ventral surfaces of body of the latter; the nostril a little nearer the eye than middle of the upper lip edge; the canthus indistinct or absent; the absent or very indistinct inner tarsal fold; the larger outer metatarsal tubercle; lesser webbing of the hand; and the greater thickness of the snout with a narrower interorbital distance.

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Courtship of the Plethodontid Salamander *Ensatina eschscholtzii*

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THE courtship of plethodontid salamanders, as so far observed, consists of a series of instinctive reactions that form a well defined and predictable pattern of behavior. The complexity of this pattern supports the generally accepted view that the Plethodontidae are a terminal group in phylogeny.

Information on plethodontid courtship stems in large part from the observations of Noble (1929) and Noble and Brady (1930) on captive animals. In studying a number of genera and species, principally from eastern North America, they observed that the general pattern of nuptial behavior was essentially the same even though some species were aquatic and others were terrestrial. They studied the following forms: *Eurycea bislineata, E. guttolineata* (= *E. longicauda guttolineata*), *Manculus quadridigitatus, Desmognathus fuscus, D. phoca, D. quadramaculatus, Stereochilus marginatum, Plethodon glutinosus, P. cinereus, Hemidactylium scutatum, Hydromantes genei* and *H. italicus*. *Eurycea bislineata* and *Stereochilus* were studied in greatest detail.

I have recently had opportunity to observe the behavior of a western North American species, *Ensatina eschscholtzii,* a form not represented in the

foregoing study. The pattern is an intricate one, differing in certain details from that described by Noble and Brady but agreeing in a general way with their summarization. As a basis for comparisons I quote from their summary:

> In all species, so far as determined, there is a series of preliminary rubbing movements during which the male applies his lips, cheeks, mental gland, or side of body to the snout of the female. This arouses the female's interest in the male. In the second phase of the courtship, the female follows the male, keeping her chin pressed closely against his tail base as they move about. . . . The male, especially when he is not moving forward, undulates the base of his tail from side to side . . . .
>
> At the height of the courtship, after the female has assumed her position behind the male, the latter often turns and pushes the female in the cloacal region with his nose. This causes the pair to move in circles about the aquarium. Another posture and movement not previously reported is the lifting of the body and arching of the tail of the male while the female is following him. This may tend to raise the fore part of the female from the floor. Another peculiar attitude during the same period is the turning forward of the tail of the female in some species, particularly in *Eurycea b. cirrigera* and *Stereochilus*. Still another distinctive position, noted especially in *Stereochilus* and *Hydromantes,* is the forcing of the mental glands tightly over the nostrils of the female while the male maintains a position directly over her back.

Observations of courtship and spermatophore pick-up were observed on several occasions in captive *Ensatina eschscholtzii xanthoptica* from the vicinity of Berkeley, Contra Costa County, California. The behavior in each instance was essentially the same. A typical sequence of steps in courtship is illustrated in Plates I and II, Figures 1 to 10. The diagrams are composite to the extent that the activity of the same courting pair has not been followed through the entire series. On several occasions the behavior of the animals was observed to step 4 in which the male is attempting to induce the female to follow him. And at other times the animals were discovered in the "tail walk," stage 5, and were watched to the culmination of courtship, at stage 10.

A large adult female with ova approximately 2.5 mm. in diameter was placed in a terrarium (14″ x 36″ x 16″) on November 25, 1948, with an adult male. The animals were observed daily and were frequently watched at night when they came out from cover to forage. On February 6, 1949, at 3:45 A.M., the first courtship activity was seen. The pair was found in the "tail-walk" (Noble, 1931: 389), stage 5 (Plate I). The observation was made under the illumination of a red Christmas tree light placed at one end of the terrarium. The animals appeared to be disturbed by the sudden illumination and by my movements. The female broke away from the male after 10 minutes and both animals sought the shelter of a board at one end of the tank. I moved them into the open and, despite handling, the male immediately again showed an interest in the female as she crawled toward cover. He moved quickly to her side, crouching low with his chest nearly touching the ground, whereupon she paused momentarily (Fig. 1). He then proceeded stealthily forward with his snout turned toward her. He appeared to touch her lightly with his nose but I am not certain that contact was made. As his head was brought near hers, his forward progress became almost imperceptible and he seemed to nose her gently along the side of the face. He brought his nose up against her gular area whereupon she raised her head, assuming

