottony white. The general shape of the cap is a flattened ellipsoid, but is variable and may be almost spherical. On the top, a slight fold runs from the anterior to the posterior end dividing the cap into two approximately equal halves (fig. 9). The jelly-like stalk has a blunt apex and a relatively wide base. The total height ranges from 6.3 to 8.5 mm; stalk length 3.6 to 6.6; base width 5.1 to 8.2; stalk at narrowest point 1.0 to 2.5; cap depth 1.0 to 2.6; cap length 2.6 to 3.1; and cap width 2.0 to 2.9.

Several spermatophores were examined microscopically the morning following deposition. The cap was found to be composed of cellular strands of two sizes. Apparently spermatozoa should have been found between these strands, but none was seen. Between the strands may be found extremely abundant colonies of protozoa (Sarcodina, Ciliata, and Mastigophora), vegetative hyphae of a phycomycete, and filaments and individual cells of green algae. The gelatinous stalk contains lesser quantities of these organisms.

Oviposition

Courtship is not a necessary prelude to egg laying. Females collected on land before the breeding season may lay unfertilized eggs when placed in aquaria at room temperature (20° C). This phenomenon occurred with all three females tested, but Professor Cagle (personal communication) kept several gravid females in aquaria two months and oviposition did not result. A female placed in a terrarium containing only damp sand resorbed her eggs. The appearance of the ovaries of this female was essentially like those of *Ambystoma jeffersonianum*, described by Clanton (1934). Infertile eggs apparently are rare in nature as only one was observed. Under conditions in the concrete pit, several clusters contained one to many unfertilized eggs. Oviposition usually takes place at night, but one female was observed to lay eggs in the outside pit during a cloudy afternoon.

Eggs may be laid on any substrate in the breeding pond, but there is a decided preference for small twigs approximately one-eighth inch in diameter which are oriented at an angle to the surface. No definite preference was shown for a particular water depth. Areas containing many twigs and sticks seem to be preferred. Eggs were sometimes deposited on twigs near the surface of the pond at times of high water and, with the lowering of the water level, left hanging in the air.

Positions assumed during oviposition vary, depending on the substrate and its orientation in relation to the surface. If oviposition occurs on the bottom of the pit, the female assumes a position in which the cloacal lips are pressed firmly to the substrate and begins to wave the tail slowly. When the waving decreases or ceases one to several eggs may be deposited. If the female does not move during deposition, the form the eggs will assume after water absorption is a large spherical clump; if she moves slowly during deposition, using all four feet, the eggs will appear after water absorption as a long, single strand.

Several individuals have been observed laying eggs on the vertical walls of the concrete pit. The female's head is always pointed toward the surface and a grip on the roughened concrete is kept by all four feet. The tail undulates slowly before the initial deposition. The female appears to rest after laying one to six eggs; during this time, the tail waving is resumed. After

laying a clump of eggs the female returns to the floor of the pit.

If a twig is oriented at an angle to the surface of the water the female will swim up to the twig at a point about 10 to 15 cm from the floor, and grasp it with her hind legs. While waving her tail, she gradually turns under the twig with ventrum up. Using only the hind legs and feet for traction, she moves slowly along the twig toward the surface depositing eggs. The tail undulates slowly except during actual deposition. The trunk of the body may at times be nearly at a right angle to the twig. By alternately shifting the tail and body, and moving slowly between times of deposition, the eggs may be laid in a wave-like pattern along the underside of the twig. This method of laying was observed frequently, and many eggs in the natural pond because of their location on twigs appeared to have been laid in this fashion. Females do not always turn over to lay eggs on slanting twigs.

The eggs are laid in small clusters. Often many clusters appear on the same twig. These clusters may or may not be laid by one female. On one occasion a female was seen laying eggs between clusters of eggs deposited previously by another female. The number of eggs in 75 individual clusters ranged from one to 37. One marked female laid eggs during three consecutive nights in the concrete pit. More than one night is probably required for all the eggs to be laid. Two females took 15 and 22 minutes to lay 17 and 18 eggs, respectively, before returning to the bottom where they remained motionless for more than an hour.