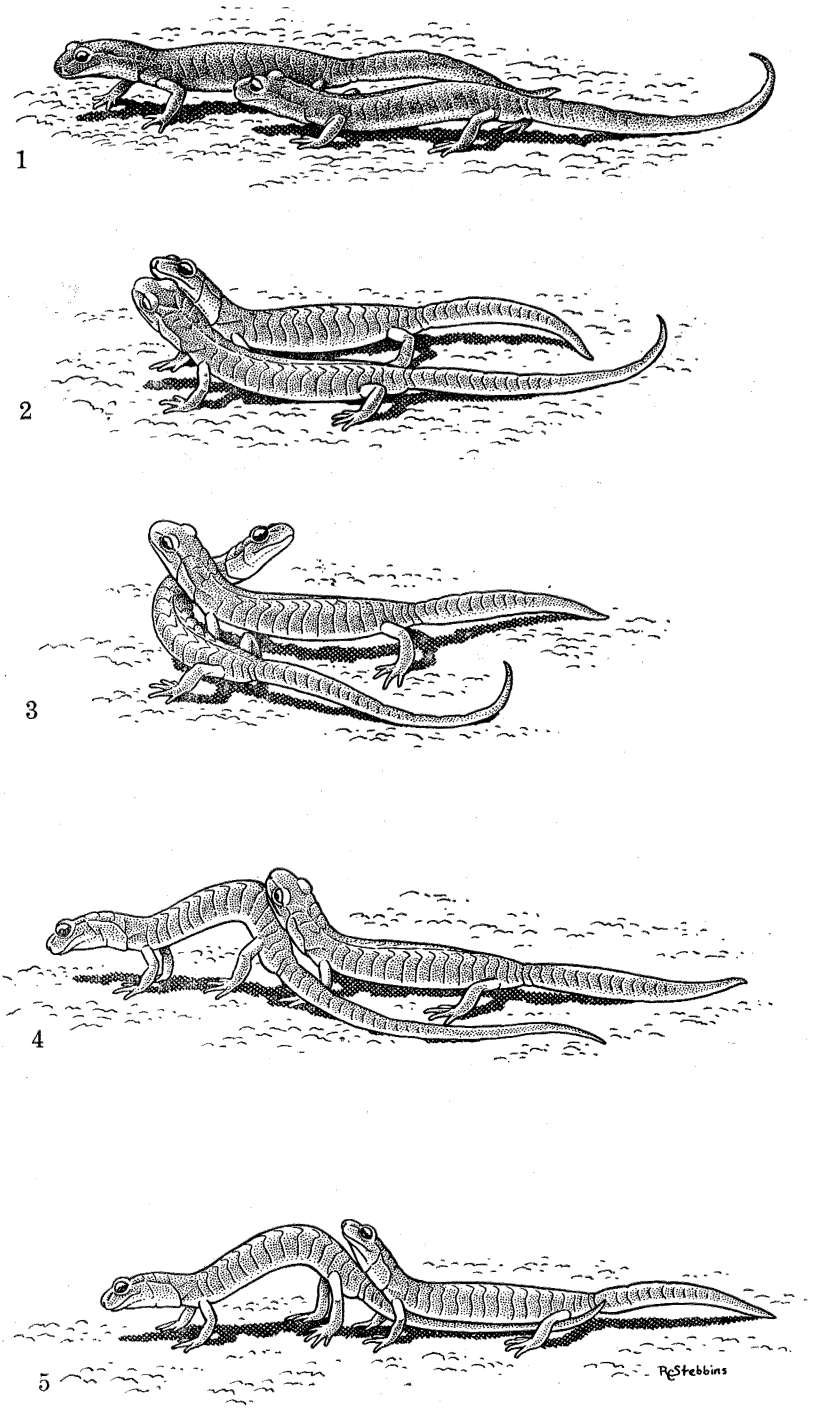
the pose shown in Figure 2. Both animals remained in this position for several seconds until the female turned aside and sought shelter. The male pursued her.

The next night, at 3:35 A.M., the pair was again found in the "tail walk" but a few seconds after the red light was turned on the animals separated.

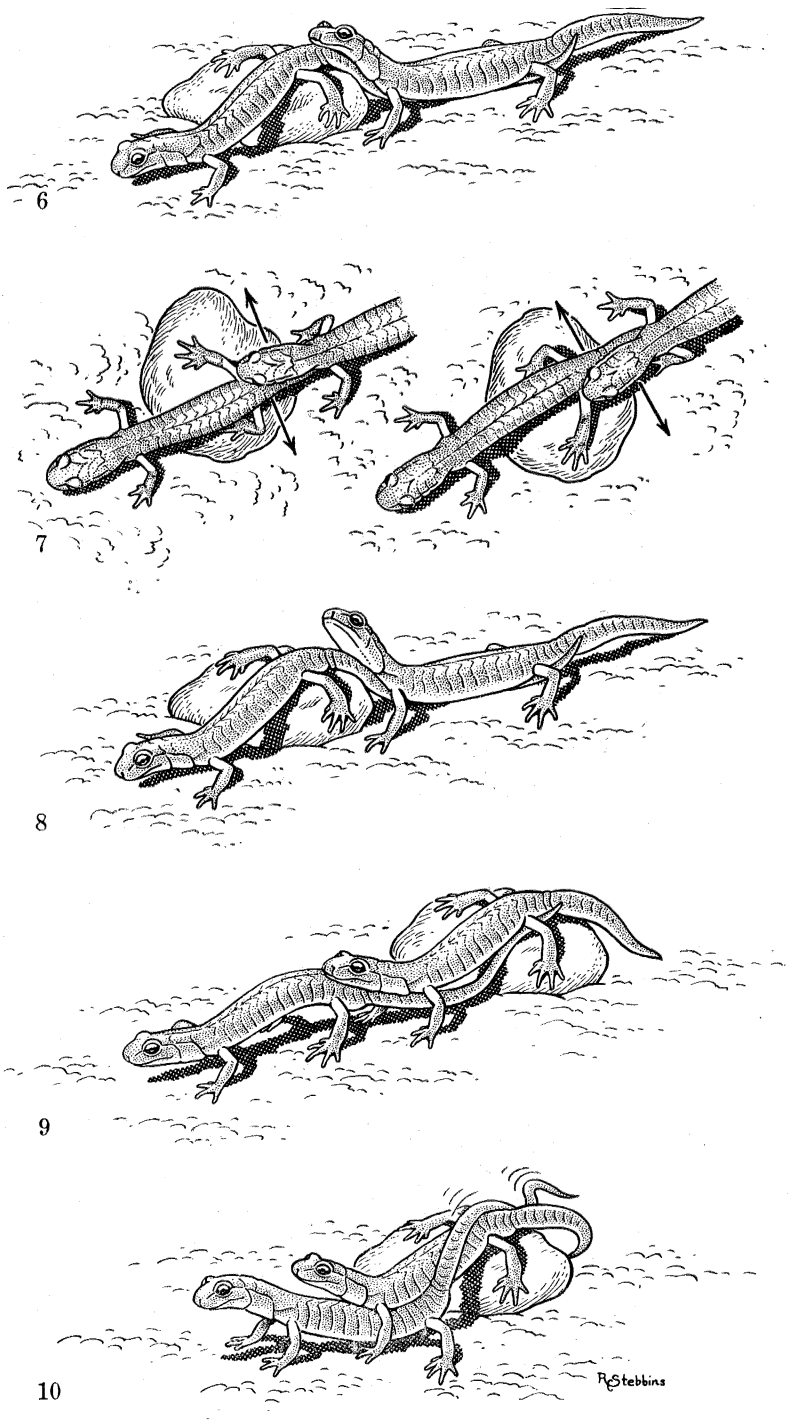
Again on February 8 the animals were found courting. The sides of the terrarium had now been darkened with sheets of black paper with a small opening at one side for observation. A 15-watt photographic ruby light replaced the Christmas tree bulb and was placed 4 feet directly above the terrarium. Several thicknesses of cloth covered the top of the tank producing a subdued diffuse light, thereby eliminating the point source of illumination that previously appeared to have been disturbing to the animals. The male stalked the female intermittently from 11:30 P.M. until 4:30 A.M. After this, on subsequent nights, his interest in her began to wane. On March 15, 1949, he was killed and the vasa deferentia were found to lack sperm. The animal had been in captivity since January 8, 1949, at room temperatures of approximately 70 to 80 degrees. He probably was rendered sterile by these temperatures since field animals were found heavily laden with spermatozoa throughout this period.