Eggs

Only one series of adults collected on land before the breeding season is in the Tulane collections. This series (TU 13584), consisting of 33 specimens, was collected near the Siren Ponds on the same day, before water was present in the ponds. Fourteen are females containing enlarged ova within the ovaries. The number of ripe ova of each specimen varies from 226 to 401. From figure 10, one can see that the largest individual or the smallest did not produce the largest or smallest number of eggs, respectively. More data are needed to show a correlation, if any, between length and size

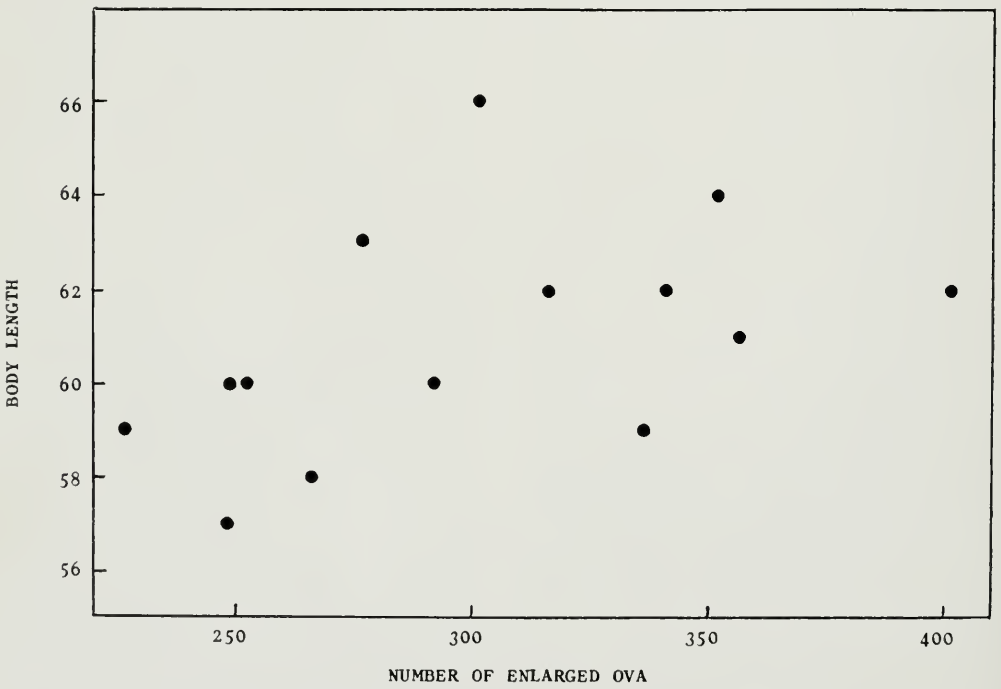

Figure 10. Graphical representation of body length in mm plotted against total number of enlarged ova.

of the egg complement. In no case was the number of ova in the two ovaries the same. Wilder (1924) showed in the salamander *Eurycea bislineata* that the number of large ova found in gravid females is consistent with the numbers of eggs deposited in the field.

The eggs and their envelopes are essentially as described by Mosimann and Uzzel (1952). Each is surrounded by a vitelline membrane plus two envelopes. A gelatinous covering or matrix is common to all eggs in a cluster. A sample of 25 fertile eggs deposited in captivity varied less than ± 0.4 mm from the egg pictured by Mosimann and Uzzell.

Discussion

Breeding season.—Blanchard (1930) and Baldauf (1952) indicated that adults of *A. maculatum* may be found in breeding ponds for a period of about two weeks or more, and that the salamanders move in waves to the pond because freezing temperatures and dryness often hinder the migration. *A. talpoideum* may spend considerably less time in the breeding pond.