On February 12, 1949, I placed another male, fresh from the field, with the female. On February 14, at 10:00 P.M., I turned on the red light to find both animals out on redwood leaf litter that had been placed at one end of the tank. The male, unconditioned to the light, immediately sought cover. Some minutes later he came out again and crawled near the female. He courted her for about an hour but she was refractory. He followed the same pattern of stealthy approach and exploratory nosing of the female engaged in by the other male, but he carried the courtship further. After getting the female into position 2 (Fig. 2), with her head held high, he slid his head past hers, holding it against her gular area, moving forward until his neck was against her throat. He then shifted backward. The movement was repeated several times, resulting in a stroking of her gular area by the dorsum and sides of his head and neck. Throughout this activity the female remained quiet, holding her head at an angle of approximately 45° (Fig. 2). The male then moved his body slowly forward and around to her other side, at the same time maintaining contact with her throat. In this position his body assumed the form of a C that opened toward her and embraced her neck and chest (Fig. 3). He moved until his sacral region passed under her throat. When in this position, he elevated his hindquarters, arching his lower back upward and straightened his hind limbs (Fig. 4). He now began a massaging motion with his sacral area pressed against her throat. He moved his rump forward, down, upward, and back without changing the position of his hind limbs. Since her head rested passively against his back, it tended to shift with his movements. The male seemed to be trying to interest her in this area of his body.

The female was entirely passive, showing no interest in the male, and after a few moments began to crawl forward, stepping on his tail. When he detected her movements, he turned quickly, bending his body sharply, and



A typical sequence of steps in the courtship of *Ensatina eschscholtzii*. Explanation of the figures will be found in the text.



A typical sequence of steps in the courtship of *Ensatina eschscholtzii*. Explanation of the figures will be found in the text.

brought his nose against her gular area again. This arrested her momentarily but she soon turned away. Although she had moved several inches from him, he seemed to be unaware of her absence until she came into view to one side of him. He approached her and repeated the sequence of acts just described but again failed to induce her to follow him. The animals separated and sought cover. No other courtship by this pair was seen, despite the fact that both animals were implanted with adult *Ensatina* pituitaries on February 21.

Another male, fresh from the field, was placed with the above female on February 26. He was observed courting her from 10:00 P.M., intermittently, until 4:25 A.M. when both animals sought cover. Several times during this period he induced her to follow him but no spermatophore deposition occurred.

On March 12 an adult male and female were obtained in the field and were placed in the terrarium on the 13th at 7:00 P.M. The animals were watched for an hour under the illumination of the red light. During this time they took no interest in one another but were intent upon getting out of the terrarium. I resumed my observations at 12:15 P.M. The light had been on since 7:00 P.M. The male now was leading the female about in the "tail walk" (Fig. 5). Forward movement was slow although he was continuously active. This activity consisted of an alternate lifting of the feet and a lateral pendulum-like movement of the body while the hindquarters remained essentially stationary. He stepped sideways with his fore feet until the long axis of his body projected at an angle of about 45° from an anterior projection of the long axis of the body of the female. He then reversed his position, shifting a similar distance to the opposite side, thereby describing an arc of about 90° that commonly required from 12 to 14 seconds for its execution. At the same time the hind legs were lifted alternately, in a walking motion, or successively on one side and then the other or in an irregular manner. One or the other of the hind limbs was lifted at intervals varying from 3 to 54 seconds but commonly at 5 to 8 seconds during peaks of activity. Through all this the lower back was sharply convex. The limb movements suggested an animal walking on a hot surface. During the lateral sorties of the male, the female rested with most of her body against the ground with his tail extending between her legs. His movements resulted in some stroking of her gular area, since she tended to keep her head directed forward while his sacral region shifted slightly from side to side as he moved his foreparts. Perhaps movements of the hind limbs have something to do with expelling the secretion from the abdominal glands, observed to have a hedonic function in other species.

The pair followed a circuitous route about the terrarium. The male, on a number of occasions, made a sharp 180° turn, one time crawling over the hindquarters of the female. She was obliged to bend nearly double in her tenacious effort to maintain the sacral contact. The "tail walk" lasted until 2:10 P.M. During this period of approximately 2 hours, the animals covered 10 or 12 feet. The male's activity was incessant but the female stepped forward only as necessary to maintain her position in relation to him. Throughout the process, his tail curled upward behind one or the other of her

hind legs. Contact here may have helped to keep the female with the male as he moved forward. Probably of greater importance, however, is some attracting substance in the skin of the sacral area of the male since in another pair a male with a tail too short to reach the hind limbs of the female was followed. The sacral region appeared to glisten more in courting males than the remainder of the dorsum, suggesting greater secretory activity in this area of the skin. During the last half hour of courtship, prior to spermatophore deposition, the male became increasingly active and appeared to be uneasy. Several times he elevated his fore parts against the side of the terrarium. Finally he came to a rock, over which he crawled. When his hindquarters came into contact with it, he stopped. He now extended his hind legs laterally and rested his fore parts on the ground beyond. The female stood quietly in the "tail walk" position (Fig. 6). With his vent against the rock, the male began a rhythmic swaying motion of his pelvis accomplished by rocking from side to side on his hind limbs. The feet were not moved during the process. The movements at first were so slight as to be almost undetectable but they increased in scope, though not notably in rate, until the sacral area of the male was moving approximately 6 mm. As the movements of the male became pronounced, the female responded by moving her head laterally, counter to his movements. At first I thought her strokes an illusion because of the movement of the male in relation to her, but with increase in their extent they became unmistakable. At the peak of her performance she moved her head approximately 6 to 10 mm. laterally. As the female assumed the rhythm, the movements of the male subsided. The female stroked the sacral area of the male 72 times, counting from the time when the strokes first became noticeable. She moved at the same rate as the male, at somewhat under 1 second. At no time was there appreciable acceleration or retardation of movement although there was a marked rise and fall in intensity. Shortly after the male ceased his activity, the female began to reduce the intensity of hers and finally lifted her head, breaking contact with his sacral area (Fig. 8). For several seconds both animals were motionless. Then the male began to crawl forward. As he moved, the female resumed the "tail walk" position (Fig. 9). Lifting of the gular area from the lower back of the male may have been the signal for this step. As the animals crawled forward, I tried to see the spermatophore but their bodies concealed it. The male took a few deliberate steps, in contrast to his earlier behavior in the "tail walk." He stopped when the cloacal region of the female was directly over the spermatophore. Neither member of the pair looked backward nor was there any exploration of the area by the female prior to the assumption of the new position. As soon as her vent was over the spermatophore the male suddenly and vigorously shifted his entire body posteriorly, slipping beneath her and momentarily lifting her fore parts above the ground. Her head now was just behind his shoulders. At the same time, he swung his hindquarters laterally and drew his tail from beneath her body, whipping it up over her back. His tail writhed violently in a series of grotesque contortions, while its base was pressed against her sacral area and lower back, seemingly aiding her in pressing against the rock with her cloaca. The tail