Blanchard (1930) stated that rain and not temperature is the main stimulus to the breeding migration of *Ambystoma maculatum* in Michigan. He believed that rain occurring before the ground thaws, or daytime rains, would have no effect. In a footnote to Blanchard's paper, A. H. Wright wrote, "I regard the most necessary condition for each species as humidity above a more or less specific minimum temperature." Concerning *maculatum,* Bishop (1941), stated, "I would qualify this theory by adding that, in eastern New York, migration of this species and *A. jeffersonianum* may be initiated by rain during the day and even by the rapid runoff of snow water following a pronounced rise in temperature." Wright and Allen (1909) stated that an air temperature of 50° F or more was required to cause the emergence of *maculatum* from hibernation, whereas Baldauf (1952) claimed a slightly higher minimum of 55° F. Baldauf believed temperature and humidity to be the most important factors in stimulating the breeding migration of the spotted salamander. In all of the above considerations, temperature and moisture are considered important.

The role of temperature in the stimulation of the breeding of *talpoideum* may be opposite to that of *maculatum.* A warming trend after freezing temperatures is required by *maculatum,* but *talpoideum* apparently requires a cooling trend. Unfortunately, temperatures of water in the breeding ponds were not recorded by the previous authors. Since breeding takes place underwater, water temperatures would be of considerable value. Perhaps, either *maculatum* or other species of *Ambystoma* and *talpoideum* breed when the water temperatures are essentially the same.

Courtship.—The courtship of *Ambystoma talpoideum* differs from that described for several other eastern ambystomatids. Bishop (1941) observed the courtship of *Ambystoma jeffersonianum* in New York. The male grasped the female in an axillary embrace at the beginning of the courtship. Kumpf and Yeaton (1932) stated that the male then rubs the head of the female with his chin, undulates his body and tail, and eventually swims and walks ahead of the female to deposit a spermatophore. Before the spermatophore is released, the female applies her snout to the male's cloacal region. Mohr (1931) reported that *jeffersonianum* undulates the tail and body while depositing spermatophores.

Of *A. maculatum,* Bishop and others stated that the species often engage in a *Liebesspiel* upon arrival at the breeding site. Mohr (1931) believed the courtship of *maculatum* does not differ in important details from that of *jeffersonianum,* but Wright and Allen (1909) saw males rubbing the dorsal surface of their heads along the ventrum of the females. Following each performance of this kind the males swam away, deposited a spermatophore and returned to nose the females. Eventually the female picked up a spermatophore cap with her cloacal labia.

Noble and Brady (1933) found that a male *A. opacum* attempts to push his head under the cloacal region of a female, and the female does the same to the male. The pair may revolve in a circular movement which they described as the "waltz." The female may then pick up a spermatophore deposited by the male. The entire courtship takes place on land.

Ambystoma tigrinum is the most widely distributed member of the genus. Kumpf

(1934) has described the courtship dance of *tigrinum* in some detail. When depositing a spermatophore, this species raised the tail at right angles to the body. The female assumed the same posture when picking up the spermatophore. The male always pushed his head under the cloaca of the female before stalking ahead to deposit a spermatophore.

According to Tihen (1958) *A. talpoideum* is most closely related to *A. opacum.* These species may have arisen from the *maculatum* group stock. The vertebral proportions of *talpoideum* and *opacum* are intermediate between *tigrinum* and *maculatum,* however. Since *opacum* and *talpoideum* are closely related, one might assume that the courtship patterns would be similar, and indeed they are. The "waltz" of *opacum* is also executed by *talpoideum* at the beginning of the courtship. The undulating tail of the male, according to Noble (1931), is used to waft the secretions of the abdominal gland toward the female. Obviously, in a terrestrial situation such as that of *opacum,* this part of the courtship is impossible. If the recorded courtship patterns of *tigrinum* and *maculatum* are compared to those of *talpoideum,* many aspects of the courtship of the tiger salamander appear similar to that of *talpoideum.* Yet certain aspects of the courtship of *jeffersonianum* are also similar. More observations are needed to clarify the courtship differences of the *maculatum* and *tigrinum* groups.