behaved much like a severed tail. Its movements were at first fast, perhaps 2 or 3 per second, with greatest activity at the tip. Initially the base of the tail was moved in a slapping motion but it soon quieted while the tip palpated the base of her tail and sacral area (Fig. 10). A loop repeatedly formed at the tip of the tail which facilitated the stroking action. No movements of the pelvic region of the female were noted during the caudal activity of the male nor was there any gular contact. The female now lost interest in the male and moved away from him. She did this at first deliberately and rather slowly but after completely disengaging herself she seemed suddenly to become nervous and began to move actively about the terrarium, seeking escape. The male immediately pursued her in the manner shown in Figure 1. His tail was still writhing and continued to do so for a half minute or more after their separation. He followed her to cover.

At 3:00 A.M. I returned for further observations and found the pair again in the "tail walk." They continued this performance until 6:10 A.M. when, after some minutes of obvious uneasiness, the female began crowding the male. She repeatedly stepped on his hind legs and finally left him to seek shelter. The male followed. It had been growing steadily lighter since 5:50 A.M. and by 6:10 the red glow in the terrarium had been replaced by daylight. The female found cover at 6:20 A.M., with the male still intent upon courtship despite the well illuminated surroundings. At 9:20 A.M. I examined her and found a whitish sperm capsule protruding from her vent. A small patch of gelatinous material was present on the surface of the rock. On March 15, at 8:00 A.M., about 24 hours later, a remnant of the capsule was still evident in the vent of the female.

On the night of March 16–17, the same pair courted again and at 7:30 A.M. on March 17, the female was found with a second sperm capsule.

On March 18 at 11:45 P.M., I discovered one of two captive males courting the female obtained November 25, 1948. She previously had been persistently disinterested in sexual activity. Perhaps pituitary implants performed February 21 were responsible for her activation. Spermatophore deposition was observed at 4:45 A.M., 5 hours from the time the "tail walk" was first seen. The nuptial pattern was essentially as observed in other pairs. One aspect of courtship not noted earlier was the behavior of the male when the gular-sacral contact was lost during the "tail walk." Six times during the "tail walk" the male made a sharp turn, causing his sacral area to swing away from the throat of the female. Each time separation occurred, he stopped his pendulum action (p. 277) and forward motion and waited until the female replaced her gular area. When she delayed in this, he engaged in a lateral massaging motion, rubbing his sacral region against her until she moved her head into place. During spermatophore pick-up by the female, the male stroked her rhythmically and slowly (about 1½ to 2 seconds per movement) with the distal 25 to 30 mm. of his tail. At the same time he raised and lowered her body in time with the tail movements by moving his hindquarters. After a minute or so this movement was terminated but the tail strokes continued for 2 or 3 minutes. The spermatophore was deposited on the ground in a level area. At 8:00 A.M. I examined the female and found

that insemination had been unsuccessful. The sperm capsule adhered to her body 4 mm. to one side of her vent.

In comparing the courtship pattern of *Ensatina* with that of other plethodontids as summarized by Noble and Brady (1930), I may call attention to the following:

(1) As reported by these authors for other species, there is in *Ensatina* a series of preliminary rubbing movements during which the male applied his lips, cheeks, and side of the body to the snout or gular area of the female. This seems to arouse the interest of the female in the male. There is no indication that male *Ensatina* possess a mental gland. Inspection of the intermandibular area under the dissecting microscope and observations of behavior have failed to indicate such a structure. Micro-sections are required to settle this matter.