Although female *talpoideum* exhibit difficulty in picking up spermatophores or spermatophore caps, the lack of infertile eggs in the breeding ponds shows the success of courtship activities. Extremely murky water in North Siren Pond in 1959 did not prevent successful courtship. Total potential reproductive capacity (as defined by Allee, *et al.,* 1959) of the breeding population appears to be almost realized, but the mortality rate of developing embryos and larvae may be high.

Spermatophores.—The spermatophore of *A. talpoideum* differs most markedly from other ambystomatids by possessing a long, thin stalk of less diameter than the sperm cap, and by possessing a mid-dorsal fold running the length of the sperm cap. *A. maculatum* produces a spermatophore which may be simple, branched, or compound; one-fourth to one-half of one inch in height; and the seminal fluid may cover the supporting jelly (Bishop, 1941). The stalk is as wide as the cap. There may be 100 or more spermatophores in one group, although one male produces only 40. Wright and Allen (1909) observed 32 deposited in only 45 minutes.

The spermatophores of *A. jeffersonianum* are widely scattered according to Bishop (1941). As Bishop pictured the spermatophore, the stalk is larger than the cap and the entire structure is smaller than that of *A. maculatum.* Mohr (1931) wrote that the stalk is pyramidal.

Lantz (1930) first described the spermatophore of *A. opacum,* and it is figured by Noble and Brady (1933). It measures 4.0 to 5.5 mm in height, 6.0 mm at the base, and 2.0 mm at the apex. The summit is quadrangular or pentangular.

Details of the spermatophore of *A. tigrinum* appear to be lacking. Generally, the height is about three-fourths of an inch with a thick stalk (Stine, Fowler and Simmons, 1954).

Oviposition.—Oviposition resembles that of most other members of the genus *Ambystoma* where this phenomenon has been described. The description of females turning over to lay eggs resembles Hamilton's (1948) account of the egg laying *A. tigrinum nebulosum.*

Many other ambystomatids use the hind feet primarily when laying eggs on twigs. Tail waving also appears to be common in this group.

Summary

The breeding habits of *Ambystoma talpoideum* were studied from October, 1957, until February, 1960. Mole salamanders breed in southeastern Louisiana during the winter for a period of six to fifteen days. The breeding migration is correlated with the coincidence of low temperatures and rains.

All mole salamanders collected in the breeding ponds during the breeding period were sexually mature. The mean total length of these specimens (99.5 mm) was greater than the maximum recorded total length; one specimen measured 122 mm.

Males apparently remain in the breeding pond throughout the breeding period in contrast to the females which depart from

the pond soon after oviposition; therefore, noncontinuous sampling may give an erroneous indication of the sex ratio of the breeding population.

The courtship pattern of *Ambystoma talpoideum* is most like that of its nearest relative, *Ambystoma opacum*. The courtship of the mole salamander differs from the described patterns of *A. opacum* and other species of *Ambystoma* in one or more respects.

A dorsal fold and a long, thin stalk differentiates the spermatophore of *A. talpoideum* from those of other ambystomatids. Oviposition resembles that of other species of *Ambystoma*, however. The eggs of the mole salamander have been described previously. No essential differences from the original description were found.

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Abstract

Breeding habits of a population of mole salamanders, *Ambystoma talpoideum*, were studied near Slidell, St. Tammany Parish, Louisiana. Only sexually mature individuals moved to the ponds to breed during a period of six to fifteen days during the winter. Breeding was coincident with rain and low temperatures. The courtship behavior was described and compared with that of other members of the genus. The courtship pattern was most like that of the nearest relative, *Ambystoma opacum*. The spermatophore of *A. talpoideum* is distinct.