(2) The courting pair engages in a "tail walk" essentially as described by Noble and Brady (1930) but there was no lateral undulation of the tail nor any nosing of the cloacal region of the female by the male. Although there was lifting of the body of the male during spermatophore pick-up, this was not observed during the "tail walk" as mentioned by Noble and Brady. There was likewise no arching of the tail of the male nor turning forward of the tail of the female. The tail was used, however, in stimulating the female during spermatophore pick-up.

In all races of *Ensatina eschscholtzii* there is marked sexual dimorphism in length and thickness of the tail. Females have stout tails, usually shorter than the body, while the tail of the male is slender and as long or longer than the body. In some individuals, as one mentioned by Gnaedinger and Reed (1948), the tail of the male may be one and one-half times as long as the body. Prior to the present observations I had found no explanation for this difference. It is clear now that the long whip-like tail functions importantly in courtship.

(3) Whether there are hedonic glands in this genus is not known. In view of their widespread occurrence in plethodontids, they are expected. Examination of the skin of the two sexes under the dissecting microscope reveals no clear differences in glandular equipment, although the swollen lips of the male may result from more extensive glandular development about the nasolabial grooves. *Ensatina* may resemble *Aneides* (*aeneus* and *lugubris*) in which apparently homologous glands have been found in both sexes.

(4) There are no obvious sexual differences in size or form of the teeth. Dentitional dimorphism has been reported in *Hydromantes, Aneides, Eurycea,* and others. In *Ensatina* the teeth were not used in stimulating the female. Noble and Brady (1930) suspect their use by male *Hydromantes.*

Courtship of *Ensatina* has not been observed in the field. In the vicinity of Berkeley, it is known to occur over a considerable period, however, since sperm capsules have been found in the vents of females on the following dates: November 13 and December 4, 1948, and February 5 and 12 and March 12, 1949. Males possess spermatozoa in large quantities in their sperm ducts upon their first appearance following the fall and winter rains in October and November. Active spermatozoa are present throughout the

period of surface activity which for the adults is largely over by April (as based on a three-year study of a local marked population). The long period of reproductive activity, the ability of the females to store spermatozoa, and repetition of the act of courtship, help to insure fertilization of eggs that are not laid until late spring or early summer. Intensive study of a local population reveals that fully adult individuals are scarce, are of scattered occurrence, and are inclined to solitary habits. Furthermore, activity on the surface is profoundly affected by thermal and moisture conditions, which may fluctuate considerably. These factors militate against successful impregnation of the females but their effect is offset by the aforementioned traits of the animals.

Summary

Courtship in *Ensatina eschscholtzii* consists of a sequence of instinctive acts that form an integrated and predictable pattern of behavior. For clarity this pattern may be considered in a series of stages. (See Plates I and II.)

(1) Stealthy approach by the male, during which he stalks the female, crouching low and moving slowly to her head region.

(2) Massage of the throat and snout of the female by a rubbing action of the male's head and neck.

(3) The "tail walk" in which the male leads the female about with his back arched upward and his tail between her legs. She applies her gular area to his sacral region throughout this process.

(4) Spermatophore deposition, accompanied by a lateral swaying of the hindquarters of the male, followed by a stroking movement of the throat of the female against the sacral area of the male.

(5) Insemination accomplished by a forward movement of the pair in the "tail walk" until the vent of the female is over the spermatophore. The female then squats on the spermatophore and is stimulated by the male who shifts posteriorly beneath her and who at this time strokes her back with his tail.

Throughout the nuptial activity the male is the aggressor and appears less sensitive than the female to stimuli unrelated to courtship. He may pursue the female under daylight conditions, when her only interest seems to be to seek cover.

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